ARTICLE

Herbivore regulation of savanna vegetation: Structural complexity, diversity, and the complexity–diversity relationship

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Abstract

Large mammalian herbivores exert strong top-down control on plants, which in turn influence most ecological processes. Accordingly, the decline, displacement, or extinction of wild large herbivores in African savannas is expected to alter the physical structure of vegetation, the diversity of plant communities, and downstream ecosystem functions. However, herbivore impacts on vegetation comprise both direct and indirect effects and often depend on herbivore body size and plant type. Understanding how herbivores affect savanna vegetation requires disaggregating the effects of different herbivores and the responses of different plants, as well as accounting for both the structural complexity and composition of plant assemblages. We combined high-resolution Light Detection and Ranging (LiDAR) with field measurements from size-selective herbivore exclosures in Kenya to determine how herbivores affect the diversity and physical structure of vegetation, how these impacts vary with body size and plant type, and whether there are predictable associations between plant diversity and structural complexity. Herbivores generally reduced the diversity and abundance of both overstory and understory plants, though the magnitude of these impacts varied substantially as a function of body size and plant type: only megaherbivores (elephants and giraffes) affected tree cover, whereas medium- and small-bodied herbivores had stronger effects on herbaceous diversity and abundance. We also found evidence that herbivores altered the strength and direction of interactions between trees and herbaceous plants, with signatures of facilitation in the presence of herbivores and of competition in their absence. While megaherbivores uniquely affected tree structure, medium- and small-bodied species had stronger (and complementary) effects on metrics of herbaceous vegetation structure. Plant structural responses to herbivore exclusion were species-specific: of five dominant tree species, just three exhibited significant individual morphological variation across exclosure treatments, and the size class of herbivores responsible for these effects varied across species. Irrespective of exclosure treatment, more

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species-rich plant communities were more structurally complex. We conclude that the diversity and architecture of savanna vegetation depend on consumptive and nonconsumptive plant–herbivore interactions; the roles of herbivore diversity, body size, and plant traits in mediating those interactions; and a positive feedback between plant diversity and structural complexity.

INTRODUCTION

Savanna ecosystems—defined by the coexistence of grasses and trees—cover roughly 20% of the Earth's land surface and account for up to 30% of global net primary production (Sankaran et al., 2005, 2008; Scholes & Archer, 1997). In Africa alone, savannas cover nearly half the continent (Osborne et al., 2018) and contribute more than US $9B annually to local economies through livestock grazing, food production, and tourism (Ryan et al., 2016). The functioning and services of savanna ecosystems are thought to be tightly linked to the physical structure of their vegetation. Tree cover, for example, is strongly correlated with aboveground carbon storage (Davies & Asner, 2019; Holdo et al., 2009; Pellegrini et al., 2017), predation risk for wildlife and livestock (Davies et al., 2016; Ford et al., 2014; Riginos & Grace, 2008), abundance and diversity of small animals (Guy et al., 2021; McCleery et al., 2018; Pringle, 2008), and various other ecological processes (Hill & Hanan, 2010). Similarly, herbaceous vegetation structure influences animal behavior (Long et al., 2017), carbon sequestration (Wigley et al., 2020), and fire regimes (Cardoso et al., 2022). Changes in vegetation structure thus have profound effects on ecosystem function, with implications for human well-being and biodiversity conservation (Osborne et al., 2018). However, "structure" is a complex three-dimensional variable that is difficult to measure comprehensively. Most proxies used in previous research are one- or two-dimensional metrics and are often in different units for herbaceous and woody plants (e.g., understory biomass, mean tree height, and percent canopy cover).

While fire and rainfall are major determinants of tree cover and herbaceous biomass in savannas (Lehmann et al., 2014; Sankaran et al., 2005; Staver et al., 2011a, 2011b), grazing and browsing by large mammalian herbivores also strongly influence savanna vegetation structure, most conspicuously in Africa, which supports many of the world's last intact megafauna communities (Augustine & McNaughton, 1998; Laws, 1970; Malhi et al., 2016; Pringle et al., 2023; Sankaran et al., 2008). All African megaherbivores (adult mass > 1000 kg) have strong effects on vegetation structure (Owen-Smith, 1988). For example, savanna elephants (*Loxodonta africana*) can significantly reduce tree cover across landscapes (Davies & Asner, 2019; Nasseri et al., 2011) and modify individual tree morphology through destructive feeding (Coverdale et al., 2016). Giraffes (*Giraffa* spp.) similarly alter the vertical profile of trees through height-selective foraging (Fornara & Du Toit, 2007; Staver et al., 2012). White rhinoceros (*Ceratotherium simum*) and hippopotamus (*Hippopotamus amphibius*) have strong effects on the herbaceous layer, where they maintain open, short-statured grazing lawns through repeated foraging and nutrient influxes from dung and urine (Hempson et al., 2015; Voysey et al., 2023; Waldram et al., 2008).

Alongside these often-conspicuous impacts of megaherbivores, a variety of smaller ungulates are ecologically influential in African savannas (Staver et al., 2021); however, comparatively few studies have experimentally dissected the roles of small and medium herbivores from those of megaherbivores in regulating physical vegetation structure (but see Staver & Bond, 2014; van der Plas et al., 2016). The effects of smaller ungulates on the composition and diversity of herbaceous plants can rival or exceed those of megaherbivores (Burkepile et al., 2016, 2017; van der Plas et al., 2016) and may likewise be principal determinants of the physical structure of the understory (Eldridge et al., 2016). For example, herbivory can directly and indirectly alter the physical structure of herbaceous vegetation by shifting the balance of dominant growth forms (e.g., grasses vs. forbs; Koerner, Burkepile, et al., 2014; Koerner, Collins, et al., 2014; Ratajczak et al., 2022; Smith et al., 2016), by reducing light limitation and thereby increasing plant diversity (Borer et al., 2014; Eby

et al., 2014; Koerner et al., 2018; Price et al., 2022), and by suppressing plant height and biomass through trampling and consumption (Augustine, 2003; Koerner & Collins, 2013; Koerner, Collins, et al., 2014; van der Plas et al., 2016). These mechanisms are analogous to the ways in which browsing megaherbivores influence the physical structure of tree communities: shifting dominant growth forms (Staver et al., 2012; Wigley et al., 2015), changing community composition (Ford et al., 2014; Pringle et al., 2016), and altering the spatial distribution and abundance of plants (Asner & Levick, 2012; Davies et al., 2018).

At present, all of Africa's megaherbivores along with numerous smaller ungulate species are threatened with extinction (Ripple et al., 2015), and many wild herbivore populations are declining even within protected areas (Daskin & Pringle, 2018). Large-herbivore declines have already resulted in major changes in savanna vegetation structure (Daskin et al., 2016; Hempson et al., 2015; Sankaran et al., 2013; Staver et al., 2021). Many of these changes (notably increases in tree cover or shrub encroachment) have mirrored those predicted by long-term herbivore-exclosure experiments, which locally simulate herbivore extirpation (Asner et al., 2009; Bakker et al., 2016; Coverdale et al., 2021; Goheen et al., 2018). However, our ability to predict how savanna vegetation structure will respond to ongoing changes in the composition and abundance of large herbivores—and, in turn, how changes in structure will affect ecosystem function—is hampered by key knowledge gaps (Bakker et al., 2016; Forbes et al., 2019; Pringle et al., 2023). We highlight four related issues that collectively form the context for our study.

First, browsing and grazing impacts vary across herbivore species with different traits, notably body size (Kartzinel et al., 2015; Pringle et al., 2014; Staver et al., 2021; but see Veblen et al., 2016). Yet, the standard experimental method for quantifying effects of herbivore loss—fenced exclosures—typically consists of only total-exclusion and totally unfenced treatments, which obscures the effects of particular species and size classes (Jia et al., 2018; Staver et al., 2021; Wigley et al., 2014; but see Asner & Levick, 2012; Goheen et al., 2018; Staver & Bond, 2014). This limitation is problematic given that human-caused changes in herbivore communities are typically size-biased (with large species decreasing more rapidly than smaller species) and characterized by reduced diversity and abundance rather than total extinction (Dirzo et al., 2014).

Second, plant responses to herbivores vary among species and growth forms. This variation is not well characterized, which makes it difficult to anticipate or even measure the effect of herbivores on plant community composition and vegetation structure. Many studies investigate such variation in the context of herbivore impacts on plant diversity and community composition (Augustine, 2003; Coverdale et al., 2016; Staver et al., 2021; Wigley et al., 2014), but fewer focus on vegetation structure, and fewer still of those account for specificity of responses across plant types and spatial scales. Studies of vegetation structure typically focus on individual plant morphology using field surveys (Coverdale et al., 2018; Pringle, 2008; Staver et al., 2012; Staver & Bond, 2014) or landscape-scale patterns using remote sensing (Asner et al., 2009; Daskin et al., 2016; Davies & Asner, 2019; Staver et al., 2011a, 2011b); few studies have integrated responses across spatial extents, measured the understory and overstory in comparable units, or quantified structure in all three spatial dimensions simultaneously (Staver, 2018). Even studies using Light Detection and Ranging (LiDAR), which enables multidimensional measurement of structure at multiple scales, are generally unable to distinguish plant species or growth forms in the absence of field data (Davies & Asner, 2014; Levick et al., 2009).

Third, herbivores can indirectly affect vegetation communities and structure by altering plant–plant interactions, but often in context-dependent ways. For example, herbivores reduce light limitation in the understory, which increases the diversity of herbaceous plants in resource-rich grasslands but has little effect otherwise (Borer et al., 2014; Burkepile et al., 2016; Price et al., 2022). In savannas, trees can facilitate herbaceous plants by reducing their apparency or accessibility to herbivores (Coverdale et al., 2016; Louthan et al., 2014) or, alternatively, reduce herbaceous biomass and diversity through competition for light, water, or nutrients (Belsky, 1994; Dohn et al., 2013; Ludwig et al., 2001). These plant–plant interactions likely depend on the presence, identity, and body size of large herbivores: competition might predominate in the absence of herbivores (e.g., if thick tree cover reduces herbaceous biomass, diversity, and/or complexity) while facilitation may prevail in their presence (e.g., if associational refuges are important). Mega-browsers such as elephant could intensify either of these effects by having outsized effects on tree cover (Laws, 1970) or by damaging trees in ways that create associational refuges (Coverdale et al., 2016).

Fourth, the physical structure of savanna vegetation is likely to be a key correlate of other ecological properties and processes—but because structure is so difficult to quantify, we have limited understanding of these associations and how they are influenced by herbivory (Pringle et al., 2023). One relationship of particular interest is the potentially reciprocal relationship between structural complexity and species diversity (Coverdale & Davies, 2023). Given that savanna plant communities comprise a variety of

growth forms (e.g., grasses, forbs, shrubs, lianas, and trees), more diverse assemblages may be more likely to contain species with unique contributions to structural complexity (Naeem & Wright, 2003). More complex habitats may also sustain greater plant diversity due to the provisioning of more heterogeneous microhabitats. Consistent with both of these mechanisms, Coverdale and Davies (2023) found that plant diversity and vegetation structural complexity are positively correlated across a wide range of ecological contexts. In megafauna-dominated savannas and grasslands, however, the occurrence and form of this relationship may depend on herbivory: herbivores might alter vegetation structure by increasing or decreasing plant diversity (Borer et al., 2014; Price et al., 2022; Staver et al., 2021) and/or alter plant diversity by changing vegetation architecture (e.g., via structural damage or plant morphological plasticity; Coverdale et al., 2016). While some prior studies have simultaneously evaluated herbivore impacts on metrics of plant structure and diversity, these are generally limited to particular plant groups (e.g., herbaceous taxa) and scales (e.g., 1-m^2 plots); it is unclear whether structure–diversity relationships are robust across scales, strata, and herbivory regimes.

Developing a more comprehensive understanding of how herbivore loss affects savanna vegetation thus hinges on determining how herbivore impacts on plant structure vary as a function of herbivore body size, how plant responses vary as a function of species identity or growth form, the role of plant–plant interactions in governing these outcomes, whether there is a predictable relationship between physical structure and community structure, and whether herbivores modify this relationship. Here, we quantified the effects of large-herbivore exclusion on vegetation structure in a semiarid Kenyan savanna by integrating high-resolution, airborne LiDAR data with detailed field measurements from a 13-year herbivore-exclusion experiment consisting of nested, size-selective treatments replicated across thirty-six 1-ha plots (Figure 1). We organize our results under three related aims (Table 1). We first consider (Aim 1) how herbivores affect the diversity, abundance, and structure of the tree and herbaceous layers. We then explore (Aim 2) how herbivores affect the structure of individual trees, and how interactions between trees and herbaceous vegetation vary as a function of herbivore exclusion. Finally, we evaluate (Aim 3) the relationship between vegetation structure and plant diversity for the herbaceous and tree layers
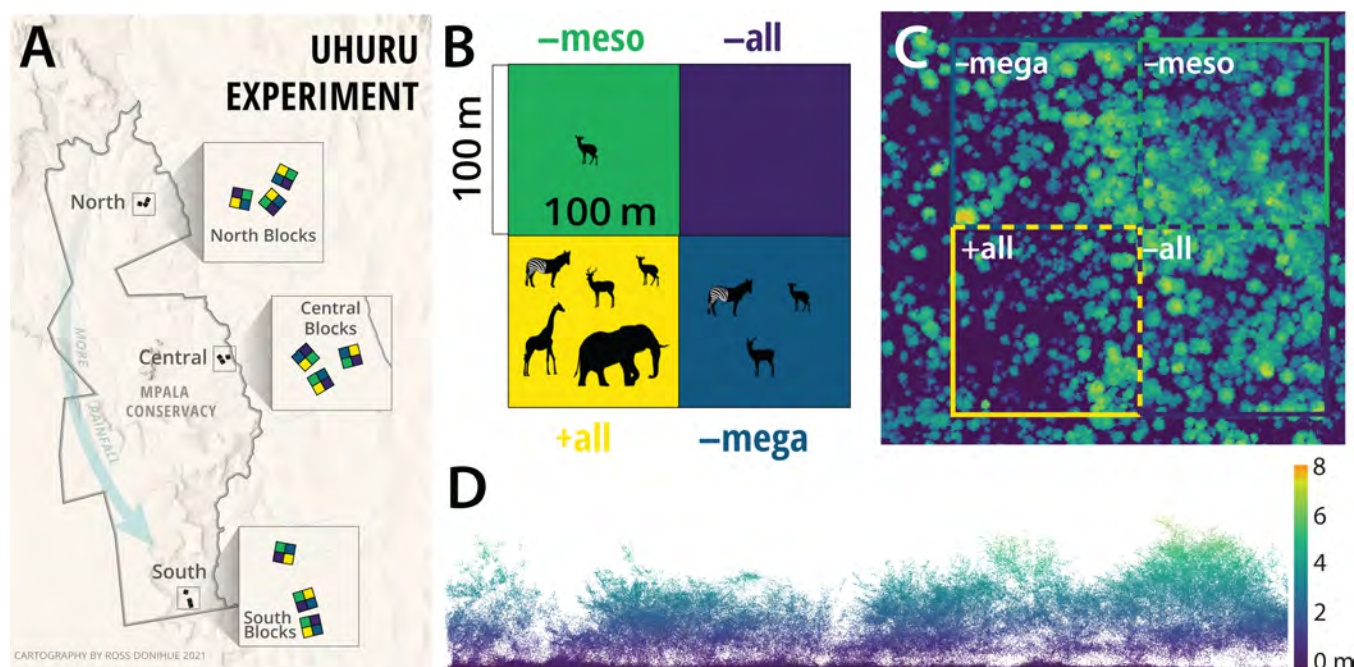

FIGURE 1 Study site and example Light Detection and Ranging (LiDAR) data. (A) Map of the study site showing the location of the UHURU large herbivore-exclusion experiment at Mpala Research Centre, Kenya (see Appendix S1: Figure S1 for more detail). (B) Schematic diagram showing the four exclosure treatments that comprise a single block of the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) herbivore-exclusion experiment. "+all": unfenced control plots; "−mega": fenced exclosures that exclude megaherbivores (≥1000 kg, i.e., elephants and giraffes); "−meso": fenced exclosures that exclude both mega- and mesoherbivores (≥20 kg); "−all": fenced exclosures that exclude all large herbivores (≥5 kg). (C) Canopy height model illustrating variation in vegetation structure in a single block of the UHURU large herbivore-exclusion experiment (North Block 1). (D) Representative LiDAR cross section showcasing the high point density of the Harvard Animal Landscape Observatory (HALO) remote sensing system. Cartography credit in (A): Ross Donihue.

TABLE 1 Aims and descriptions of analyses conducted in this study.

Aims and analysis	Result summary	Data type	Scale of analysis	Figure(s)
Aim 1: Quantify herbivore effects on the abundance, diversity, and structure of trees and herbaceous vegetation				
Effects of herbivore-exclosure treatment on tree cover and density	Megaherbivores reduced tree cover; tree density did not vary as a function of herbivore exclosure	Remote sensing and field surveys	10 × 10 m subplot	Figure 2A,B
Effects of herbivore-exclosure treatment on tree diversity	Tree diversity increased monotonically with increasing herbivore exclosure	Field surveys	1-ha plot	Figure 2C
Effects of herbivore-exclosure treatment on herbaceous abundance (DPM and pin frame)	Medium- and small-bodied herbivores reduced herbaceous abundance	Field surveys	1-ha plot	Figure 3A
Herbaceous diversity (species density, species richness, and Shannon index)	Herbivores had idiosyncratic effects on herbaceous diversity, but all measures of diversity tended to increase with increasing herbivore exclosure	Field surveys	1-ha plot	Figure 3B,C
Effects of herbivore-exclosure treatment on herbaceous community composition	Site (South, Central, and North) had the strongest effect on herbaceous community composition; within sites, communities tended to be most similar within the same exclosure treatment	Field surveys	1-ha plot	Appendix S1: Figure S4
Effects of herbivore-exclosure treatment on tree-only vegetation structure (six metrics)	Megaherbivores (elephant and giraffe) reduced four of six structural complexity metrics; no other herbivores affected tree structure	Remote sensing	1-ha plot	Figure 4
Effects of herbivore-exclosure treatment on herbaceous-only vegetation structure (six metrics)	All herbivore size classes affected some aspects of herbaceous vegetation structure; rumple and mean height did not vary across exclosure treatments	Remote sensing	1-ha plot	Figure 5
Effects of herbivore-exclosure treatment on whole plot (all plants) vegetation structure (six metrics)	All herbivore size classes affected some aspects of whole community vegetation structure; rumple did not vary across exclosure treatments	Remote sensing	1-ha plot	Appendix S1: Figure S6
Aim 2: Quantify herbivore effects on individual tree structure and tree-herbaceous interactions				
Effects of herbivore-exclosure treatment on height and canopy area of five dominant tree species	Large- and medium-bodied herbivores reduced the height and canopy area of three of five dominant tree species	Field surveys	Individual plant	Figure 6A,B
Vertical biomass profile and CV of height of individual trees	Megaherbivores reduced CV of height for two of five dominant species and the center of gravity (vertical profile) of one tree species	Remote sensing and field surveys	Individual plant	Figure 6C,D
Effects of trees (presence/absence) and herbivore-exclosure treatment on herbaceous abundance (DPM and pin frame)	Trees had a positive effect on herbaceous abundance in the presence of herbivores, but a negative or neutral effect in their absence	Remote sensing and field surveys	1 × 1 m quadrat	Figure 7A; Appendix S1: Figure S5
Effects of trees (presence/absence) and herbivore-exclosure treatment on herbaceous diversity (species richness)	Trees had a positive effect on herbaceous diversity in the presence of herbivores, but a neutral effect in their absence	Remote sensing and field surveys	1 × 1 m quadrat	Figure 7B

(Continues)

TABLE 1 (Continued)

Aims and analysis	Result summary	Data type	Scale of analysis	Figure(s)
Aim 3: Quantify whether vegetation structure varies as a function of plant diversity				
Relationship between tree species richness and vegetation structure (six metrics)	Tree species richness was positively correlated with five of six measures of vegetation structural complexity	Remote sensing and field surveys	10 × 10 m subplot	Figure 8; Appendix S1: Table S1
Relationship between herbaceous species richness and vegetation structure (six metrics)	Herbaceous species richness was positively correlated with all measures of vegetation structural complexity	Remote sensing and field surveys	1 × 1 m quadrat	Figure 9; Appendix S1: Table S2 and Figure S7

Abbreviation: DPM, disc pasture meter.

and the consistency of this relationship across exclosure treatments.

MATERIALS AND METHODS

Study site and experimental design

Mpala Research Centre (MRC) encompasses ~20,000 ha of semiarid thorn-scrub savanna in Laikipia County, Kenya ($0°36'4''$ N, $36°87'8''$ E), most of which is underlain by infertile red sandy loams (Figure 1A). The overstory community on this soil type is dominated by spinescent *Acacia* s.l. (including *Senegalia* and *Vachellia* spp.) trees and shrubs—predominantly *A. brevispica*, *A. etbaica*, and *A. mellifera*—with ~40 additional species at lower densities (e.g., *Balanites rotundifolia* and *Croton dichogamus*). The understory includes several hundred species of grasses, forbs, and subshrubs (Coverdale et al., 2016; Gill et al., 2019; Kartzinel et al., 2014). The large-herbivore community incudes more than 20 species of native wildlife ≥5 kg, of which elephant (~3000 kg km^{-2}), impala (*Aepyceros melampus*, ~800 kg km^{-2}), dik-dik (*Madoqua* cf. *guentheri*, ~700 kg km^{-2}), zebras (*Equus quagga* and *E. grevyi*, ~370 kg km^{-2} combined), and giraffe (*G. camelopardalis reticulata*, ~250 kg km^{-2}) attain the highest biomass densities (Augustine, 2010). Five species of domesticated livestock are also present at MRC but are only rarely present in our experimental plots (Goheen et al., 2013).

The UHURU experiment was initiated in 2008 and comprises replicate blocks of four treatments in southern, central, and northern MRC (Goheen et al., 2013; Figure 1; Appendix S1: Figure S1). Total exclosures (−all) exclude all herbivores ≥5 kg using 1-m tall chain link fence together with 2-m tall fences of alternating electrified and ground wires. Mesoherbivore exclosures (−meso) have the same electric-fence design but without the lower chain link fence, excluding all herbivores larger than ~10 kg. The main difference between −all and

−meso is that the latter allows unfettered access by dik-dik, the most numerically abundant ungulate at MRC (up to ~140 km^{-2}; Augustine, 2010). Megaherbivore exclosures (−mega) consist of electrified wires at 2 m, excluding elephant and giraffe but allowing all other herbivores. Therefore, −meso and −mega differ in the presence of multiple species, but impala and zebras are each several-fold more abundant than any other mesoherbivore, and impala are roughly twice as abundant as zebra (Augustine, 2010). Unfenced plots (+all) are marked with wooden posts and accessible to all species. The difference between −mega and +all is the exclusion of elephant and giraffe. The impact of excluding each herbivore size class can be assessed by comparing exclosure treatment pairs, while the collective impact of successively larger bodied herbivore groups can be assessed by comparing each treatment to +all (Goheen et al., 2013).

Plant community composition and abundance data are collected regularly within the 36 UHURU plots. Full details of the experimental design and sampling protocols are available in Goheen et al. (2013), and raw data from 2008 to 2019 are available in Kartzinel et al. (2014) and Alston et al. (2022); see also detailed schematics in Figure 1; Appendix S1: Figure S1A. Briefly, within each 1-ha (100 × 100 m) plot is a 60 × 60 m grid of 49 permanently marked stakes (total $N = 1764$; Goheen et al., 2013). At each stake, plant abundance and species composition are surveyed twice annually in 1-m^2 quadrats. Understory abundance/biomass is estimated in two complementary ways: with a standard disc pasture meter (DPM; converted to kilograms per hectare following Zambatis et al., 2006) and a ten-pin frame (canopy-intercept method; Frank & McNaughton, 1990). We include data from both methods to test replicability of our results, because DPM data are comparable with those collected in other savannas, and because we did not independently validate the form and fit of the relationship between DPM and pin-frame data in this study (prior work at MRC shows that the total number of pin hits is highly correlated, $r^2 > 0.87$, with harvested dry

biomass; Augustine, 2003; Coverdale et al., 2016). Understory community composition is measured by recording the identity and percent cover of all species in each quadrat. At the same locations, an 8-m telescoping pole is positioned vertically in the center of each quadrat and the number, height (in centimeters), and species identity of all plants touching the pole are recorded from the ground through the top of the canopy, quantifying abundance of all species in the same currency.

Woody plants are monitored in two ways. First, a subset of common trees (~10 per species per plot of *A. etbaica*, *A. mellifera*, *A. brevispica*, *C. dichogamus*, and *B. rotundifolia*) have been monitored since the start of the experiment in 2008. Here, we analyzed height and canopy area of 1504 trees ($N = 113$–360 trees per species). Second, species identity and height class (<1 m, 1–2 m, 2–3 m, 3–4 m, and >4 m) of all large trees, shrubs, and succulents ($\geq$2 m tall at maturity) are measured in 36 subplots (10×10 m) within the central grid of each plot (Appendix S1: Figure S1A). We used field data from October to November 2021, 13 years after the start of the experiment and three months before the collection of LiDAR data.

Remote sensing of vegetation structure

In January 2022, with permission from the Kenya Civil Aviation Authority (KCAA/OPS/2117/4), we collected high-resolution LiDAR data of all UHURU plots using the Harvard Animal Landscape Observatory (HALO). HALO is equipped with a Riegl VUX-1LR LiDAR sensor (integrated by Phoenix LiDAR Systems, Austin, Texas, USA), which was flown using a Freefly Alta-X rotary-wing unoccupied aerial vehicle (UAV; Freefly Systems, Woodinville, Washington, USA). At each site (north, central, and south), an area of ~100 ha was flown that encompassed all three blocks of plots; multiple flights of ~15 min each were made to fully cover the landscape surrounding the exclosure plots. The UAV was flown at 8 m/s in a serpentine pattern at 50 m altitude above ground with a line speed of 114 lines/s and an 820 kHz pulse rate. Flight trajectories were corrected during post-processing using GPS data from a nearby mobile base station. LiDAR data from multiple flights at each site were denoised, classified (Axelsson, 2000), and aligned using the Terrasolid software suite (Terrasolid Ltd, Espoo, Finland). After denoising, the average vegetation point density was ~300 points/m^2. We created digital terrain models at 25-cm resolution for each site using a triangulated model of ground points. The height above ground was then computed for each point based on its vertical distance to the ground surface model.

The resulting point cloud contained both tree and herbaceous vegetation. We used field data on the vertical position and identity of plants within the 1764 permanent monitoring quadrats (Alston et al., 2022) to determine whether trees and herbaceous vegetation could be differentiated based on height alone. This dataset contained 16,645 height measurements, of which 8461 were trees, 6956 were herbaceous species, and 1228 were lianas (which we excluded from the analysis because they originate in the herbaceous layer and climb into the overstory). For each plot, we then separately calculated the mean and 95% CI of height for tree and herbaceous heights (Appendix S1: Figure S2A). Across all plots, the 95% CI of tree heights was >1 m, while the 95% CI for herbaceous heights was <1 m. We therefore classified all LiDAR points >1 m above ground as trees and all LiDAR points <1 m above ground as herbaceous vegetation (Appendix S1: Figure S2B). To create a canopy height model (CHM) for trees only, we calculated the maximum heights of first-return points after removing all points <1 m; to create a CHM for herbaceous vegetation only, we did the same after removing all points >1 m. This yielded tree and herbaceous-only rasterized CHMs with a pixel size of 25×25 cm (Appendix S1: Figure S3).

We then calculated six common structural metrics for each vegetation stratum using the tree- and herbaceous-only CHMs and the classified, denoised LiDAR point clouds: rumple, rugosity, maximum height (measured as 98th percentile height), mean height, CV of height, and percent cover. Rumple, the ratio of the outer canopy surface to the ground surface (a measure of 3D canopy "roughness"), was calculated using the rumple_index function in the R package *lidR* (Roussel et al., 2020). Rugosity, the SD of rasterized maximum canopy height, was extracted directly from each CHM (following Parker & Russ, 2004). To measure percent cover, we classified pixels as having herbaceous vegetation if maximum height was <1 m and >5 cm (to exclude bare-ground points); similarly, we measured tree cover by calculating the proportion of pixels in the tree-only CHM with points >1-m high. Ground and noise points were removed prior to assigning each point a height above ground and calculating height percentiles for each 1-m^2 quadrat (for herbaceous vegetation) or 100-m^2 subplot (for trees). We then used the tree-only point-cloud data to calculate canopy density within $25 \times 25 \times 25$ cm cubic voxels, which we used to estimate vertical vegetation biomass profiles for a subset of individual trees. Canopy density for a given voxel was defined as the ratio of the number of points within that voxel to the total number of non-ground points in the voxel column.

Most of these structural metrics are positively correlated, reflecting shared reliance on aspects of vegetation height (Pearson's *r*: range −0.15 to 0.94, mean 0.41, for trees; range 0.16–0.88, mean 0.56, for herbaceous layer; Appendix S1: Tables S2 and S3). We include all of them to provide the most comprehensive assessment, and for three additional reasons. First, recent studies advocate the use of standardized metrics, including those analyzed here, to facilitate cross-study comparisons (Loke & Chisholm, 2022; Moudrý et al., 2023). Second, this suite of metrics captures potentially nonoverlapping categories of structural diversity proposed by Atkins et al. (2018)— namely height, distribution, and heterogeneity of vegetation, which are linked to ecosystem functions in savannas (Godlee et al., 2021). Finally, while these metrics have been used extensively in forests, the feasibility of measuring them—as well as their utility and applicability— outside of forested ecosystems remains to be tested.

Data analysis

Several datasets were non-normally distributed (Shapiro–Wilk tests; see Appendix S1: Table S1). Because linear models tend to be robust to violations of normality (Schielzeth et al., 2020), and because standard transformations did not normalize the data, we present parametric analyses of non-transformed data in the main text and in all figures. To test the sensitivity of our results to this choice, we analyzed non-normal data with nonparametric tests (Kruskal–Wallis rank-sum tests and post hoc contrasts with Bonferroni–Holm corrections). These tests confirmed the qualitative robustness our conclusions (Appendix S1). We also note that data were collected across all three sites in UHURU (south, central, north), which differ in rainfall, some soil properties, and primary productivity (Figure 1; Alston et al., 2022; Goheen et al., 2013). Because our goal was to understand the effects of herbivory, we accounted for this environmental variation in the random-effects structure of our models (parsing interactive effects of herbivory and environmental context on our responses would require a separate study). For transparency, we reanalyzed data with site as a fixed effect in otherwise identical models (Appendix S1: Table S1). All analyses were performed in R (v.4.0.3; R Core Development Team, 2023).

of trees and herbaceous vegetation abundance and species richness (Table 1). For trees, we supplemented our LiDAR-derived measurements of plot-level tree cover with measurements of tree density from field surveys; we also recalculated tree cover at the subplot level (using LiDAR data) to ensure that tree cover and density measurements were at comparable spatial scales. Since we used a 1-m height threshold to delineate tree cover in LiDAR point clouds, we excluded trees <1 m from the field data (i.e., only trees in 1–2 m, 2–3 m, 3–4 m, and >4 m height classes were included in density measurements). This combination of metrics allowed us to directly test the effect of herbivores on tree cover and indirectly assess whether differences in tree cover were due to individual trees growing larger (i.e., structural effects) and/or an increase in tree density (i.e., abundance effects). We assessed herbivore effects on tree diversity by comparing the species richness of each plot from field surveys of 100-m^2 subplots. We similarly compared herbivore impacts on herbaceous abundance and diversity by comparing plot-level estimates of biomass (DPM and pin frame) and three measures of diversity (species density, species richness, and Shannon diversity). Comparisons of herbivore impacts on the abundance and diversity of trees and herbaceous vegetation used separate mixed models with exclosure treatment as a fixed effect and random intercepts grouped by site and block nested within site, which we fit in *lmer* (Bates et al., 2015). We visualized differences among treatments and sites in herbaceous community composition using nonmetric multidimensional scaling (NMDS).

To investigate the effects of different large-herbivore size classes on woody and herbaceous vegetation structure, we compared the effects of exclosure treatment on vegetation structure (six metrics described above) with separate mixed models, with exclosure treatment as a fixed effect and random intercepts for site and block within site. For comparison, we also calculated the same six metrics at the plot level for the full plant community (i.e., using non-truncated CHMs and point clouds) to test whether size-specific herbivore effects on vegetation structure could be detected without separating the plant community into tree and herbaceous components. We used Tukey's honestly significant difference (HSD) tests for pairwise comparisons between treatments.

Aim 1: Herbivore effects on abundance, diversity, and structure of trees and herbaceous vegetation

We investigated the effects of small-, medium-, and megaherbivores on the abundance and species richness

Aim 2: Herbivore effects on individual tree structure and tree-herbaceous interactions

We used a combination of field and LiDAR data to determine how different subsets of the herbivore community affected individual tree structure. First, we compared the

individual height and canopy area of the five common trees species measured in field surveys across exclosure treatments. We used separate mixed models (fixed effect of treatment and random effects of site, block nested within site, and plot) for each tree species. We then delineated all tree canopies using a modified watershed transformation (following Beucher & Meyer, 2018) and matched the locations of 93 *A. etbaica* and 84 *A. mellifera* from field surveys with segmented tree canopies in the LiDAR data. For each tree species, we averaged the voxel-based vertical biomass profiles within each exclosure treatment. We compared the effects of exclosure treatment on height profiles using separate pairwise Kolmogorov–Smirnov tests to determine whether herbivore effects on vertical biomass distribution varied as a function of herbivore size class. We also analyzed the effects of herbivores on vertical biomass variability (CV of vegetation height) using separate mixed models for each species (with treatment as a fixed effect and random effects of site, block nested within site, and plot).

To evaluate the hypothesis that herbivores indirectly impact herbaceous abundance and diversity by modifying the strength and/or direction of tree-herbaceous interactions, we assessed the interactive effect of trees and herbivory on herbaceous biomass and diversity. We reasoned that a positive effect of tree cover on herbaceous biomass/diversity indicates facilitation, and a negative effect indicates competitive interactions, with effect size reflecting interaction strength. We quantified the independent and interactive effects of herbivores and trees on herbaceous abundance (DPM and pin frame) and species richness using separate mixed models, with exclosure treatment and tree presence–absence (and their interaction) as fixed effects, and random effects of site, block nested within site, and plot; data were analyzed at the level of 1-m^2 quadrats. We consider a greater abundance and diversity of herbaceous vegetation beneath trees (relative to outside trees) to be consistent with facilitation and consider the magnitude of this difference to be evidence of the strength of the woody-herbaceous interaction.

Aim 3: Relationship between vegetation structure, herbivory, and plant diversity

Finally, we tested whether more diverse plant communities were more structurally complex (Coverdale & Davies, 2023), and whether herbivores of varying body size affected the strength and direction of this relationship. For both trees and herbaceous plants, which had replication of 1296 100-m^2 subplots and 1764 1-m^2 quadrats, respectively, we elected to use a conservative approach that first pooled data within each plot. For trees, we averaged all measures of structural complexity for each level of species richness (from 0 to 10 species per subplot) within each plot ($N = 36$ plots). Of the 360 possible combinations of species richness and plot identity, our data include 278 estimates (e.g., only 9 of 36 plots contained one or more subplots with zero trees). For herbaceous vegetation, we similarly averaged our estimates of structural complexity collected in quadrats by species richness at the plot level, and our dataset included 275 of 360 possible combinations; as for trees, some plots did not contain quadrats with all levels of species richness (e.g., only 21 of 36 plots had one or more quadrats with no herbaceous species). We separately analyzed all structural metrics for trees and herbaceous vegetation with linear mixed models, with exclosure treatment and species richness (and their interaction) as fixed effects and random effects of site and block nested within site. For both vegetation types, subplots or quadrats with no vegetation were excluded from comparisons involving CV of height (which cannot be calculated for bare patches). A significant (and positive) effect of species richness would suggest that more diverse plant communities tended to be more structurally complex. A significant effect of exclosure treatment would suggest that structural complexity varies with herbivore exclosure (compare to analyses in Aim 2). A significant interactive effect of exclosure treatment and species richness would suggest that herbivores affected the strength or direction of the relationship between plant diversity and structure.

Because the 1-m height threshold we used to separate trees and herbaceous vegetation could have introduced structural artifacts in the herbaceous layer (e.g., by truncating taller understory plants and creating a horizontal canopy top at 1 m), and because trees can influence herbaceous structure without affecting diversity (e.g., by causing phenotypic shifts through shading; Coverdale & Agrawal, 2021), we also compared structural metrics across the subset of quadrats that did not have overlying trees (i.e., herbaceous structural metrics derived from non-truncated CHMs and point clouds). We classified quadrats as being outside tree canopies if the 98th percentile height of all points in the cloud was <1 m above ground; all others were classified as having overlying trees. This approach yielded the same result as classifying quadrats based on the presence of trees in field surveys for ~85% of quadrats, but since the field surveys included tree seedlings and saplings (which are unlikely to have comparable effects to trees >1-m tall), we elected to use the classification based on LiDAR vegetation height. Across all plots, 1263 quadrats were overlain by trees and 501 were not. We analyzed the effects of herbivory and species richness on structural complexity for

non-truncated herbaceous data using the same linear mixed models, described above.

RESULTS

Aim 1: Herbivore effects on abundance, diversity, and structure of trees and herbaceous vegetation

Herbivores, especially megaherbivores (elephants and giraffes), had a strong negative effect on tree cover ($F_{3,24} = 24.01$, $p < 0.0001$). Tree cover was lowest in

unfenced (+all) plots (mean ± 1 SEM: $15.5 \pm 0.9\%$) and roughly threefold higher in all other treatments, which did not differ from each other (Figure 2A). Tree density, likewise, was lowest in +all plots (1240 ± 71 trees ha^{-1}) and highest in −meso plots (2043 ± 95) but differed only marginally across treatments ($F_{3,24} = 2.62$, $p = 0.073$; Figure 2B). Tree species richness increased with the stringency of herbivore exclusion ($F_{3,24} = 10.06$, $p = 0.0002$), being lowest in +all plots (3.4 ± 0.1 species/ subplot) and highest in −all plots (5.4 ± 0.1 species/subplot; Figure 2C).

Biomass of herbaceous vegetation—whether estimated with DPM ($F_{3,30} = 13.08$, $p < 0.0001$) or pin frame
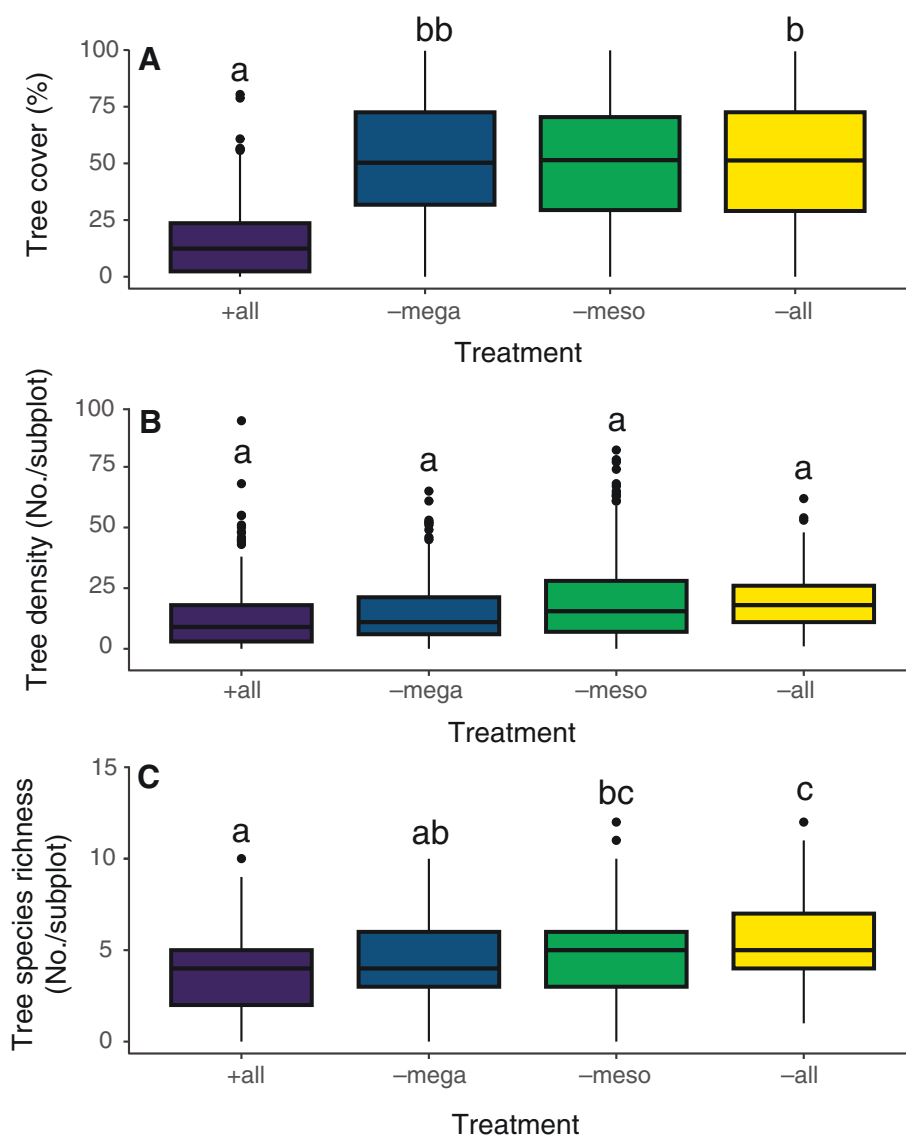

FIGURE 2 Effects of herbivore exclusion on tree abundance and species richness. (A) Tree cover across exclosure treatments calculated from Light Detection and Ranging-derived canopy height models. (B) Tree density across exclosure treatments calculated from field surveys. (C) Species richness across exclosure treatments calculated from field surveys. All data were measured at the subplot level (10 × 10 m); boxplots show median (central bar), IQR (bottom and top bars), 1.5 × Interquartile Range (IQR; whiskers), and outliers (>1.5 × IQR from first or third quartile). Letters above bars denote significant differences between treatments in post hoc contrasts (Tukey's honestly significant difference).

($F_{3,32} = 5.33$, $p = 0.004$)—was also higher where herbivores were excluded. In contrast to the effects on tree abundance, the greatest pairwise differences between treatments was between −mega and −meso (DPM) and −meso and −all (pin frame), suggesting that medium- (notably impala, zebra) and small-bodied (dik-dik) species had a greater effect on herbaceous abundance than did megaherbivores (Figure 3A; Appendix S1: Figure S4A). The effects of herbivore exclusion on herbaceous diversity were more idiosyncratic. Per quadrat species richness (species density) increased monotonically with exclosure treatment: −all plots had ~65% more species per m^2 than +all plots ($F_{3,24} = 7.98$, $p = 0.0007$; Appendix S1: Figure S4B). Plot-level species richness

(cumulative number of species per 1-ha plot; $F_{3,30} = 7.17$, $p = 0.0009$) and Shannon diversity ($F_{3,24} = 12.01$, $p < 0.0001$), however, were both greatest in −all and −mega plots, and significantly lower in +all and −meso (Figure 3B,C). NMDS ordination revealed that although herbaceous community composition was most strongly influenced by site (North, Central, and South), communities from the same exclosure treatment tended to be most similar to one another (and dissimilar from other treatments) within sites (Appendix S1: Figure S4C).

Megaherbivores (elephants and giraffes) had dramatic effects on the structural complexity of the tree layer (Figure 4): maximum height ($F_{3,24} = 5.41$, $p = 0.0054$), mean height ($F_{3,30} = 7.85$, $p = 0.00051$), rugosity ($F_{3,30} = 22.70$,
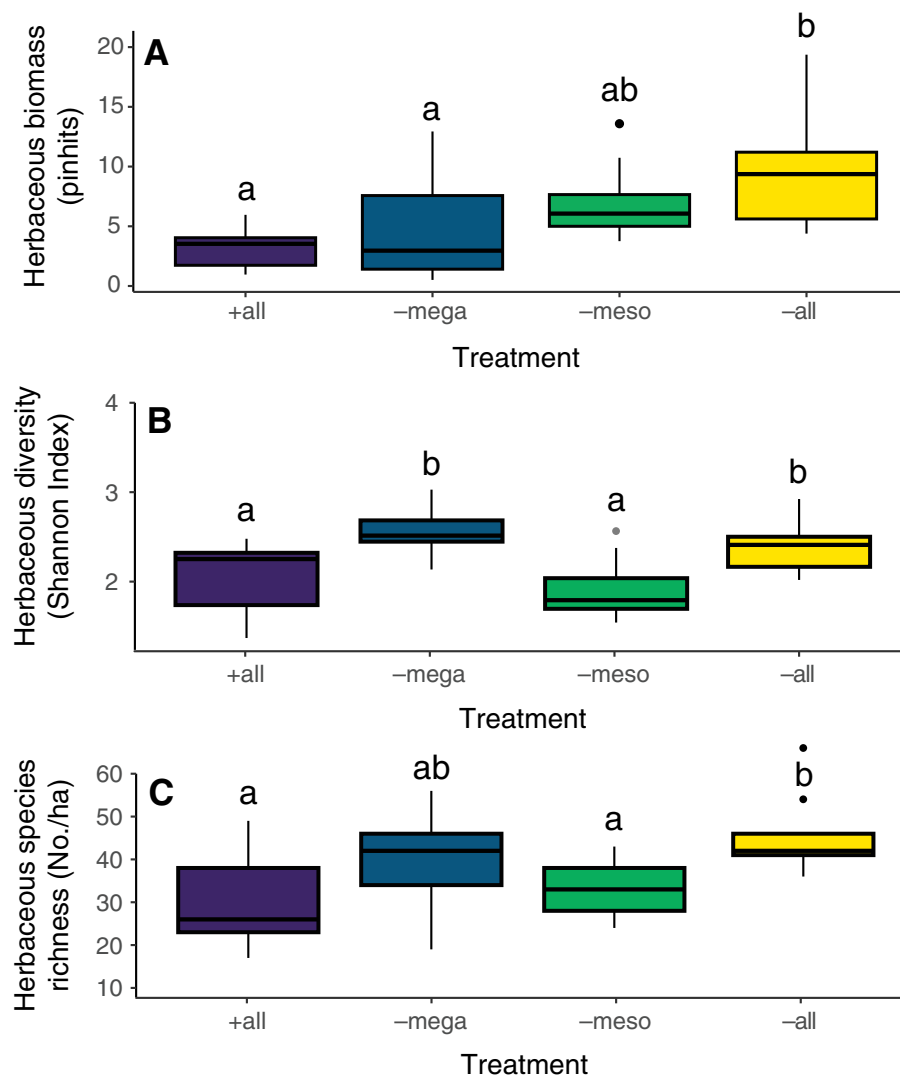

FIGURE 3 Effects of herbivore exclusion on herbaceous biomass and diversity calculated from field surveys. (A) Herbaceous biomass across exclosure treatments calculated from pin hit surveys. (B) Herbaceous diversity (Shannon Index) across exclosure treatments. (C) Species richness across exclosure treatments. All data were measured at the quadrat level (1 × 1 m); boxplots show median (central bar), IQR (bottom and top bars), 1.5 × IQR (whiskers), and outliers (>1.5 × IQR from first or third quartile). Letters above bars denote significant differences between treatments in post hoc contrasts (Tukey's honestly significant difference).
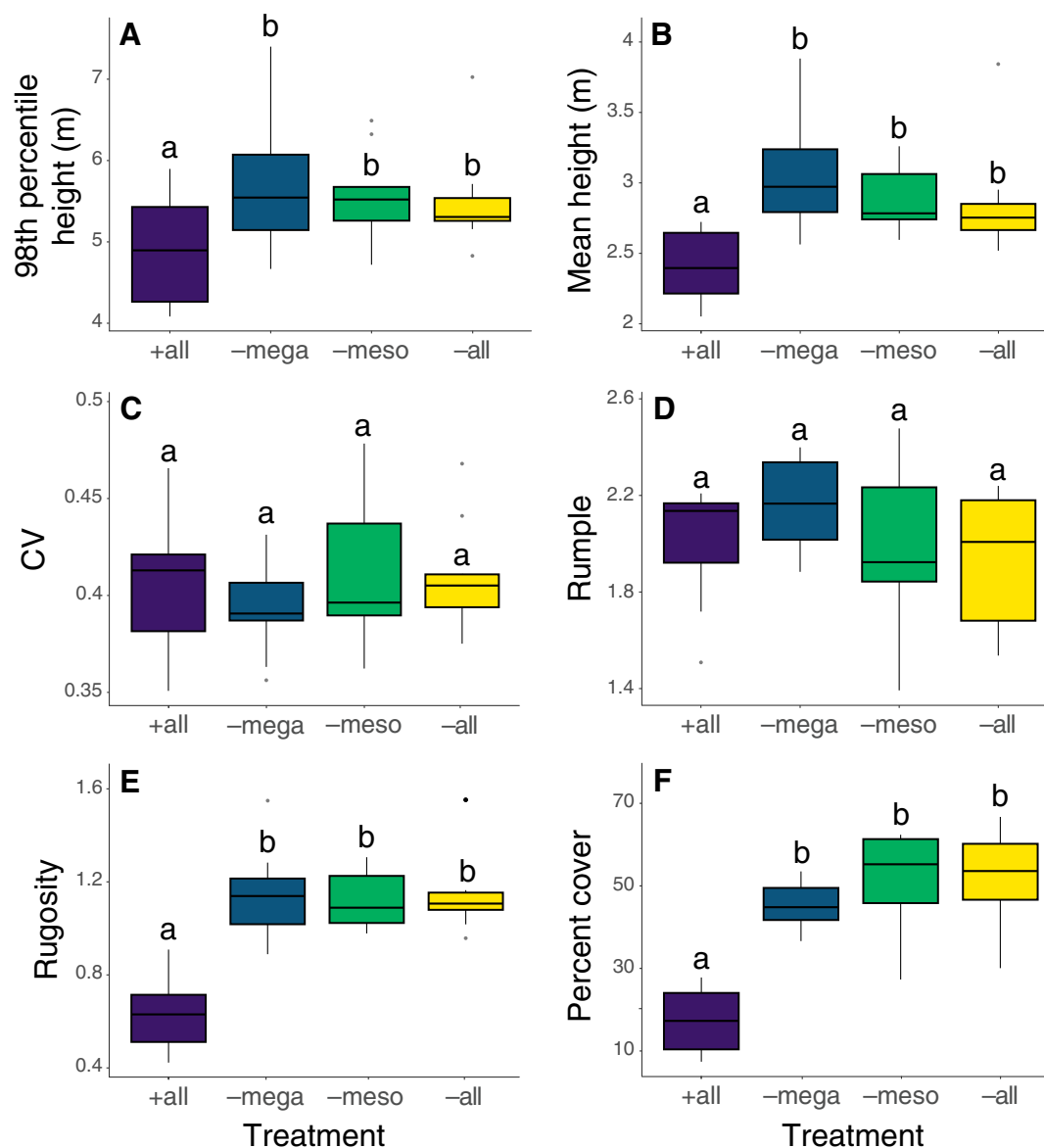
FIGURE 4 Effects of herbivore exclusion on metrics of structural complexity in the tree layer. (A) 98th percentile (maximum) height, (B) mean height, (C) CV of height, (D) rumple (a measure of 3D canopy roughness), (E) rugosity (the SD of maximum canopy height), and (F) areal percent cover. All metrics were calculated at the whole-plot level (1 ha, $N = 36$ plots); boxplots show median (central bar), IQR (bottom and top bars), $1.5 \times$ IQR (whiskers), and outliers ($>1.5 \times$ IQR from first or third quartile). Letters above bars denote significant differences between treatments in post hoc contrasts (Tukey's honestly significant difference).

$p < 0.0001$), and cover ($F_{3,24} = 33.67$, $p < 0.0001$) were all significantly greater in the absence of megaherbivores and statistically indistinguishable in all other treatments. The CV of tree height ($F_{3,24} = 1.91$, $p = 0.15$) and rumple ($F_{3,30} = 1.57$, $p = 0.22$) did not vary across treatments. In other words, megaherbivores were the only group to affect tree structure; we found no effects of smaller bodied herbivores on any structural metric.

In contrast, herbivores of all size classes had nonredundant effects on structural complexity of the herbaceous layer (Figure 5). As with trees, rumple of the herbaceous layer did not vary across treatments

($F_{3,32} = 0.60$, $p = 0.62$), and neither did mean height ($F_{3,30} = 0.77$, $p = 0.52$). Maximum height of herbaceous vegetation was greatest in +all and −mega and lowest in −all ($F_{3,30} = 3.72$, $p = 0.022$): elephants and giraffes had no detectable effect on peak herbaceous height, whereas smaller ungulates did. The CV of herbaceous vegetation height was similarly greatest in the presence of all herbivores and decreased monotonically with progressively stricter exclosure treatments ($F_{3,30} = 10.16$, $p < 0.0001$). Conversely, rugosity ($F_{3,24} = 27.33$, $p < 0.0001$) and herbaceous cover ($F_{3,32} = 109.71$, $p < 0.0001$) were lowest in the presence of all herbivores and increased monotonically
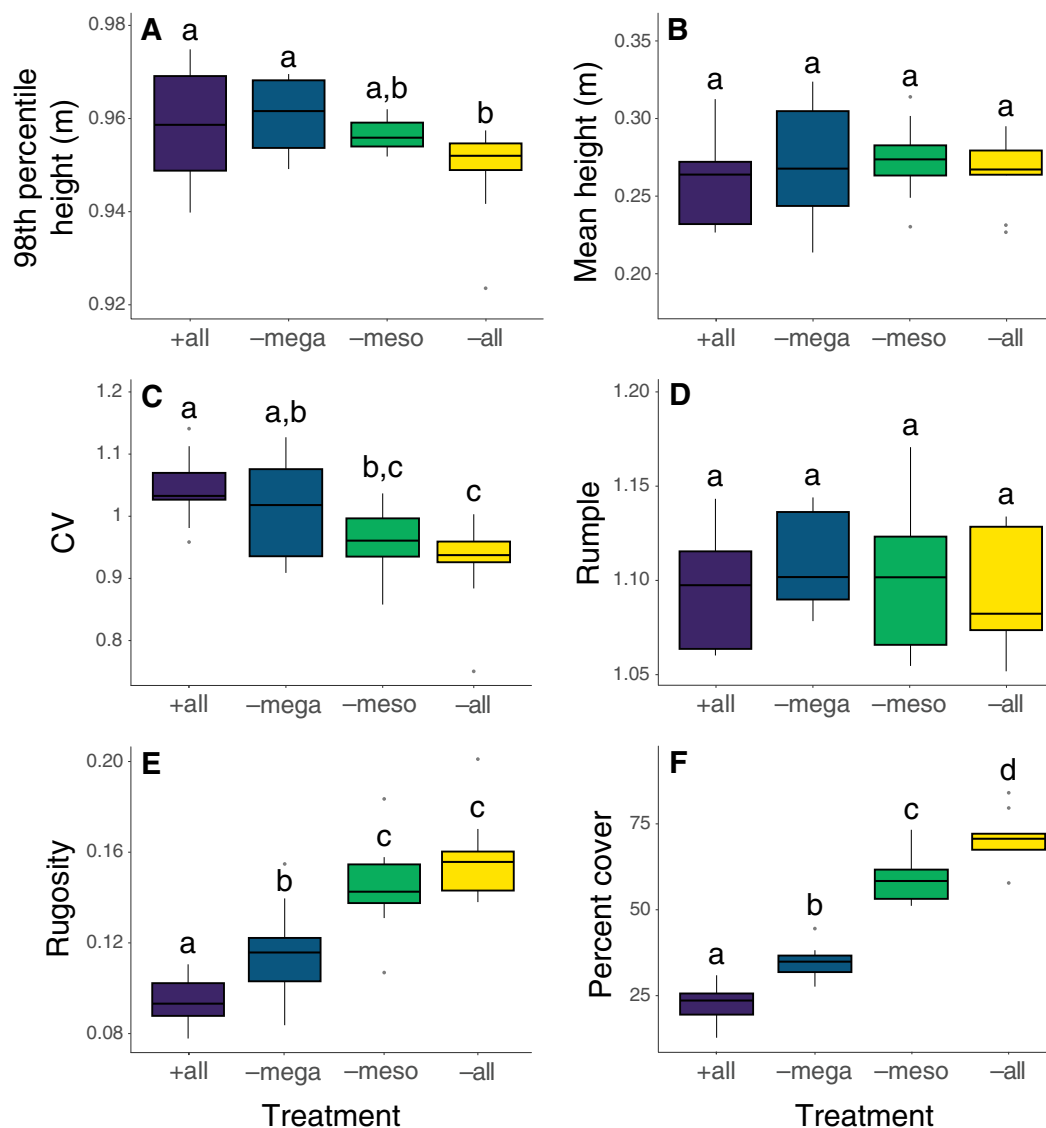
FIGURE 5 Effects of herbivore exclusion on metrics of structural complexity in the herbaceous layer. (A) 98th percentile (maximum) height, (B) mean height, (C) CV of height, (D) rumple (a measure of 3D canopy roughness), (E) rugosity (the SD of maximum canopy height), and (F) areal percent cover. All metrics were calculated at the whole-plot level (1 ha, $N = 36$ plots); boxplots show median (central bar), IQR (bottom and top bars), $1.5 \times$ IQR (whiskers), and outliers ($>1.5 \times$ IQR from first or third quartile). Letters above bars denote significant differences between treatments in post hoc contrasts (Tukey's honestly significant difference).

with each additional size class excluded, and all treatments differed significantly from one another except for rugosity in −meso and −all (Figure 5E). Thus, megaherbivores (elephant, giraffe) and mesoherbivores (impala, zebra) were the main drivers of variation in herbaceous rugosity, whereas the smallest but most abundant antelope (dik-dik) had little additional effect despite feeding exclusively below the 1-m mark. Herbaceous cover, which was nearly three-fold greater in −all plots than +all plots, responded significantly to each successive reduction in the herbivore community, with a particularly large difference between −mega and −meso, showing that herbivores of all sizes contributed to the net impact on this structural metric.

In comparisons of the same structural metrics for the entire plant community (i.e., trees and herbaceous vegetation combined), herbivores had strong effects on all structural metrics except rumple ($F_{3,32} = 0.43$, $p = 0.73$; Appendix S1: Figure S6). Two metrics (maximum height and rugosity) were lowest in +all plots and similarly high (i.e., no significant pairwise differences) in −mega, −meso, and −all treatments (both $F > 6.0$, $p < 0.004$). Percent cover was similarly lowest in +all plots but was intermediate in −mega and highest in −meso and −all treatments ($F_{3,30} = 129.7$, $p < 0.0001$). The CV of height was lowest in −mega and similarly high in all other treatments ($F_{3,24} = 8.05$, $p = 0.0007$), while mean height was

lowest in +all, greatest in −mega, and intermediate in −meso and −all. For all metrics other than rumple, the greatest pairwise differences were between +all and −mega treatments, indicating that elephants and giraffes predominantly influence vegetation structure at this resolution and that the effects of medium- and small-bodied herbivores stand out only when the tree and herbaceous communities are considered independently.

Aim 2: Herbivore effects on individual tree structure and tree-herbaceous interactions

The effects of herbivores on individual tree morphology varied among tree species but were broadly consistent with an overriding effect of elephant and giraffe (Figure 6). For *A. etbaica* and *B. rotundifolia*—the two species defended by long, straight spines or thorns— exclosures had a negligible effect on individual height and canopy area ($F < 1.6$, $p > 0.21$; Figure 6A,B). For *A. mellifera* and *A. brevispica*, both of which have short, recurved spines, exclusion of elephants and giraffes (+all vs. −mega) vastly increased height (both $F > 28.7$, $p < 0.0001$) and canopy area (both $F > 5.7$, $p < 0.004$), with no additional effect of smaller herbivores; *C. dichogamus* (spineless but aromatic and phytochemically rich) increased in height and area with both mega- and mesoherbivore exclusion ($F_{3,14.3} = 14.3$, $p < 0.0001$). In keeping with these results, herbivores did not affect the vertical biomass profile of *A. etbaica* ($p > 0.83$ for
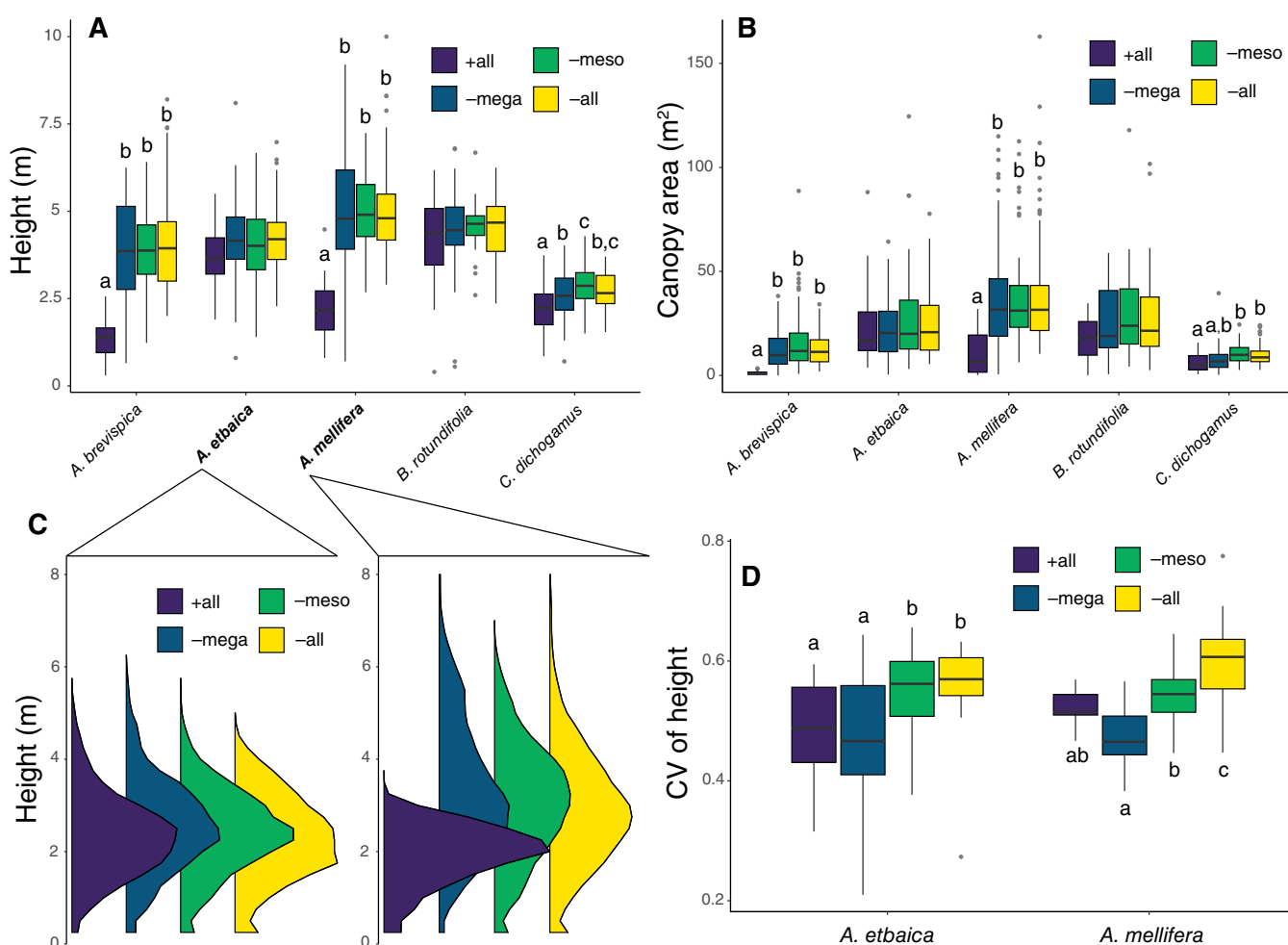

FIGURE 6 Herbivore effects on individual tree morphology. (A) Heights of five of the most common tree species measured in field surveys across all experimental treatments. (B) Canopy area of the same five tree species measured in field surveys across all exclosure treatments. Significant differences between treatments in post hoc contrasts (Tukey's honestly significant difference [HSD]) within a species are indicated by letters above bars; letters are omitted for nonsignificant contrasts. (C) Vertical height profiles for *Acacia etbaica* (left) and *A. mellifera* (right) derived from Light Detection and Ranging (LiDAR) point clouds. Profiles represent averages of multiple trees sampled across replicate plots of each treatment. (D) CV of height for *A. etbaica* (left) and *A. mellifera* (right) derived from LiDAR point clouds. Boxplots show median (central bar), IQR (bottom and top bars), 1.5 × IQR (whiskers), and outliers (>1.5 × IQR from first or third quartile). Letters above and below bars denote significant differences between treatments in post hoc contrasts (Tukey's HSD).

all pairwise comparisons), but elephants and giraffes significantly shifted the modal height and truncated the overall vertical distribution of *A. mellifera* biomass ($p < 0.005$ for each fenced treatment compared against +all; Figure 6C). The CV of height was greater in −all and −meso plots, where both extremes of height were well represented, than in +all plots (which had few large trees) and −mega plots (which had relatively fewer saplings) for *A. etbaica* ($F_{3,18.4} = 5.1$, $p = 0.01$) and *A. mellifera* ($F_{3,29} = 16.9$, $p < 0.0001$; Figure 6D).

Patterns of herbaceous abundance and diversity were further shaped by the interactive effects of herbivores and trees. In the pin-frame data, trees had weakly positive associations with herbaceous biomass in +all, −mega, and −meso plots (exclosure × tree: $F_{3,1741.9} = 7.46$, $p < 0.0001$; Appendix S1: Figure 7A), suggesting that interactions were generally neutral-to-facilitative in the presence of ungulates; however, this effect diminished with increasing level of herbivore exclusion and was reversed in −all, suggesting progressively stronger competitive relative to facilitative interactions as more herbivores were removed. DPM-based

estimates of biomass showed a qualitatively similar pattern (exclosure × tree: $F_{3,1739.8} = 2.28$, $p = 0.077$; Appendix S1: Figure S5), with the strongest positive effect of trees in −meso plots. Herbaceous species richness was markedly greater beneath trees in +all, −mega, and −meso treatments, but negligibly different in −all plots (exclosure × tree interaction: $F_{3,1743.1} = 4.37$, $p = 0.005$; Figure 7B). These community-level outcomes are consistent with previous species-level experiments conducted in UHURU, where neighbor removals have shown directly that plant–plant interactions are typically positive in the presence of herbivores and switch to being competitive when herbivores are removed (Coverdale et al., 2016, 2018, 2021; Louthan et al., 2014).

Aim 3: Relationship between vegetation structure, herbivory, and plant diversity

For five of the six metrics of vegetation structure, more diverse tree communities also tended to be more structurally complex (Figure 8): maximum height ($F_{3,265.2} = 18.5$,
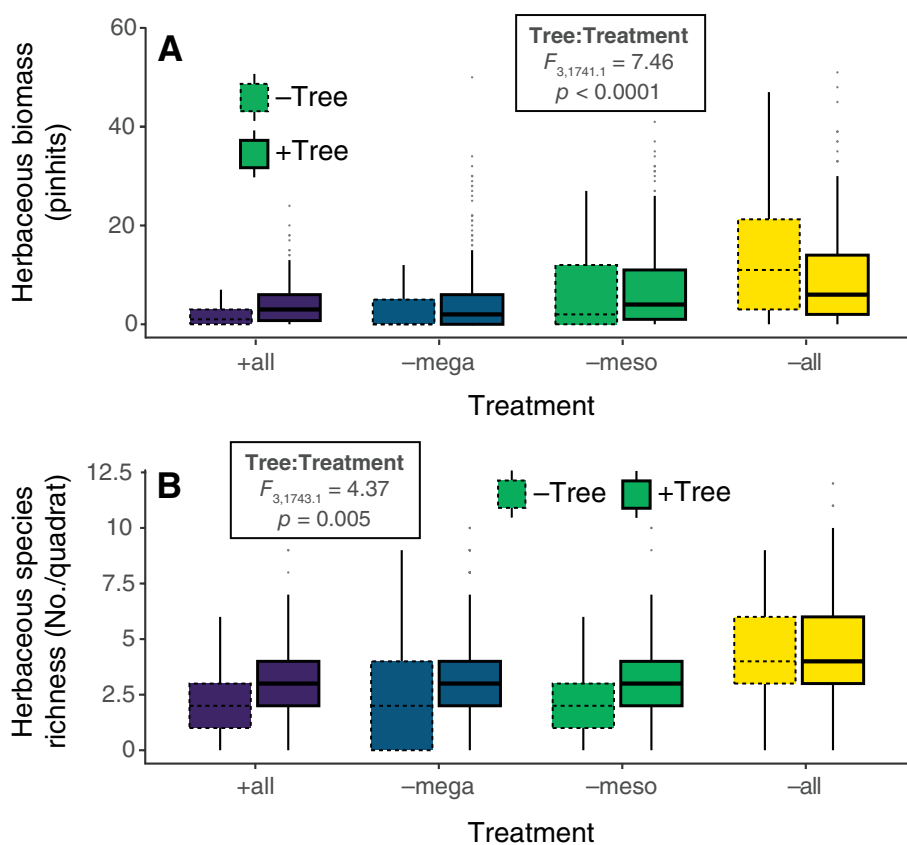

FIGURE 7 Interactive effects of herbivores and trees on herbaceous biomass and species richness. (A) Herbaceous biomass calculated from field surveys using a pin frame from quadrats without (dashed boxplots) and with (solid boxplots) overlying trees across exclosure treatments. (B) Herbaceous species richness calculated from field surveys from quadrats without (dashed boxplots) and with (solid boxplots) overlying trees across exclosure treatments. Boxplots show median (central bar), IQR (bottom and top bars), 1.5 × IQR (whiskers), and outliers (>1.5 × IQR from first or third quartile).
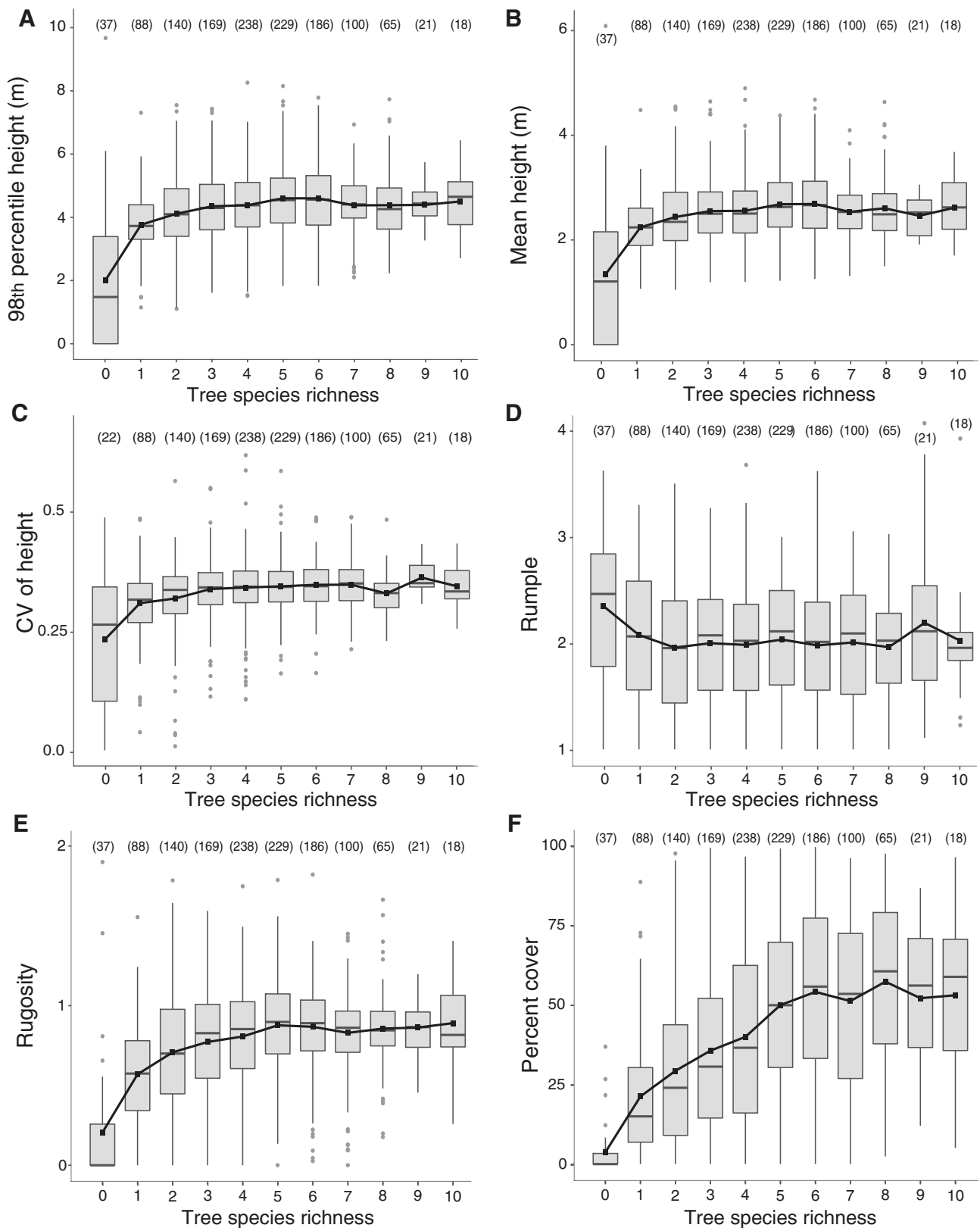
FIGURE 8 Relationship between tree species richness (unique species per subplot) and six metrics of structural complexity. (A) 98th percentile (maximum) height, (B) mean height, (C) CV of height, (D) rumple (a measure of 3D canopy roughness), (E) rugosity (the SD of maximum canopy height), and (F) percent cover. All metrics were calculated at the subplot level (10 × 10 m) using Light Detection and Ranging data; boxplots show median (central bar), IQR (bottom and top bars), 1.5 × IQR (whiskers), and outliers (>1.5 × IQR from first or third quartile). Black squares show mean values of structural metrics for each level of species richness and are connected by segmented lines (black). Numbers above each boxplot indicate the number of replicate subplots for each level of species richness.

$p < 0.0001$), mean height ($F_{3,269.8} = 11.5$, $p < 0.0001$), CV of height ($F_{3,257.8} = 14.6$, $p < 0.0001$), rugosity ($F_{3,267.6} = 47.0$, $p < 0.0001$), and percent cover ($F_{3,265.7} = 115.0$, $p < 0.0001$). All of these metrics saturated in subplots containing five or more species (100 m^{-2}); the three height metrics peaked rapidly (Figure 8A–C), whereas rugosity and percent cover increased more gradually with richness (Figure 8E,F). Rumple was slightly greater at lower levels of species richness, but this trend was not statistically significant ($F_{3,269.7} = 0.89$, $p = 0.35$; Figure 8D).

The same five metrics also responded strongly to herbivore-exclosure treatment (Appendix S1: Figure S7): maximum height ($F_{3,263.0} = 16.8$, $p < 0.0001$), mean height ($F_{3,263.6} = 11.6$, $p < 0.0001$), CV of height ($F_{3,254.2} = 10.9$, $p < 0.0001$), rugosity ($F_{3,264.2} = 21.4$, $p < 0.0001$), and percent cover ($F_{3,263.0} = 8.8$, $p < 0.0001$) tended to be greatest in −all plots and lowest in +all plots. These effects of herbivore-exclosure treatment on tree complexity were qualitatively similar to those presented in Aim 2; however, we note that the present models were, by necessity, less conservative in order to allow us to compare the interactive effects of species richness and exclosure treatment (i.e., data could not be pooled at the level of plot as in Aim 2). As before, rumple did not vary as a function of herbivore-exclosure treatment ($F_{3,263.6} = 2.4$, $p = 0.07$; Appendix S1: Figure S7D).

With only one exception, the generally positive relationship between tree diversity and structural complexity was not affected by herbivory (Appendix S1: Figure S7): negligible interactions between exclosure treatment and species richness for maximum height ($F_{3,263.3} = 0.92$, $p = 0.43$), mean height ($F_{3,264} = 0.67$, $p = 0.57$), CV of height ($F_{3,254.6} = 1.80$, $p = 0.15$), rumple ($F_{3,263.9} = 0.35$, $p = 0.79$), and rugosity ($F_{3,264.7} = 1.49$, $p = 0.22$) all indicate that the diversity–complexity relationship was not modified by exclosure treatment. The sole exception to this pattern was percent cover (exclosure × species richness interaction: $F_{3,263.2} = 3.27$, $p = 0.02$), which increased as a function of species richness in −mega, −meso, and −all plots, but was lower and comparatively constant in +all plots.

As with trees, more diverse herbaceous communities tended to be more structurally complex (Figure 9): maximum height ($F_{3,257.1} = 21.4$, $p < 0.0001$), CV of height ($F_{3,245.8} = 24.4$, $p < 0.0001$), rugosity ($F_{3,265.5} = 19.5$, $p < 0.0001$), and percent cover ($F_{3,264.8} = 34.3$, $p < 0.0001$) all tended to increase with increasing species richness. Only mean height ($F_{3,266.4} = 0.09$, $p = 0.76$) and rumple ($F_{3,265.7} = 2.47$, $p = 0.12$) were comparatively insensitive to variation in species richness. Overall, these relationships were similar but more variable in form than those for the tree layer; rugosity and percent cover appeared to saturate in quadrats containing at least 5 species (per square meter),

whereas maximum height and CV of height increased more or less monotonically with richness. Excluding quadrats with overlying trees did not qualitatively change these results (Appendix S1: Figure S8A–F).

Increasing herbivore exclusion also tended to increase structural complexity in the herbaceous layer (Appendix S1: Figure S9): maximum height ($F_{3,265.8} = 13.4$, $p < 0.0001$), mean height ($F_{3,261.3} = 6.9$, $p < 0.0001$), CV of height ($F_{3,244.7} = 5.5$, $p = 0.001$), rumple ($F_{3,260.9} = 3.2$, $p = 0.02$), rugosity ($F_{3,260.7} = 7.0$, $p < 0.0001$), and percent cover ($F_{3,261.0} = 21.6$, $p < 0.0001$) were greatest in −all, −meso, or −mega treatments and tended to be lowest in −all treatments (compare with the more conservative analysis presented in Appendix S1: Figure S9).

Herbivores had a strong effect on the relationship between diversity and herbaceous height (Appendix S1: Figure S9). Maximum height (exclosure × species richness interaction: $F_{3,258.5} = 4.6$, $p = 0.003$) increased as a function of species richness in +all, −mega, and −meso plots but was high and comparatively constant in −all plots. The interaction between species richness and exclosure treatment was also significant for mean height (exclosure × species richness interaction: $F_{3,263.1} = 3.43$, $p = 0.018$), but in contrast to maximum height, the differences across treatments were more idiosyncratic (Appendix S1: Figure S9B). As for trees, the relationship between all other metrics of herbaceous structure and species richness did not vary across herbivore-exclosure treatment (all exclosure × species richness interactions: $F < 1.6$, all $p > 0.19$).

DISCUSSION

Our study combines data that are simultaneously both uncommonly granular (3D imaging and hundreds of field measurements at the scale of individual plants within each of four nested exclosure treatments) and uncommonly large in experimental scale ($36 \times 10,000$-m^2 plots distributed across an environmental gradient for 13 years; Figure 1). This powerful combination enabled us to reexamine ideas that have been proposed and tested in other systems (often at smaller scales, with narrower taxonomic focus and/or coarser data) and to test for the first time whether and how large herbivores modify the relationship between plant diversity and structure.

Disaggregating effects of herbivores on plant communities and vegetation structure (Aims 1 and 2)

Determining the extent to which savanna herbivore species and size classes are functionally redundant or
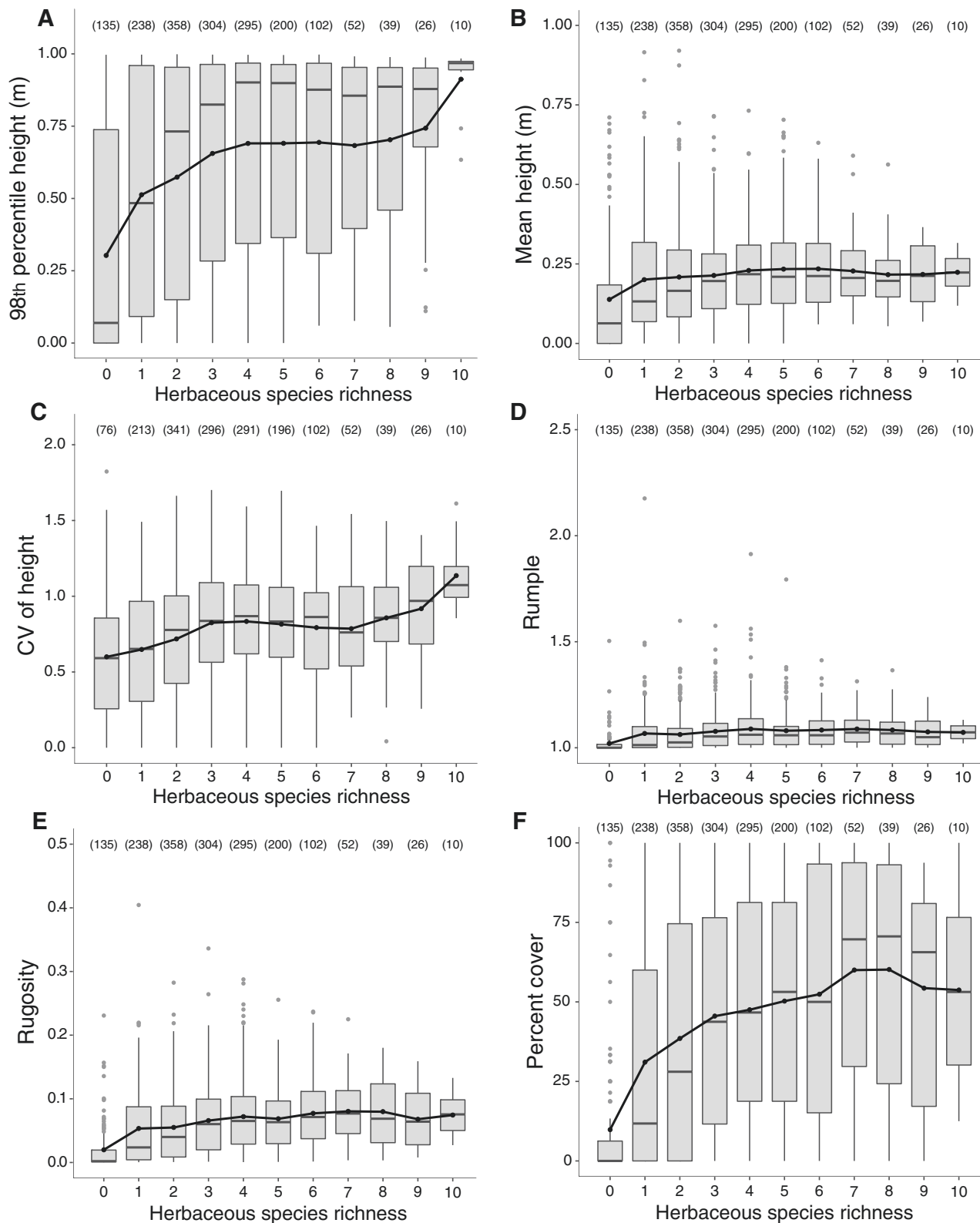
FIGURE 9 Relationship between herbaceous species richness (unique species per square meter and six metrics of structural complexity. (A) 98th percentile (maximum) height, (B) mean height, (C) CV of height, (D) rumple (a measure of 3D canopy roughness), (E) rugosity (the SD of maximum canopy height), and (F) percent cover. All metrics were calculated at the quadrat level (1 × 1 m); boxplots show median (central bar), IQR (bottom and top bars), 1.5 × IQR (whiskers), and outliers (>1.5 × IQR from first or third quartile). Black squares show mean values of structural metrics for each level of species richness and are connected by segmented lines (black). Numbers above each boxplot indicate the number of replicate quadrats for each level of species richness.

instead have unique impacts on ecosystems is critical for understanding and predicting the effects of size-biased herbivore declines (Lundgren et al., 2024; Pringle et al., 2023). Previous studies have found that herbivores of different sizes have nonredundant impacts on particular species or structural metrics (Asner & Levick, 2012; Coverdale et al., 2016, 2021; Pringle et al., 2014; van der Plas et al., 2016). We show that high functional complementarity also characterizes herbivore impacts on savanna plants as a whole, including aspects of abundance, species composition, and physical structure. In keeping with previous work, we found that mega-browsers alone drove structural changes in the tree layer (Figure 4), with the majority of this effect almost certainly attributable to elephants (Asner & Levick, 2012; Davies & Asner, 2019; Laws, 1970): in the presence of elephants, tree height, cover, and rugosity were significantly lower. These changes were broadly consistent whether structural metrics were calculated from the tree-only LiDAR data (Figure 4) or the full dataset (Appendix S1: Figure S6).

The high resolution of our UAV-LiDAR data (Boucher et al., 2023) also enabled us to detect nonredundant impacts of different-sized herbivores on the diversity and structure of the herbaceous layer. For example, medium-sized species (e.g., impala and zebra) regulated biomass accumulation and helped maintain herbaceous diversity, whereas larger (elephant, giraffe) and smaller (dik-dik) species had negligible impacts on biomass and reduced diversity (Figure 3). Moreover, we found that medium- and small-bodied species have effects on herbaceous vegetation structure that are analogous to those of megaherbivores on trees: herbaceous cover, maximum height, and rugosity responded more strongly to medium- and small-bodied species than to megaherbivore exclusion (Figure 5). This latter result is consistent with the foraging behavior of megaherbivores at MRC, with overstory plants comprising an estimated 68% of elephant diet and 95% of giraffe diet (Coverdale et al., 2021; Kartzinel et al., 2019; Kartzinel & Pringle, 2020). Our study adds to the evidence that diverse herbivore assemblages are crucial to ecological process in savannas, where the unique impacts of small ungulates are often overlooked relative to the dramatic effects of megaherbivores.

Just as the impacts of herbivores varied as a function of body size, plant responses varied as a function of species identity and growth form. After 13 years of herbivore exclusion, tree cover was more than threefold greater in the −mega, −meso, and −all exclosure plots (mean tree cover: 51%) than in the unfenced +all plots (mean tree cover: 16%; Figure 2A). However, the total density of trees did not vary across treatments

(Figure 2B), indicating that observed changes in tree cover were primarily driven by increases in the size of individual tree canopies rather than an increase in the number of trees. Thus, our results support the idea of a "browse trap" (Staver & Bond, 2014): the bottleneck on tree demography imposed by herbivores is not on recruitment from seeds or seedlings (which may in fact often be facilitated by ungulates: Goheen et al., 2010), but rather on the escape of saplings from indefinite suppression and arrested development in the understory (Holdo et al., 2022; Pringle et al., 2016; Prins & Van Der Jeugd, 1993). By examining the responses of the five most common tree species, which collectively accounted for ~75% of all individuals in 2021, we further show that plot-level differences in tree cover were disproportionately caused by structural changes in just three species: *A. brevispica* and *A. mellifera*, which had greater canopy area in the absence of elephants and giraffes, and *C. dichogamus*, which was most strongly affected by mesoherbivores (Figure 6B). The specificity of tree responses again mirrors their prevalence in herbivore diets: *A. brevispica* and *A. mellifera* were present in the diets of 100% and 69% of 80 elephants sampled at MRC from 2013 to 2016, respectively while *C. dichogamus* occurred in only 8% of elephant diet samples but in 13%–25% of samples from each of six bovid mesoherbivore species (Gill et al., 2019; Kartzinel et al., 2015). In contrast, *B. rotundifolia* (which was present in <4% of samples across all herbivore species at MRC) and *A. etbaica* (which is often browsed but strongly avoided relative to its abundance; Hutchinson et al., 2022) were insensitive to exclosure treatment. *A. etbaica* and *B. rotundifolia* are physically defended with long spines and thorns, respectively, which reduce palatability to ungulates (Ford et al., 2014); the unresponsiveness of these species suggests that elongated physical defenses are a more effective defense against browsers than short recurved spines (*A. brevispica*, *A. mellifera*) or secondary chemistry (*C. dichogamus*) (Wigley et al., 2019).

Predicting the responses of particular plant species or growth forms to shifts in herbivore community structure is a major challenge in the study of African savannas (Staver et al., 2021), and our results suggest that this is due, in part, to the distinct ways in which herbivores affect different plant species. Across African savanna ecosystems more broadly, even the direction of herbivore impacts on plant diversity and abundance is variable: whereas our results from an infertile, semiarid savanna show that herbivores decrease both diversity and abundance in both the tree and herbaceous layers, herbivores typically increase herbaceous diversity in high-productivity systems dominated by a small number of

competitively vigorous species (Burkepile et al., 2017; Eby et al., 2014; Eskelinen et al., 2022; Koerner et al., 2018). Combining remote sensing and field data, as we have done here, is a promising approach for quantifying these responses and predicting the consequences of human impacts on wildlife assemblages in African savannas (Coverdale & Davies, 2023).

Relationship between plant diversity, herbivory, and vegetation structure (Aim 3)

The species richness of tree and herbaceous plant communities was positively correlated with almost all metrics of vegetation structural complexity (Figures 8 and 9). The relationships between plant diversity and structure were broadly consistent for trees and herbaceous vegetation, despite the former comprising roughly an order of magnitude fewer species than the latter (Gill et al., 2019). In part, this congruence likely reflects the similar species richness for each growth form at the different spatial scales at which we surveyed them: >90% of 1-m^2 quadrats and 100-m^2 subplots contained 0–10 herbaceous plant and tree species, respectively. Regardless, the strong positive relationship between richness and complexity is consistent with the general mechanisms invoked to explain positive biodiversity-ecosystem function relationships, namely niche complementarity and the higher likelihood that more diverse communities contain species with outsized contributions to structure (Loreau et al., 2001). Several notable patterns emerged from this analysis.

First, for several structural metrics (e.g., maximum height, mean height, CV of height, and rugosity), the greatest difference was between zero and one species, after which the addition of more species had progressively smaller effects. This saturating pattern is broadly consistent with relatively high redundancy among plant species' contributions to vertical structure, as might be expected in a savanna plant community with lower overall height and greater overlap between species vertical profiles than is found in many mesic savannas and forests (Ishii et al., 2004). However, for both trees and especially herbaceous vegetation, several structural metrics continued to increase across the full range of species richness, suggesting a lower level of functional redundancy (Figures 8 and 9).

Second, rumple (a measure of 3D canopy roughness, or topological heterogeneity) did not vary across tree communities of varying diversities. In forested ecosystems, rumple and rugosity are thought to be positively correlated with habitat area and complexity, both of

which shape the diversity and abundance of arboreal species. Additional research in non-forested systems will be necessary to elucidate the value and applicability of standard remotely sensed structural metrics for describing non-forest vegetation, but our results suggest that canopy-level metrics like rumple may not be as useful for describing the structure of discontinuous tree canopies as they are in forests. Forests and savannas differ considerably in overall vegetation height, openness, and other aspects of physiognomy (Ratnam et al., 2011). Horizontal and vertical heterogeneity tends to be greater in savannas than in forests (Asner et al., 2009; Augustine, 2003), particularly forests managed for silviculture where increased canopy heterogeneity (i.e., rumple and rugosity) is associated with reduced economic value (Hardiman et al., 2011; Milodowski et al., 2021). The general utility of all standard structural metrics outside forest ecosystems will be improved with further data collection in these systems.

Finally, we note that all the structural metrics we report (following Atkins et al., 2018; Loke & Chisholm, 2022; Moudrý et al., 2023) are strongly correlated with one another (Tables S2 and S3), in part because they depend to some degree on vegetation height. Correlation among metrics is common in studies of vegetation structure (Coverdale & Davies, 2023) and inherently increases the odds of discovering common patterns across metrics (e.g., positive relationship with species richness). Nonetheless, these metrics capture distinct aspects of vegetation structure—maximum height, variation in height, canopy shape, areal cover—that have different functional implications, and the varying form and strength of their relationships with species richness in different vegetation strata underscore that they convey complementary information.

The positive relationship between diversity and structural complexity has the potential to advance the understanding of herbivore impacts on savanna function. We suggest that this relationship may reflect an additional, indirect mechanism by which savanna herbivores affect plants: herbivores had strong, negative effects on both tree (Figure 2C) and herbaceous (Figure 3B,C) species richness, which were greatest in −all plots and lowest in +all plots. At the same time—and irrespective of herbivore-exclosure treatment—more diverse plant communities were more structurally complex (and vice versa; Figures 8 and 9). Moreover, the relationship between diversity and structure varied as a function of herbivore-exclosure treatment for only three of the six structural metrics we investigated for both trees and herbaceous vegetation (tree cover and mean and maximum herbaceous height; Appendix S1: Figures S7F and S9A,B). This suggests that the generally positive relationship between plant diversity and structure at our study site is robust to the effects

of herbivory and contributes to a growing body of evidence that diversity–structure relationships are likely driven by classic biodiversity-ecosystem functioning mechanisms (Coverdale & Davies, 2023). While we are unable to definitively determine the directionality of this relationship, basic principles suggest that the relationship is probably bidirectional. On the one hand, more diverse plant assemblages are more likely to contain structurally complex species (e.g., erect subshrubs and prostrate forbs) and thus have higher overall structural complexity. This suggests a positive effect of diversity on structure, in keeping with biodiversity-ecosystem function theory (Naeem & Wright, 2003; Tilman et al., 2014). On the other hand, structurally complex vegetation clusters are likely to increase local plant diversity by boosting patch heterogeneity (and hence available niche space) and providing spatial refuges from herbivores. For example, we found that overhanging tree canopies significantly increased herbaceous species richness, but only in the presence of herbivores (Figure 7B). This latter result is consistent with previous research at MRC showing that plants protect their neighbors from large herbivores by reducing apparency and/or accessibility (Coverdale et al., 2016; Louthan et al., 2014) and suggests a positive effect of structural complexity on plant diversity. We postulate that the most likely mechanism for this pattern is that trees (especially shrubby and/or spinescent taxa) impede herbivores and reduce consumptive pressure beneath their canopies and that in the absence of herbivores, this facilitative relationship shifts toward competition for light and/or water (Belsky, 1994).

The future of vegetation structure in African savannas

The savanna biome is defined by its uniquely heterogeneous, dual-layered vegetation community. Accordingly, changes in vegetation structure are likely to have cascading effects on other savanna dynamics, including herbivore foraging behavior (Atkins et al., 2019; Daskin et al., 2023; Walker et al., 2023), predator–prey interactions (Davies et al., 2016; Ford et al., 2014), fire frequency and intensity (Smit et al., 2010), carbon cycling (Davies & Asner, 2019; Grace et al., 2006), and the distribution and abundance of plants and animals (Coverdale et al., 2016; Louthan et al., 2014; Pringle, 2008; Treydte et al., 2009). The nonredundant effects of various large herbivores on vegetation structure documented here show that large mammals play a critical role in regulating the physical structure of vegetation and all of its downstream effects. Similarly, the impacts of large herbivores on vegetation structure may differ across spatial scales: We found a negative effect of herbivores on nearly all aspects of vegetation structural complexity, but previous research at larger

spatial scales suggests that herbivores tend to have a positive effect on structural complexity, potentially by increasing landscape-scale habitat heterogeneity (Asner et al., 2009; Levick et al., 2009).

Greater structural complexity is often positively linked to ecological functions such as microclimate regulation, primary productivity, faunal diversity, and habitat provisioning (Coverdale & Davies, 2023). Our results show that different subsets of the large-herbivore assemblage affect structural complexity in different ways, both negative and positive, and that the strong and diverse ecological impacts of wild large herbivores are not always simplistically aligned with metrics viewed as indicators of ecosystem health. Similarly, at different scales and in different places, large herbivores can increase or decrease the diversity and abundance of other species (Burkepile et al., 2017; Coverdale et al., 2016; Daskin & Pringle, 2016; Eby et al., 2014; Guy et al., 2021; Pringle et al., 2007) and augment or diminish carbon storage (Davies & Asner, 2019; Holdo et al., 2009; Pellegrini et al., 2017). Understanding the direction and magnitude of these impacts, and their scale and context dependence, is necessary for predictive ecology and adaptive management alike.

To date, most research on the link between structural complexity and ecosystem function has occurred in forests, where increasing complexity does not fundamentally alter ecosystem physiognomy and where remediation efforts are often motivated by historic losses of complexity resulting from deforestation or silviculture (Hardiman et al., 2011; Milodowski et al., 2021). In contrast, the integrity of African savannas is threatened by a suite of human impacts (e.g., land-use and atmospheric change, overharvesting, and afforestation; Buitenwerf et al., 2012; Daskin et al., 2016; Davies & Asner, 2019; Stevens et al., 2017) that have collectively increased woody cover and shrub density, which can fundamentally alter savanna processes and even lead to alternative stable states (Ratnam et al., 2011; Sankaran et al., 2005). In forests, increasing complexity through management intervention has emerged as a powerful tool to increase biodiversity and restore a broad suite of degraded ecosystem functions (Camarretta et al., 2020). In contrast, restoration efforts in grassy ecosystems should focus on restoring lost ecological processes (e.g., herbivory and fire), which in some cases could result in decreased vegetation structural complexity, at least at localized scales.

Conclusions

By combining high-resolution LiDAR and field data from a long-term exclosure study, we found that large African herbivores exert strong top-down control on the

abundance, diversity, and structure of savanna vegetation. Herbivores tended to reduce both the diversity and abundance of trees and herbaceous plants, though the strength of these effects varied as a function of both herbivore body size and plant type. Vegetation structural complexity—in both the overstory and herbaceous layer—similarly varied in response to the exclusion of different subsets of the large-herbivore community, highlighting the nonredundant effects of different herbivore size classes on an important determinant of ecosystem function. Structural complexity was positively related to plant species richness among both trees and herbaceous plants, consistent with the possibility of a positive feedback loop between these properties. We also found evidence that herbivores modify the structure–diversity relationship by enhancing the benefits to herbaceous plants of spatial association with trees. The low functional redundancy of herbivore impacts on vegetation structure, along with the marked interspecific variation in plant responses to herbivore exclusion, underscore the roles of both animal and plant species diversity in determining the emergent properties and functions of African savanna landscapes.

AUTHOR CONTRIBUTIONS

Tyler C. Coverdale and Andrew B. Davies conceived and designed the research plan. Jacob R. Goheen, Todd M. Palmer, and Robert M. Pringle conceived and coordinated the UHURU experiment. Tyler C. Coverdale, Peter B. Boucher, Jenia Singh, and Andrew B. Davies collected, processed, and analyzed remote sensing data. Tyler C. Coverdale analyzed field data and drafted the manuscript. All authors approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Coverdale et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.rfj6q57jp.

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SUPPORTING INFORMATION

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