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ARTICLE

Multidimensional resource partitioning by Serengeti herbivores

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Abstract

The enchanting diversity of large mammalian herbivores in African savannas has long challenged ecologists: How can so many species of large, generalist plant eaters coexist? Variation in body size and craniofacial/dental anatomy are key morphological determinants of ecological niche differentiation, shaping foraging behavior in ways that stabilize coexistence by limiting interspecific competition for space and food. Variation in water requirements may be another important dimension of niche differentiation, but whether and how variability in water requirements affects the partitioning of other resources is unknown. Here, we investigate how body size, dental morphology, and water requirements interactively affect space use and diet of 15 large-herbivore species in Serengeti National Park. Water requirements predicted space use in relation to permanent water sources, while diet type (percentage grass) was best predicted by dental morphology. Food partitioning was best predicted by a combination of all three traits in both wet and dry seasons. Furthermore, the total explained variation of diet dissimilarity explained almost tripled when these three traits were combined compared to single traits, emphasizing the importance of multiple dimensions of niche differentiation. Our results show that variation in water requirements is strongly associated with spatial and dietary niche differentiation among large herbivores, emphasizing the importance of spatial heterogeneity in surface water and vegetation structure for maintaining the world's last mega-diverse megafaunal assemblages. Integrating multiple dimensions of resource partitioning is a crucial step toward predicting how species will respond to homogenization of savanna landscapes due to changes in land use, surface water availability, and rainfall.

KEYWORDS
African savannas, eDNA, megafauna, species coexistence theory, surface water distribution, water requirements

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INTRODUCTION

The long search for mechanisms explaining the coexistence of diverse herbivore assemblages in African savanna ecosystems has identified multiple key dimensions of resource partitioning (Figure 1; Hopcraft et al., 2010; Jarman, 1974; Lamprey, 1963; McNaughton & Georgiadis, 1986; Potter et al., 2022; Sinclair et al., 2003). First, different herbivore species eat different plants, with the grazer-browser continuum—proportional consumption of grasses and other monocots—forming the primary axis of variation in diet composition and food partitioning (Codron et al., 2007; Kartzinel et al., 2015; Owen-Smith, 2015; Pansu et al., 2019, 2022). Species' positions on the grazer-browser continuum correspond with morphological traits, especially craniofacial anatomy and dentition, that influence the relative efficiency of extracting nutrients from graminoids versus woody plants and forbs (Codron et al., 2019; Damuth & Janis, 2011). A second axis—the forage quality-quantity continuum—arises from the fact that larger herbivores require more food but have diets of lower nutritional quality (Bell, 1971; Clauss et al., 2013; Clauss & Hummel, 2005; Potter et al., 2022; Potter & Pringle, 2023; Wilmshurst et al., 2000). In general, smaller herbivores utilize short-statured, nutrient-rich vegetation, whereas large herbivores are forced to use areas of abundant vegetation biomass with lower average quality (Anderson et al., 2010; Hopcraft et al., 2012; Owen-Smith, 2015). These two continua have formed a framework for explaining resource partitioning based on interspecific differences in body size and morphology (Du Toit & Olff, 2014; Gordon & Prins, 2008; Hopcraft et al., 2010; Olff et al., 2002).

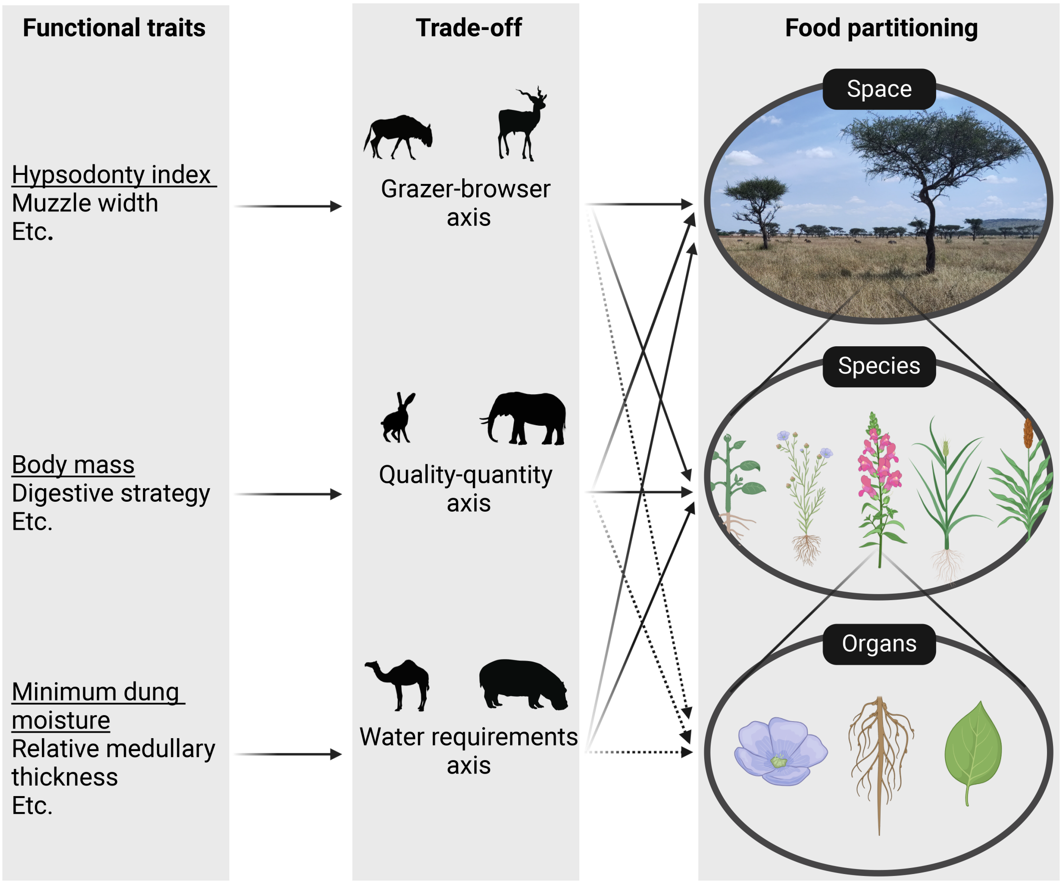


FIGURE 1 Multidimensional resource partitioning by large herbivores. Herbivores can reduce interspecific competition for food by selecting different sites (space), different plant taxa, and different plant organs. In this graphic, herbivores partition space, plant species, and organs in relation to three key trade-offs: Grazer-browser continuum, forage quality–quantity continuum, and water requirements continuum. Here, we use functional traits as proxies for the positioning of 15 large-herbivore species along these three axes to integrate multiple dimensions of food partitioning. We investigate their ability to explain partitioning of space and plant taxa (we did not consider partitioning of plant parts in this study). Underlined traits have been used as proxies for the three dimensions in this study. Figure created in BioRender (Veldhuis, 2025a; https://BioRender.com/fo719sq). Animal silhouettes created by the Pringle Laboratory. Photograph taken by M.P. Veldhuis.

However, this framework does not include another potentially important dimension of resource partitioning related to water requirements, which differ markedly among herbivore species (Cain et al., 2012; De Leeuw et al., 2001; Kihwele et al., 2020; Taylor, 1968; Veldhuis et al., 2019; Western, 1975). Spatiotemporal variation in surface water availability can have profound impacts on herbivore population and community dynamics (Cain et al., 2006, 2012; Rymer et al., 2016) and is a key driver of both seasonal migration (Gereta et al., 2009; Gereta & Wolanski, 1998; Wolanski et al., 1999) and species-specific cycles of wet-season dispersal and dry-season congregation around freshwater sources (Western, 1975; Wolanski & Gereta, 2001). Some studies have combined data on herbivore locations from GPS collars or observations with the average distance to water as a proxy for differences between species in surface water dependence (Cain et al., 2012; Redfern et al., 2003, 2005; Valeix, 2011; Western, 1975). However, local herbivore distributions are influenced by other factors, such as nutritional requirements (Hopcraft et al., 2012; Owen-Smith, 2015; Smit, 2011), vulnerability to predation and sensitivity to risk (Atkins et al., 2019; Hopcraft et al., 2012, 2014; Owen-Smith, 2015), and landscape features (Cromsigt et al., 2017; de Jonge et al., 2022; Hopcraft et al., 2010; Owen-Smith & Traill, 2017). These factors are often spatially auto-correlated. For instance, grass biomass and woody cover—and hence, forage availability and risk of ambush predation—are often highest in valley bottoms, where water accumulates, and sparsest on the relatively dry hilltops. Furthermore, many savanna species spend little time drinking and may obtain much of their water from the plants they eat (Van Driessche et al., 2025) and/or commute to water over large distances (>10 km) (Cain et al., 2012). Therefore, the degree of dry-season concentration or dispersion of animals around water sources might not be a reliable indicator of surface-water dependence. Although variation among herbivore species in water requirements and space use around surface water is well established, it remains unclear how this variation relates to other dimensions of resource partitioning.

Relative differences in water requirements between large-herbivore species can be quantified through their minimum dry-season dung moisture content—a proxy for water requirements in field studies of resource partitioning (Kihwele et al., 2020; Woodall & Skinner, 1993). This metric is tightly correlated with experimentally measured minimum water requirements, urine osmolarity, medullary thickness, and evaporative water loss (all $|r| > 0.7$; see Kihwele et al., 2020), thus providing a simple, cheap, and noninvasive way to assay relative water requirements in the field and incorporate them into a more encompassing framework of niche differentiation. Understanding the implications of interspecific variation in water requirements is important not just for elucidating mechanisms of biodiversity maintenance, but also for conservation and management (Owen-Smith, 1996; Ogutu et al. 2010).

Here, we investigate the partitioning of space and diet (i.e., plant taxa) by large herbivore species in Serengeti National Park—specifically, the extent to which resource partitioning can be explained by variation along three main trait axes: body size, dental morphology, and minimum dung moisture content. Based on the literature outlined above, we expect variation between species along these three trade-off axes to explain the partitioning of resources. We selected these three functional traits because they have been widely used and shown to correlate with the three axes. We therefore test whether these three morphophysiological traits predict observed differentiation in resource use and the extent to which water availability, next to food, is a key determinant.

METHODS

Study area

Serengeti National Park comprises 14,763 km^2 and exhibits diverse habitats ranging from open grasslands in the southeast to acacia-dominated woodlands in the central and western Serengeti to Miombo woodland in the northwest (Reed et al., 2009). Annual rainfall follows a bimodal distribution with two distinct rainfall seasons: short rains in November–December and long rains between March and May, with a dry season occurring in July–October. Mean annual rainfall ranges from about 500 mm in the southeast to >1200 mm in the northwest. Four major rivers intersect the park: the Mara, Grumeti, Orangi, and Mbalageti, all of which flow westward into Lake Victoria (Gereta & Wolanski, 1998). Of these, only the Mara flows year-round and is thus a key dry-season water source for migrating herbivores (Gereta et al., 2009).

Mapping permanent surface water sources

In August 2016 (peak dry season), we conducted an intensive survey to map all surface-water sources in Serengeti National Park that are used by wildlife for drinking—that is, those with a salinity threshold of <4 parts per thousand (Wolanski & Gereta, 2001). Accompanied by long-serving and experienced park rangers, who explore the area by foot on a daily basis and thus know it extremely well, we visited each water source to record its location (Figure 2). This has been the most extensive effort to map all surface water points in the Serengeti National Park. Nevertheless, there is always the possibility that we might have missed some (smaller) surface water points in the most remote areas. During a normal season, puddles and small pools appear everywhere across the landscape following the rains. It would be exceedingly difficult and impractical to map these, but in practice we can safely assume that herbivores are always within ~1 km from water during the wet season and thus that distance to drinking water is not a limiting factor during that period.

Spatial partitioning: Animal counts

The distribution of herbivores was estimated from monthly road-based transects (for detailed methods see Fryxell et al., 2022). Two observers enumerated all large mammals within 100 m from a slow-moving vehicle (<20 km/h) along nine permanent transects (Figure 2C). Observers recorded the odometer reading at each wildlife

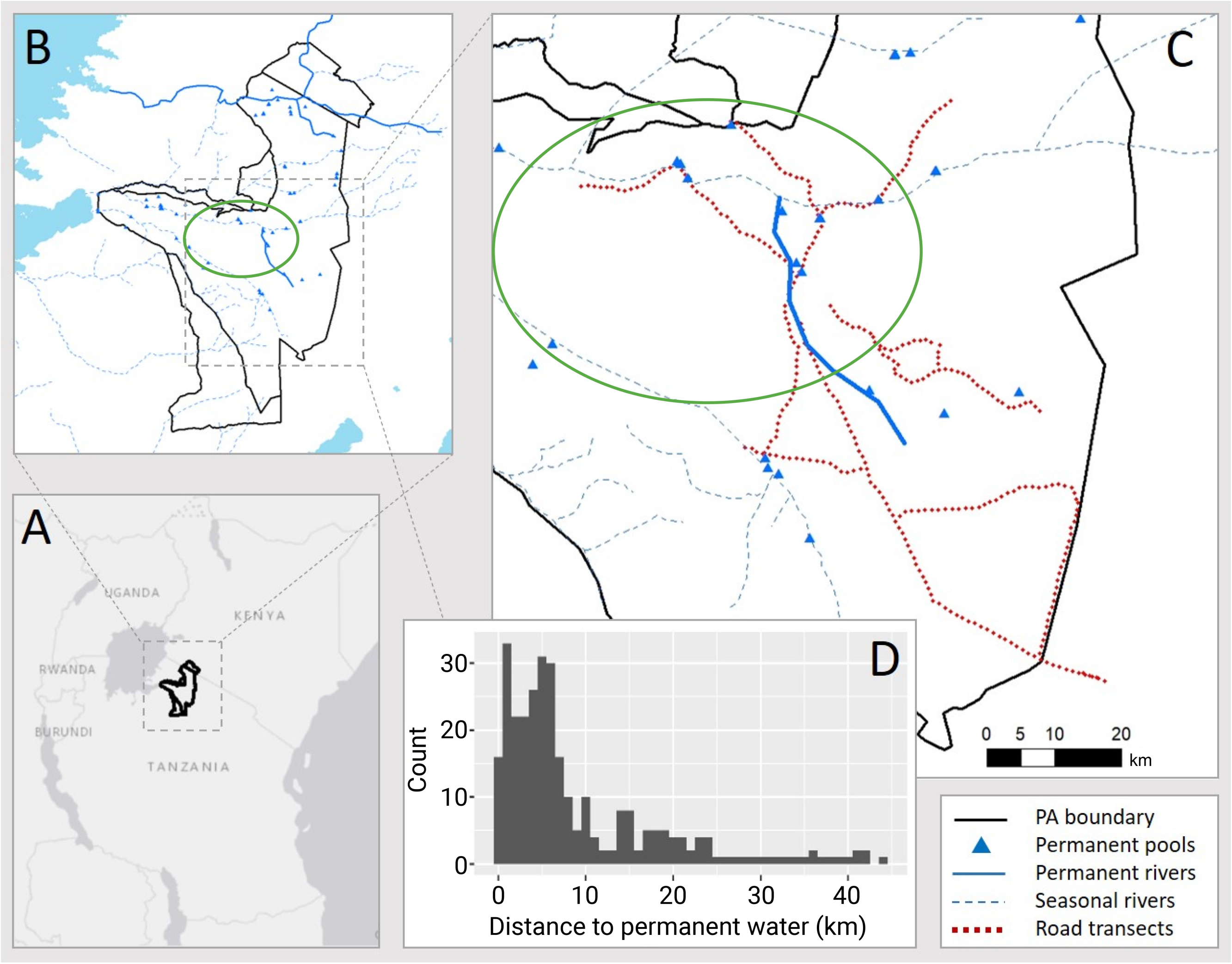


FIGURE 2 Study area, road count survey transects, and permanent water sources in 2016. (A) Location of Serengeti National Park in East Africa. (B) Overview of Serengeti National Park and adjacent protected areas (PA) with (semi-)permanent rivers and perennial pools. Water volume differs substantially among these water sources, with only the rivers in the north being sufficient to support the high abundance of wildebeest in the dry season. (C) Study area within Serengeti National Park, showing locations of road transects used for evaluating the distribution of animals in relation to permanent water sources. (D) Frequency distribution of observation points along road transects in relation to distance to permanent water sources. Transects were typically within 10 km of permanent water but included many points at greater distances (up to >40 km). Green circles in B and C indicate the area where fecal samples were collected. Seasonal rivers only provide water during the wet season and seasonal pools appear everywhere across the ecosystem during the wet season so that drinking water is no longer limiting. Figure created in BioRender (Veldhuis, 2025b; https://BioRender.com/x42x978).

sighting along each transect. Road transects were georeferenced with GPS coordinates taken every kilometer along each transect. Odometer readings were categorized to 1 km increments and translated into GPS coordinates. We estimated the distance of each animal—ungulates and elephants—to the nearest permanent water source (Figure 2C,D) using nearest-neighbor distance in the *Spatial Analyst* tool in ArcGIS 10.6. We subsetted the transect data from April to May 2015 and 2016 to investigate wet-season herbivore distributions, and from August to September 2015 to investigate dry-season distributions. We limited the analysis to these years, as they were closest to the mapping of permanent water sources. These months represent the core wet and dry seasons in the area, and hence, the maximum and minimum availability of surface water (see Appendix S1: Table S1 for a list of species and number of observations for each month).

Dietary partitioning: DNA metabarcoding

Herbivore fecal samples were collected in 2018 from March to April (wet season) and August to October (dry season). We collected samples while driving around the center of the park (Figure 2), meaning that all sampled herbivores had access to the same plant communities. Dung pellets were collected between 07:00 and 18:00 from individuals that were observed defecating to enable visual identification of the herbivore species and ensure that samples were fresh and uncontaminated.

Protocols for sample collection, processing, sequencing, and bioinformatic analysis followed a pipeline that has been used for 12 years (with minor variations and refinements) in Robert M. Pringle's laboratory. Below, we present a brief description of the processing, sequencing and bioinformatics analysis; a detailed description is included in Appendix S1.

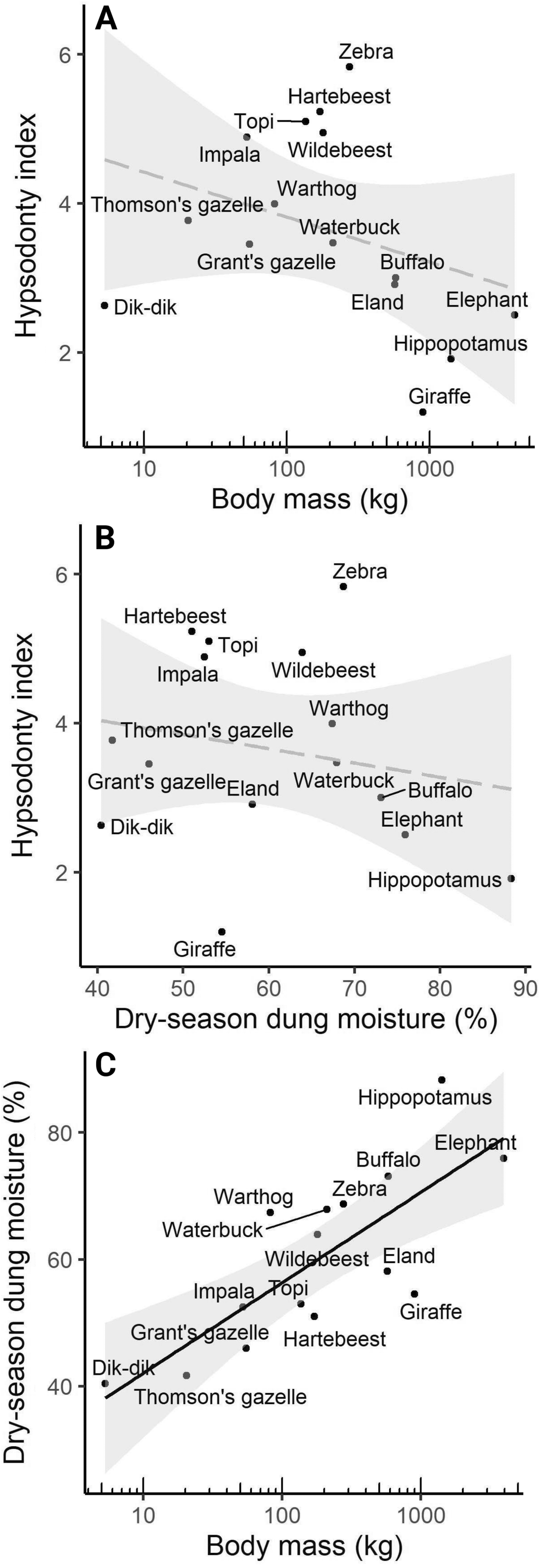
DNA was extracted from fecal samples in a Biosafety Level 2 facility. Prior to amplification, we used the Quant-iT Picogreen assay (ThermoFisher Scientific) to quantify per-sample DNA concentrations; we then used nucleic acid-free water to dilute concentrated samples and standardize DNA concentrations. We amplified the P6 loop of the *trnL*(UAA) chloroplast intron with the *g* and *h* primers (Taberlet et al., 2007). Following PCR and electrophoretic confirmation of amplification, products were pooled by plate and purified using MinElute PCR Purification kits (Qiagen), pooled into equimolar sequencing libraries prepared using a low-cycle PCR approach, and sequenced (2 × 150-bp paired-end) on Illumina platforms at Princeton University's Lewis Sigler Institute for Integrative Genomics.

We assigned taxonomic identifiers to each sequence using reference databases for the *trnL*(UAA) intron, as follows. We prioritized matches to a local database of Serengeti grasses (Anderson et al., 2024); when that match was <98%, we prioritized the best match obtained from (i) a global reference database of vascular plants (EMBL release 143); (ii) a comprehensive local database of 460 plant species from Mpala Research Centre, Laikipia, Kenya (~400 km northeast of the study area; Gill et al., 2019); and (iii) an extensive local library of 244 plant species from Gorongosa National Park, Mozambique (~1700 km south of the study area; Pansu et al., 2019). Unique plant DNA sequences remaining in the dataset after all filtering steps (see Appendix S1) were considered molecular operational taxonomic units (mOTUs). Last, we randomly rarefied each sample to 4500 reads, divided mOTU read counts by 4500 to obtain relative read abundance, and discarded mOTUs representing <1% of reads per sample. Relative read abundance of *trn*L-P6 does not perfectly reflect proportional consumption, but various lines of evidence indicate that it is a robust first-order proxy (e.g., Craine et al., 2015; Kartzinel et al., 2015; Potter et al., 2022; Reese et al., 2019; Willerslev et al., 2014), and yields similar inferences about dietary differentiation relative to presence–absence data (e.g., Kartzinel et al., 2015; Pansu et al., 2019).

The final dataset for diet composition and plant partitioning analysis included 11 species after genetically confirming the identity of four samples (see Appendix S1), with wet- and dry-season sample sizes, respectively, in parentheses: impala (*Aepyceros melampus*, 18, 16); hartebeest (*Alcelaphus buselaphus*, 16, 3); wildebeest (*Connochaetes taurinus*, 6, 15); topi (*Damaliscus lunatus*, 18, 6); plains zebra (*Equus quagga*, 17, 15); Thompson's gazelle (*Eudorcas thomsonii*, 18, 18); waterbuck (*Kobus ellipsiprymnus defassa*, 6, 2); Grant's gazelle (*Nanger granti*, 18, 4); warthog (*Phacochoerus africanus*, 18, 15); buffalo (*Syncerus caffer*, 15, 13); and eland (*Tragelaphus oryx*, 18, 1). We excluded waterbuck and eland from dry-season dietary partitioning analyses owing to sample sizes <3.

Herbivore functional traits

We sought to understand ecological niche differentiation (partitioning of space and food resources) in terms of underlying herbivore functional traits, specifically aiming to capture the three key morphophysiological dimensions identified in the introduction (Figure 1): body size, craniodental anatomy, and water requirements. While each of these attributes can be represented by various measurements, we wanted to capture ecologically



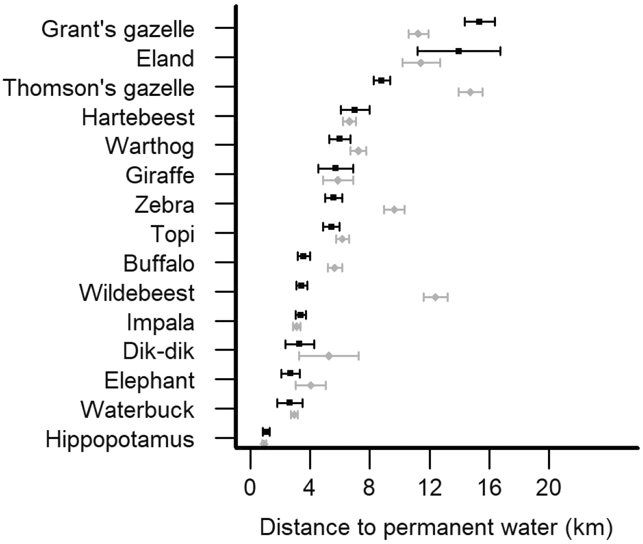


FIGURE 4 Seasonal distribution of herbivores in relation to their distance from permanent surface water sources using visual counts in Serengeti National Park. Points show mean distances of herbivores during the dry (black square) and wet (gray diamonds) season. Bars represent ±1 SE. Species are ranked according to their dry season mean distance to water.

relevant variation using a parsimonious combination of traits for which data are readily available. Following convention, we used body mass (average of male and female adults in kilograms) compiled from primary and secondary literature to index size (data from Smith et al., 2003). For dentition, we used the hypsodonty index of adult specimens, defined as the unworn crown height of the third molar divided by its occlusal width (Janis, 1988), which correlates with the grazer-browser continuum (grazers generally have high hypsodonty indices) (data from Janis, 1988). For water requirements, we used the percentage of dry-season dung moisture content, as drought-adapted species resorb more water from feces (data mean values for each species from Kihwele et al., 2020). Kihwele et al. (2020) compiled data from pri-

FIGURE 3 Relationships between three key herbivore functional traits related to three dimensions of niche differentiation. (A, B) Body mass and hypsodonty index were not strongly correlated (A; $r = -0.33$, $t = -1.26$, $p = 0.23$); neither were dung moisture content and hypsodonty index (B; $r = -0.19$, $t = -0.71$, $p = 0.49$). (C) Body mass and dung moisture content were strongly positively correlated ($r = 0.77$, $t = 4.40$, $p < 0.001$). Lines represent ordinary least squares regression with 95% CI (gray bands). Please note that body mass is presented on a logarithmic scale. Mean values were extracted from literature for all three traits (see *Methods*).

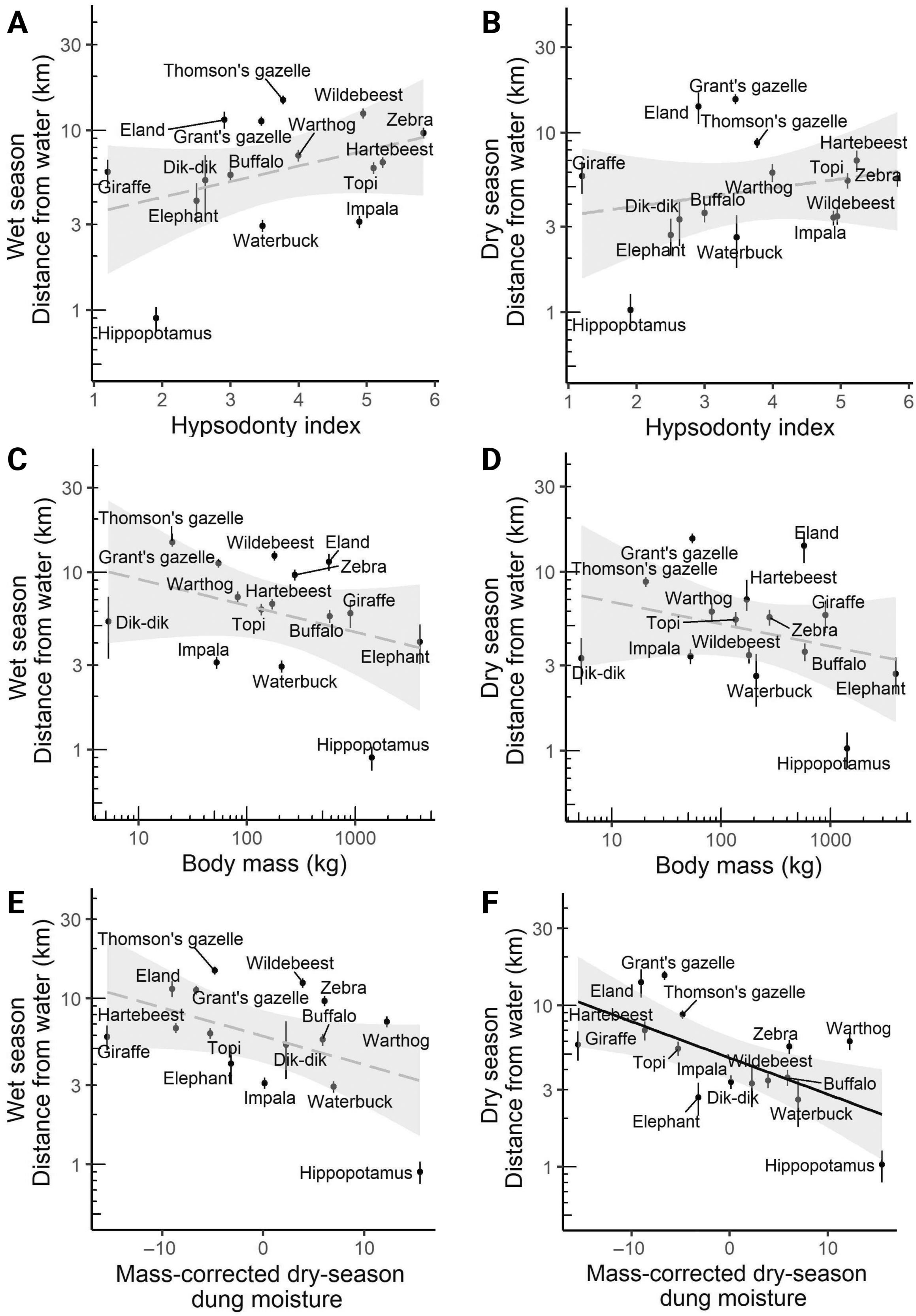


FIGURE 5 Legend on next page.

mary literature with data collected at different field sites, including Serengeti. Percentage moisture content is computed as: [1 − (dry weight/fresh weight)] × 100.

Data analysis

First, we tested the pairwise relationships between these three traits (hypsodonty index, body mass, dung moisture) using the *cor.test* function from stats in R. Body mass was $\log_{10}$-transformed. Because body mass and dry-season dung moisture were strongly correlated ($r = 0.77$, $p < 0.001$; Figure 3), we used the residuals of a linear model—with body size as the predictor and dry-season dung moisture as the response—to obtain mass-corrected dung moisture for use in further analyses.

Second, we tested how each of these three traits predicted herbivore space use (specifically, distance to permanent water sources) and proportion of grass in the diet (specifically, Poaceae DNA relative read abundance) in both wet and dry seasons. We first used linear models ($\log_{10}$-transformed distances and body mass) to evaluate the relationship between each trait alone and both response variables (distance to water, proportion grass). We then performed model selection on multiple-regression models that comprised all possible combinations of the three traits to evaluate the traits or trait–trait interactions that best predicted large-herbivore space use and dietary grass proportion. We used the *glmulti* function from glmulti in R to perform model selection and corrected Akaike information criterion (AIC_c) to evaluate models.

Third, we tested for an association between functional traits and dietary dissimilarity. We first generated species-level diets by averaging the sample-by-mOTU table for each species in each season. We then ran distance-based redundancy analyses (dbRDA; using the *capscale* function from *vegan* in R) on Bray–Curtis dissimilarity in diets as a function of functional traits (as elsewhere, body mass was $\log_{10}$-transformed), analyzed separately for wet and dry seasons. dbRDA is an extension of redundancy analysis (RDA), which itself is a form of multivariate linear regression. Unlike classical RDA, dbRDA allows for the use of non-Euclidean dissimilarity measures, making it especially suitable for ecological datasets. For associations between traits and diet dissimilarity, we selected the best dbRDA model based on adjusted R^2 considering all possible combinations of functional traits and their pairwise interactions.

All analyses were implemented in R (v. 4.4.0; R Core Team, 2024) using the packages *vegan* (v. 2.6-4; Oksanen et al., 2022), *ggplot2* (v. 3.4.1; Wickham, 2016), *DHARMa* (v. 0.4.6; Hartig, 2022), and *glmulti* (v. 1.0.8; Calcagno, 2020). Statistical test results for figure-based analyses are reported in the corresponding figure legends.

RESULTS

Correlations among functional traits

The 15 large herbivores varied multiple-fold in body size (5–3940 kg, median = 180 kg), dry season dung moisture content (40%–88%, median = 58%), and hypsodonty index (1.2–5.8, median = 3.5) (see Appendix S1: Table S2). There was no significant relationship between body mass and hypsodonty index (Figure 3A) or between hypsodonty index and dry-season dung moisture (Figure 3B). However, we did find a significant, positive relationship between body mass and dung moisture (Figure 3C), where larger herbivores generally showed higher water dependence.

Functional traits and space-use

We found strong variation in space use between herbivore species (Figure 4). Hippopotamus, waterbuck, and elephant were generally found close to permanent surface water (<4 km), while Grant's gazelle and eland were found in areas furthest (>10 km) away from water. Patterns were quite similar in both seasons, and most species occupied areas slightly closer to water during the dry season. The three migratory species (Thomson's

FIGURE 5 Relationships between functional traits and distance to water for the wet season (A, C, E) and dry season (B, D, F). Hypsodonty index did not predict distance to permanent surface water in either wet (A; linear regression; slope = 0.09 ± 0.06 SE, $F_{1,13} = 2.14$, $R^2_{\text{Adj}} = 0.07$, $p = 0.17$) or dry season (B; slope = 0.05 ± 0.06 SE, $F_{1,13} = 0.71$, $R^2_{\text{Adj}} = -0.02$, $p = 0.42$). Body mass likewise did not significantly predict distance to water in either wet (C; slope = −0.15 ± 0.11 SE, $F_{1,13} = 1.85$, $R^2_{\text{Adj}} = 0.05$, $p = 0.20$) or dry season (D; slope = −0.12 ± 0.11 SE, $F_{1,13} = 1.33$, $R^2_{\text{Adj}} = 0.02$, $p = 0.27$). There was a negative trend between distance to water and body-mass-corrected dry-season dung moisture in the wet season (E; linear regression; slope = −0.02 ± 0.009 SE, $F_{1,13} = 3.81$, $R^2_{\text{Adj}} = 0.17$, $p = 0.07$), and in the dry season this relationship was much stronger (F; linear regression; slope = −0.02 ± 0.007 SE, $F_{1,13} = 9.29$, $R^2_{\text{Adj}} = 0.37$, $p = 0.009$). Points represent means per species (±SE). Lines represent ordinary least squares regression with 95% CI (gray bands). Please note that distance to water and body mass are presented on a logarithmic scale.

gazelle, zebra, and wildebeest) stood out in that each occupied areas far from water (>10 km) during the wet season.

We then investigated whether space partitioning in relation to permanent water sources was related to the three functional traits. We found no significant relationship between hypsodonty index and distance to water in either the wet or dry season (Figure 5A,B). Excluding hippopotamus did not affect these results. Furthermore, we found no significant relationships between body mass and distance to water (Figure 5C,D). However, mass-corrected water dependence did predict the positioning of large herbivores in relation to surface water. There was a marginally significant relationship between mass-corrected dung

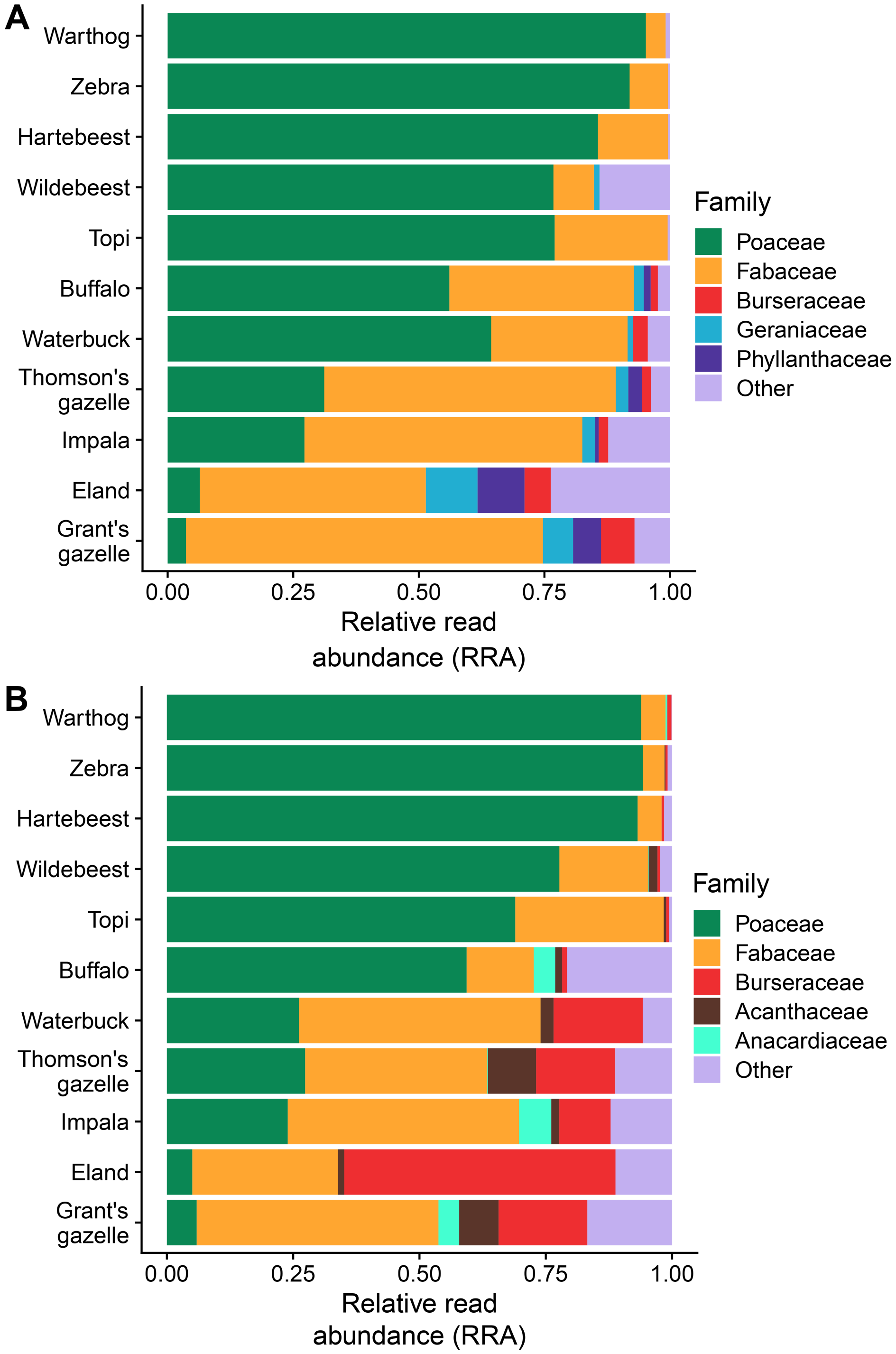
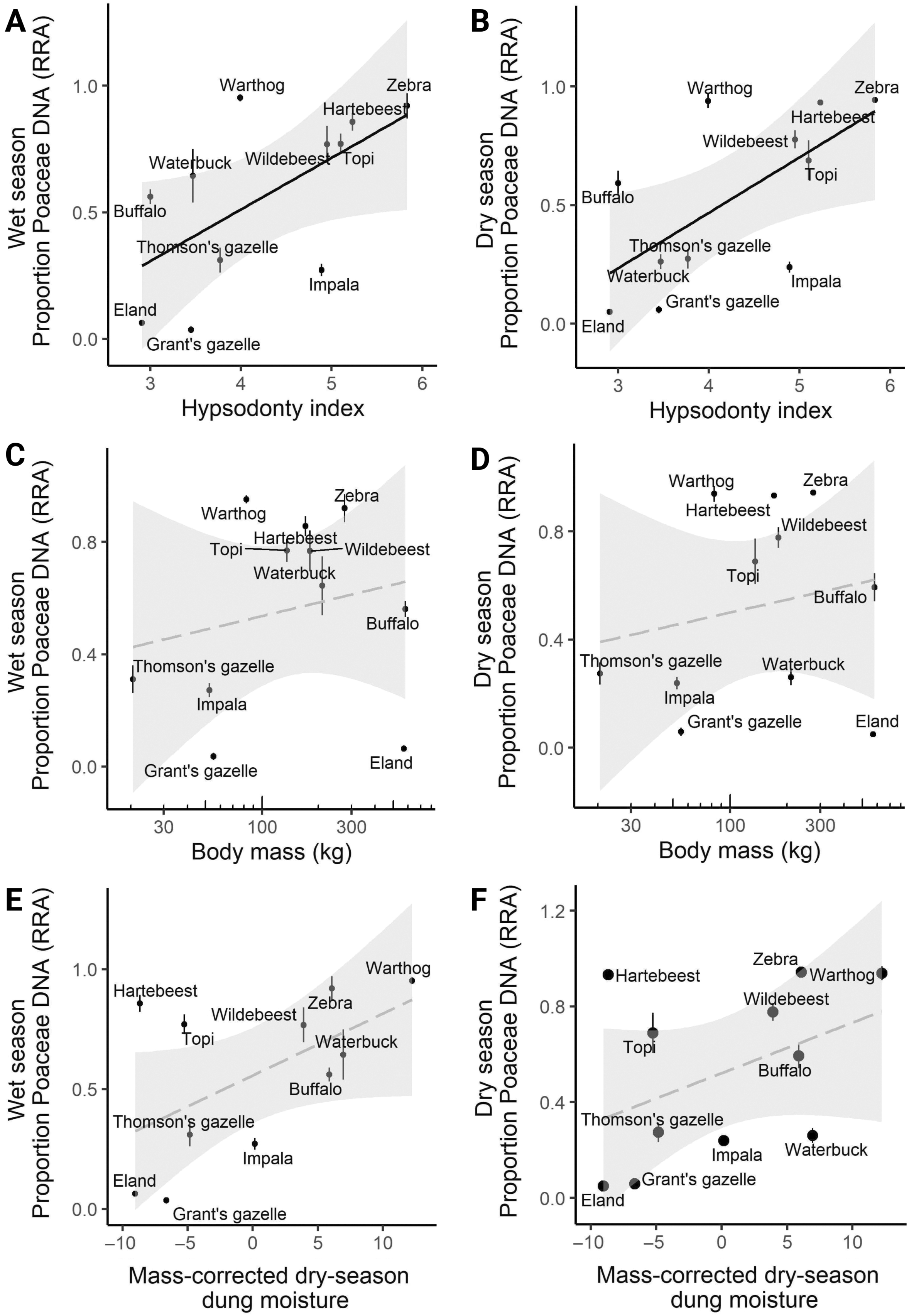


FIGURE 6 Proportion relative read abundance (RRA) of the five most dominant plant families for each herbivore species in both wet season (A) and dry season (B). Species are ranked based on their average proportion of Poaceae across both seasons.



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moisture and distance to water during the wet season (Figure 5E) and mass-corrected dung moisture decreased with distance to water during the dry season (Figure 5F). Comparison of multiple regression models reproduced these results, with the best model for the dry season containing mass-corrected dung moisture content alone (dry season: corrected Akaike information criterion weight ($\mathrm{wAIC_c}$) = 0.41; Appendix S1: Table S3) while for the wet season, a model including hypsodonty index was slightly better (wet season: $\mathrm{wAIC_c} = 0.21$; Appendix S1: Table S4) than a model with only mass-corrected dung moisture.

Functional traits and diet composition

There was strong variation in diet composition between herbivore species (Figure 6). Mean relative read abundance (RRA) of Poaceae (grasses) was highest for nonruminant grazers, warthog, and zebra and also high for the three alcelaphine species—hartebeest, topi, and wildebeest—for both the wet and dry seasons. Buffalo and waterbuck had an intermediate proportion of grass in their diets, with waterbuck strongly reducing the grass proportion during the dry season. Thomson's gazelle and impala had about 25% grass in their diets, and eland and Grant's gazelle had the lowest proportions of grass in both seasons (<7%). Besides Poaceae, Fabaceae was the most common plant family—consumed to varying degrees by all herbivore species (see Pansu et al., 2022). We observed strong differentiation in the contribution of other plant families—Burseraceae, Geraniaceae, Acanthaceae, Anacardiaceae, Phyllanthaceae—for species with lower amounts of grass in their diets (e.g., eland vs. Grant's gazelle; Figure 6).

We then investigated whether the percentage grass in the diets—the grazer-browser axis—was related to the three functional traits. Hypsodonty index best explained the percentage of dietary grass in both the wet and dry seasons (Figure 7A,B), whereas no significant relationships between body mass and proportion grass were found (Figure 7C,D). Water dependence did not predict dietary grass proportion very well (Figure 7E,F) although the wet season effect was marginally significant ($p = 0.07$). Again, model selection reproduced these results, with the best model containing hypsodonty index alone in the dry season (dry-season: $\mathrm{wAIC_c} = 0.44$; Appendix S1: Table S5) and both hypsodonty and mass-corrected dung moisture in the wet season (wet-season: $\mathrm{wAIC_c} = 0.39$; Appendix S1: Table S6).

Functional traits and diet dissimilarity

Finally, we investigated the extent to which functional traits predicted dietary dissimilarity. For the wet season, pairwise dietary dissimilarity was marginally related to hypsodonty and mass-corrected dry-season dung moisture, but not to body mass (Figure 8A,C–E), indicating that species with similar dental morphology and water requirements have more similar diets regardless of their size; model selection identified all three traits and their pairwise interactions as important predictors ($F_{6,4} = 2.26$, $p = 0.01$, adjusted $R^2 = 0.43$; Appendix S1: Table S7). Conversely, dry season diet dissimilarity was a function of body size but was not significantly related to hypsodonty or water dependence (Figure 8B,F–H); here, the best model included all three traits along with interactions between hypsodonty and both body mass and mass-corrected dung moisture ($F_{5,3} = 3.46$, $p = 0.002$, adjusted $R^2 = 0.61$; Appendix S1: Table S8). The proportion of explained variance in diet dissimilarity tripled for the wet season (13% vs. 43%) and almost tripled for the dry season (24% vs. 61%) in multiple-regression models including multiple traits relative to univariate regressions of single traits, emphasizing the multi-dimensionality of resource partitioning.

DISCUSSION

We investigated spatial and dietary resource partitioning among large-herbivore species in Serengeti National Park and tested the extent to which three morphophysiological

FIGURE 7 Relationships between functional traits and proportion grass in the diet—Poaceae DNA relative read abundance (RRA)—for the wet season (A, C, E) and dry season (B, D, F). Hypsodonty index was positively correlated with proportion grass in diet in both wet (A; linear regression; slope = 0.20 ± 0.09 SE, $F_{1,9} = 5.20$, $R^2_{\mathrm{Adj}} = 0.30$, $p = 0.04$) and dry seasons (B; slope = 0.23 ± 0.09 SE, $F_{1,9} = 6.85$, $R^2_{\mathrm{Adj}} = 0.37$, $p = 0.03$). Body mass did not significantly predict the proportion of grass in either wet (C; slope = 0.16 ± 0.25 SE, $F_{1,9} = 0.42$, $R^2_{\mathrm{Adj}} = -0.06$, $p = 0.53$) or dry season (D; slope = 0.16 ± 0.26 SE, $F_{1,9} = 0.37$, $R^2_{\mathrm{Adj}} = -0.07$, $p = 0.56$). The dietary grass proportion was marginally correlated with body-mass corrected dry-season dung moisture in the wet (E; linear regression; slope = 0.02 ± 0.01 SE, $F_{1,9} = 4.14$, $R^2_{\mathrm{Adj}} = 0.23$, $p = 0.07$), but not the dry season (F; linear regression; slope = 0.02 ± 0.01 SE, $F_{1,9} = 2.10$, $R^2_{\mathrm{Adj}} = 0.09$, $p = 0.18$). Points represent means per species (±SE). Lines represent ordinary least squares regression with 95% CI (gray bands). Please note that body mass is presented on a logarithmic scale.

traits—as proxies for three key trade-offs—suffice to predict observed differences in resource use (see Figure 1). We aimed to better understand how trait differences facilitate coexistence and, in particular, the added value of variation in water requirements relative to body size and dental morphology alone. We found that differences in water requirements allowed herbivores to spatially partition the landscape in relation to surface water, while

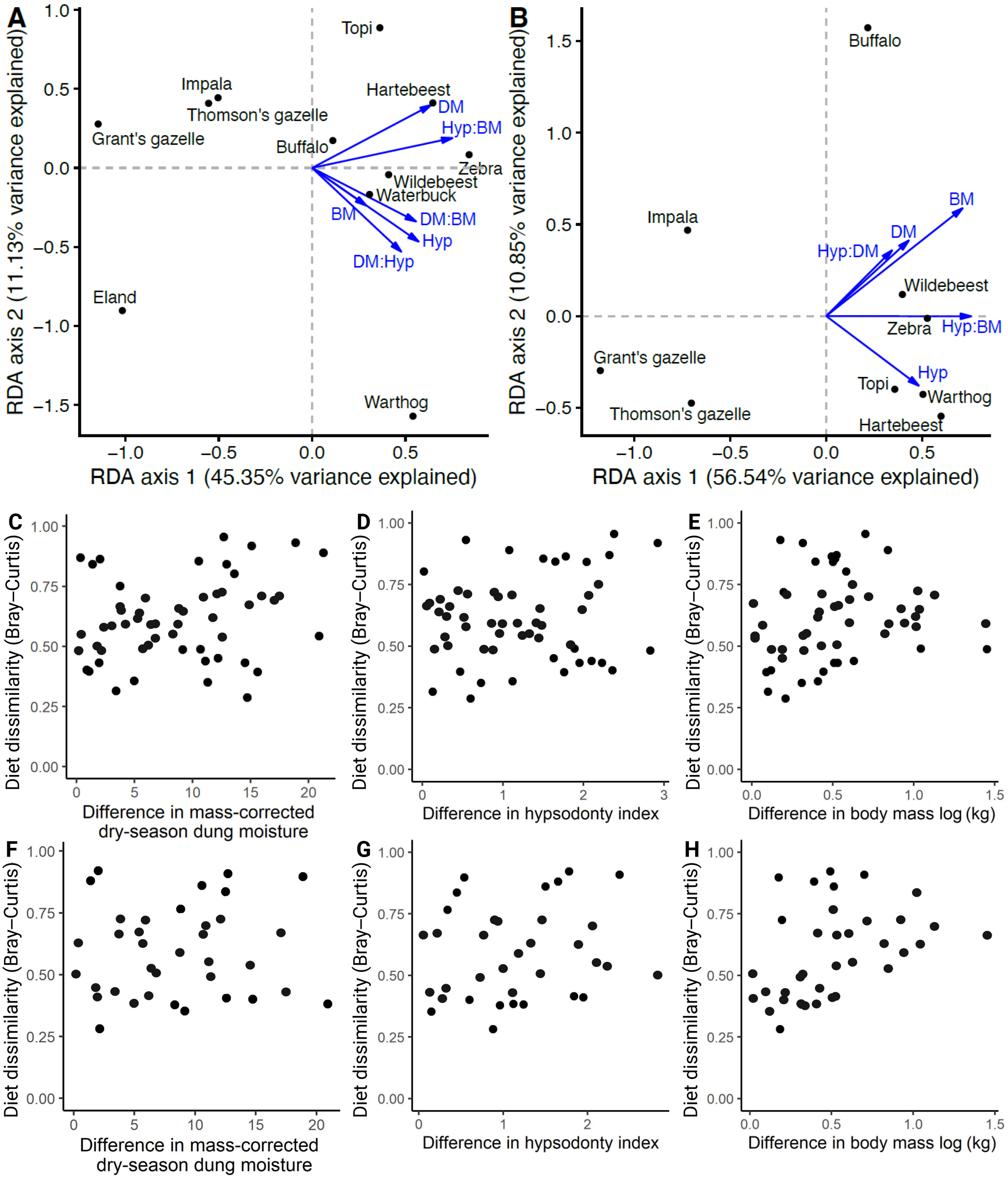

FIGURE 8 Legend on next page.

dental morphology best explained variation along the grazer-browser axis. Furthermore, all three traits were important predictors of food partitioning in both seasons.

Large herbivores showed strong variation in space use in relation to permanent water sources in both seasons (Figure 4). Overall, the distribution of species across the landscape in relation to surface water availability was explained by their water requirements (Figure 5), with highly water-dependent species occupying areas closer to water. Surface water availability has repeatedly been identified as a key driver of ungulate distributions across the landscape (Gereta & Wolanski, 1998; Smit, 2011; Western, 1975; Wolanski et al., 1999; Wolanski & Gereta, 2001). Some species—Grant's gazelle, eland, Thomson's gazelle—remained in areas far away from water sources in the dry season, which accords with their low water requirements (Kihwele et al., 2020). Most other species moved closer to permanent water, suggesting that surface water is an important dry season constraint on space use. In the wet season, drinking water is available across the landscape in small ephemeral pools (Naidoo et al., 2020) and did not limit the distribution of most herbivore species. The migratory species—wildebeest and zebra—occupied areas on the southern plains far away from permanent water sources during the wet season and subsequently moved to areas with available water during the dry season (Gereta et al., 2009; Wolanski et al., 1999). The movement toward permanent water sources in the dry season by migratory species supports the hypothesis that migratory behavior could also be explained in part by species' water requirements (Frank et al., 1998; Fryxell et al., 1988), especially in ecosystems where access to water becomes seasonally restricted to specific areas. These results strongly suggest that water requirements are a key determinant of spatial niche differentiation among large herbivores across the landscape.

The space partitioning between water-dependent and water-independent species likely interacts with the diet-based dimensions. We indeed found that water requirements affected dietary overlap in both seasons (Figure 8). Dental morphology—a proxy for grazer-browser continuum—was an important dimension of dietary niche partitioning which aligns well with previous work emphasizing the importance of feeding guilds (Codron et al., 2007; Damuth & Janis, 2011; Kartzinel et al., 2015; Owen-Smith, 2015). Body size was a strong predictor of dietary niche partitioning in the dry season (Figure 8). Differences in body size are thought to facilitate species coexistence (Cromsigt et al., 2009; Hopcraft et al., 2012; Olff et al., 2002; Owen-Smith, 2015) through a trade-off between high-quality food and abundant lower quality food. In addition, body size is correlated with predation risk such that populations of small herbivores tend to be predator regulated while the largest herbivores are not (Sinclair et al., 2003). These trade-offs become increasingly important during the dry season when high-quality food gets scarcer (Kleynhans et al., 2011) and animals may be forced to access water that is associated with riskier parts of the landscape (Sinclair & Arcese, 1995).

Surface water availability is increasingly becoming a major environmental concern, both in the Serengeti Mara ecosystem and in savannas more generally. Continuous decline in the flow level of the Mara river—the perennial lifeline of the ecosystem—as a result of land use changes (Mati et al., 2008), catchment deforestation (Kipampi et al., 2017), and irrigation demands (Gereta et al., 2009, Wolanski et al., 1999) is further compromising surface water availability throughout the ecosystem (Kihwele et al., 2021). Given the current rate of climate and land use change, the flow rates in the Mara River are likely to become more ephemeral and less predictable, with potentially long periods of no flow (Dutton et al., 2019). Model predictions suggest that severe water restrictions in the Mara could result in a collapse of the migration (Gereta et al., 2002; Holdo et al., 2011), with critical consequences for the ecosystem and its biodiversity. Wildlife managers foresee the need to provide artificial water as an intervention to maintain population numbers and tourism demands; however, this would entail distributing over 1000 m^3 (1 million liters) of water per day across the dry season range of 1.5

FIGURE 8 Relationships between the three functional traits and food partitioning. Redundancy analysis biplot of axes 1 and 2 of herbivore diet for the wet (A) and dry (B) season; DM is mass-corrected dry-season dung moisture (our proxy for water dependence), BM refers to body mass and Hyp refers to hypsodonty index. In these plots, species positioned farther away from each other have more dissimilar diets. (A) In the wet season, model selection identified all three traits and their interactions as important predictors of dietary dissimilarity ($F_{6,4} = 2.26$, $p = 0.01$, $R^2_{\text{Adj}} = 0.43$); considering each factor individually, hypsodonty ($F_{1,9} = 2.53$, $p = 0.047$, $R^2_{\text{Adj}} = 0.13$) and water dependence ($F_{1,9} = 2.27$, $p = 0.06$, $R^2_{\text{Adj}} = 0.11$) predicted dietary dissimilarity, whereas body size had no detectable effect ($F_{1,9} = 1.27$, $p = 0.24$, $R^2_{\text{Adj}} = 0.03$). (B) In the dry season, dietary dissimilarity was best predicted by interactions of hypsodonty with body mass and water dependence ($F = 3.46$, $p = 0.002$, $R^2_{\text{Adj}} = 0.61$); individually, hypsodonty ($F_{1,7} = 1.57$, $p = 0.18$, $R^2_{\text{Adj}} = 0.07$) and water dependence ($F_{1,7} = 1.31$, $p = 0.24$, $R^2_{\text{Adj}} = 0.04$) were not associated with dietary dissimilarity, but body size was ($F_{1,7} = 3.48$, $p = 0.03$, $R^2_{\text{Adj}} = 0.24$). Visualization of mean pairwise dietary dissimilarities and differences in functional trait values among larger herbivores for the wet (C–E) and dry season (F–H). Dots show dissimilarity between each pair of species.

million wildebeest and zebra (>600 km^2), which is a significant logistical challenge to say the least. Furthermore, such artificial water points can come at the cost of herbivore diversity (Harrington et al., 1999; Ogutu & Owen, 2003), pushing water-independent species toward extinction through homogenizing surface water availability to the benefit of water-dependent competitors (Cromsigt et al., 2009). Thus, to sustain biodiversity, any water-provision policy will need critical assessment and evaluation such that heterogeneity of habitat in relation to surface water availability remains intact.

CONCLUSIONS

Our study integratively assessed multiple dimensions of resource partitioning among large herbivores in savanna ecosystems and the extent to which resource partitioning can be explained by underlying morphological traits. We provide strong evidence that water requirements are an important dimension for resource partitioning among large herbivores in the Serengeti. Herbivore water requirements underpin spatial niche partitioning in relation to water sources and—together with dental morphology and body size—affect dietary resource partitioning. The resulting multidimensional framework ultimately determines which set of species can coexist with co-occurring species dispersed along these trait axes. The three key axes identified here will help predict changes in herbivore community assembly in response to changes in surface water availability due to climate change and/or establishment of artificial water points. We contend that maintaining heterogeneity in surface water availability should therefore be a key management priority in savanna ecosystems.

AUTHOR CONTRIBUTIONS

Emilian S. Kihwele, Han Olff, and Michiel P. Veldhuis conceived the ideas and designed the methodology. Emilian S. Kihwele, Damari S. Nassary, John R. Hongoa, and J. Grant C. Hopcraft collected and contributed field data and samples. Michiel P. Veldhuis and Matthew C. Hutchinson conducted the molecular work in Robert M. Pringle's laboratory at Princeton University. Matthew C. Hutchinson and Michiel P. Veldhuis analyzed the data. Emilian S. Kihwele led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Veldhuis, 2025c) are available in Zenodo at https://doi.org/10.5281/zenodo.14733315.

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SUPPORTING INFORMATION

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

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