Journal of Ecology

Potter Arjun Brandreth (Orcid ID: 0000-0002-7789-6349)
Pansu Johan (Orcid ID: 0000-0003-0256-0258)
Long Ryan (Orcid ID: 0000-0002-0124-7641)
Pringle Robert Mitchell (Orcid ID: 0000-0001-7487-5393)

Editor: Amy Austin

Mechanisms of dietary resource partitioning in large-herbivore assemblages: a plant-trait-based approach

Arjun B. Potter[1,*], Matthew C. Hutchinson[1], Johan Pansu[1,2], Bart Wursten[3], Ryan A. Long[4], Jonathan M. Levine[1], Robert M. Pringle[1,*]

1. Department of Ecology & Evolutionary Biology, Princeton, NJ, 08544, USA
2. Institut des Sciences de l'Évolution de Montpellier (ISEM), Université de Montpellier, CNRS, EPHE, IRD, F-34000 Montpellier, France
3. Meise Botanic Garden, Meise, Belgium
4. Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA

***Corresponding Authors:** Arjun B. Potter (apotter@princeton.edu) and Robert M. Pringle rpringle@princeton.edu)

ABSTRACT

1. Sympatric large mammalian herbivore species differ in diet composition, both by eating different parts of the same plant and by eating different plant species. Various theories proposed to explain these differences are not mutually exclusive, but are difficult to reconcile and confront with data. Moreover, whereas several of these ideas were originally developed with reference to within-plant partitioning (i.e., consumption of different tissues), they may analogously apply to partitioning of plant species; this possibility has received little attention.

2. Plant functional traits provide a novel window into herbivore diets and a means of testing multiple hypotheses in a unified framework. We used DNA metabarcoding to characterize the diets of 14 sympatric large-herbivore species in an African savanna and analyzed diet composition in light of 27 functional traits that we measured locally for 204 plant species.

3. Plant traits associated with the deep phylogenetic split between grasses and eudicots formed the primary axis of resource partitioning, affirming the generality and importance of the grazer-browser spectrum. A secondary axis comprised plant traits relevant to herbivore body size. Plant taxa in the diets of large-bodied species were lower on average in digestible energy and protein, taller on average (especially among grazers), and tended to be higher in tensile strength, zinc, stem-specific density, and potassium (and lower in sodium, stem dry matter content, and copper). These results are consistent with longstanding hypotheses linking body size with forage quality and height, yet they also suggest the existence of undiscovered links between herbivore body size and a set of rarely considered food-plant traits. We also tested the novel hypothesis that the leaf economic spectrum (LES), a major focus in plant ecology, is an axis of resource partitioning in large-herbivore assemblages; we

found that the LES was a minor axis of individual variation within a few species, but had little effect on interspecific dietary differentiation.

4. ***Synthesis*.** These results identify key plant traits that underpin the partitioning of food-plant species in large-herbivore communities and suggest that accounting for multiple plant traits (and tradeoffs among them) will enable a deeper understanding of herbivore-plant interaction networks.

KEYWORDS: Gorongosa National Park, Mozambique; herbivory; Jarman-Bell principle; leaf economic spectrum; dietary niche partitioning; plant functional traits; resource availability hypothesis; ungulate foraging behavior

RESUMO

1. Espécies simpátricas de grandes mamíferos diferem na composição de suas dietas, seja ao consumirem diferentes partes da mesma planta ou ao consumirem diferentes espećies de plantas. As diferentes teorias propostas para explicar essas diferenças não são mutuamente exclusivas, mas são difíceis de conciliar e validar com dados empíricos. Além disso, enquanto várias dessas idéias foram originalmente desenvolvidas tendo como foco principal o particionamento de nicho dos herbívoros em relação às plantas (ipor exemplo, consumo de diferentes tecidos), elas podem ser aplicadas de forma análoga ao particionamento de nicho ao nível de espécie, embora essa possibilidade tenha recebido pouca atenção.
2. Os traços funcionais das plantas fornecem uma nova janela para as dietas herbívoras e uma forma de testar múltiplas hipóteses por meio de uma estrutura unificada. Usamos *DNA metabarcoding* para caracterizar as dietas de 14 espécies simpáticas de herbívoros de grande

porte em uma savana africana, e analisamos a composição da dieta com base em 27 traços funcionais que medimos localmente para 204 espécies de plantas.

3. Traços vegetais associados à divergência filogenética em tempo profundo entre gramíneas e eudicotiledôneas formaram o eixo primário da partição de recursos, enfatizando a generalidade e a importância do espectro *grazer-browser*. Um segundo eixo foi formado por traços vegetais relacionados ao tamanho do corpo do herbívoro. Os táxons vegetais nas dietas das espécies de grande porte apresentaram, em média, valores mais baixos em energia digerível e proteína, além de plantas mais altas em média (especialmente entre os pastadores), e apresentaram tendência para valores mais altos de resistência à tração, zinco, densidade específica do caule e potássio (além de valores mais baixos em sódio, no teor de matéria seca do caule e na quantidade de cobre). Estes resultados são consistentes com as hipóteses já estabelecidas que conectam o tamanho do corpo à qualidade nutricional e altura da planta, mas também sugerem a existência de conexões ainda não descritas entre o tamanho do corpo do herbívoro e um conjunto de características raramente consideradas em plantas utilizadas como recurso. Nós também testamos uma nova hipótese de que o *leaf economic spectrum* (LES), muito estudado em ecologia vegetal, representa um eixo de partição de recursos em comunidades de grandes herbívoros; encontramos que o LES teve baixa importância para a variação individual dentro de algumas espécies, e teve pouco efeito na distinção interespecífica das dietas.
4. ***Síntese.*** Nossos resultados identificam os principais traços vegetais que sustentam o particionamento das espécies de plantas utilizadas como recursos por comunidades de herbívoros de grande porte e sugerem que a inclusão de múltiplos traços vegetais (e das demandas conflitantes entre eles) permitirá uma compreensão mais profunda das redes de interação herbívoros-plantas.

INTRODUCTION

An animal's dietary niche—the types and relative amounts of foods that it eats—is a key determinant of its interactions with and effects on other species. For example, differences in the dietary niches of co-occurring species can help to stabilize species coexistence by reducing the strength of interspecific competition for food (Chase & Leibold, 2003; Chesson, 2000; Pringle et al., 2019). Yet challenges inherent in identifying the foods eaten by free-ranging generalist consumers mean that diet composition is often coarsely described, which makes it difficult to discern the degree of dietary niche differentiation and the mechanisms through which it emerges (Pringle & Hutchinson, 2020).

The diversity of large-herbivore assemblages in African savannas suggests the existence of mechanisms for partitioning the resource pool (plant tissue, mostly foliage) (Lamprey, 1963; McNaughton & Georgiadis, 1986). But how does resource partitioning manifest among species with such generalized diets? Most research has focused on broad mechanisms that are based primarily on the traits and adaptations of herbivores. First, species differ in grass consumption: grazers eat mostly grasses, browsers eat mostly non-grasses, and mixed feeders eat both, producing a grazer-browser spectrum (Cerling, Harris, & Passey, 2003; Codron et al., 2007; Lamprey, 1963). Second, differences in herbivore size, morphology, and physiology create tradeoffs between the quantity and nutritional quality of food consumed. The Jarman-Bell hypothesis posits that larger-bodied herbivores tolerate lower-quality food and should thus tend to have lower-quality diets, on average, than smaller-bodied herbivores (Bell, 1971; Jarman, 1974; Müller et al., 2013). Similarly, differences in body size, digestive system, and craniofacial anatomy influence species' selectivity for small patches of high-quality forage versus larger patches with greater biomass availability (Bell, 1971; Cromsigt & Olff, 2006; Janis & Ehrhardt,

1988). Third, differences in herbivore height and anatomy influence the range of heights at which they forage, creating vertical stratification: tall species such as giraffe can crop vegetation at any height but mostly browse foliage >2m above the ground, and taller antelopes likewise typically forage at greater heights than shorter ones (du Toit, 1990; du Toit & Olff, 2014).

Common to all of these ideas is that resource partitioning emerges from the interplay of animal traits and plant traits. Yet, whereas the role of animal traits in dietary niche differentiation has been considered in detail, the treatment of food-plant traits has been piecemeal; some studies focus on a single plant trait, while others consider aggregates of traits in an implicit way. For example, differences in the morphology and behavior of grazing versus browsing ungulates is often ascribed to differences in the characteristics of grasses versus eudicots (Codron & Clauss, 2010; Gordon, 2003; Searle & Shipley, 2008; Spencer, 1995). The Jarman-Bell hypothesis has been assessed using crude protein as a proxy for nutritional quality (Clauss, Steuer, Müller, Codron, & Hummel, 2013; Kleynhans, Jolles, Bos, & Olff, 2011; Owen-Smith, 1988), where the underlying plant functional trait is leaf nitrogen content. And explanations for resource partitioning based on vertical stratification depend on the functional trait of plant height to generate a distribution of possible feeding heights (du Toit, 1990; Nichols, Cromsigt, & Spong, 2015; Wilmshurst, Fryxell, & Bergman, 2000). Although these latter two mechanisms do not require that herbivores eat different plant species—indeed, they are classically conceived as the result of herbivores eating different parts of the same plant—large herbivores nonetheless do commonly partition plant species, even within grazing and browsing guilds (Christopherson, Tremblay, Gagné, Bérubé, & St-Laurent, 2019; Churski et al., 2021; Kartzinel et al., 2015; Kleynhans et al., 2011). The bases of such differences in dietary species composition have received comparatively little attention. We reasoned that each of the above mechanisms should

influence the taxonomic composition of herbivore diets in addition to any effects they have on selection for particular plant tissues, and that plant functional traits should provide a useful lens through which to understand these compositional differences.

Exploring herbivore diets through the lens of plant traits also has the potential to identify novel mechanisms of resource partitioning. Functional traits play a key role in efforts to understand plant-community dynamics (Kraft, Godoy, & Levine, 2015; McGill, Enquist, Weiher, & Westoby, 2006), and detailed trait data exist for an ever-increasing number of plant species. Leaf traits are well-studied and should matter to large herbivores, which disproportionately eat foliage (Gwynne & Bell, 1968; Owen-Smith, 1988). However, studies of large-herbivore diets rarely consider leaf structure and function explicitly. The leaf economic spectrum (LES) describes an apparently universal set of tradeoffs in leaf traits: 'fast' plant species invest more in cell constituents that enable rapid growth while minimizing investments in leaf structure and longevity, whereas 'slow' species do the opposite (Onoda et al., 2017; Osnas, Lichstein, Reich, & Pacala, 2013; Wright et al., 2004). Traits such as leaf nitrogen content are positively related to photosynthetic rate (Evans, 1989), while structural traits such as leaf mass per area confer leaf longevity (Poorter, Niinemets, Poorter, Wright, & Villar, 2009). The relative investment in cell walls versus cell contents is relevant for animal nutrition, because cell contents are more easily digestible than cell walls (Van Soest, 1994). This suggests that plants on the 'fast' end of the LES should be better food than those on the 'slow' end. We posit two ways in which the LES might shape large-herbivore diets. First, the LES could be an axis of dietary differentiation representing nutritional quality. Smaller-bodied herbivores and ruminants tend to eat higher-quality diets and might therefore feed at the fast end, whereas larger-bodied and non-ruminant species might feed more heavily on lower-quality plants at the slow end, consistent with the

Jarman-Bell hypothesis and related ideas based on digestive physiology (Clauss et al., 2013). Alternatively, all large herbivores might feed predominantly on a shared subset of palatable plants at the fast end of the LES, resulting in high interspecific dietary overlap. This scenario would be consistent with the resource-availability hypothesis, which predicts that fast-growing plants invest in growth at the expense of defense and thus incur more herbivory, whereas slow-growing, better-defended plants resist herbivory (Bryant, Chapin, & Klein, 1983; Coley, Bryant, & Chapin, 1985; Endara & Coley, 2011; Fine et al., 2006).

We used fecal DNA metabarcoding (Kartzinel et al., 2015; Taberlet et al., 2007) to quantify the diets of 14 large-herbivore species (Table 1), and we collected data on 27 functional traits of 204 plant species in Mozambique's Gorongosa National Park. Diets and traits were assessed during the early to mid-dry season. By weighting the trait values of plant species by their relative contribution to herbivore diets, we positioned the large-herbivore community in plant-trait space. The 27 plant traits that we measured included structural traits and physical defenses as well as several aspects of foliar chemistry; we did not measure plant secondary metabolites, although these can have important effects on plant-herbivore interactions in African savannas (Schmitt, Shuttleworth, Shrader, & Ward, 2020; Scogings, Hjältén, & Skarpe, 2011).

We tested five predictions. (1) Herbivore species' diets differ in plant species composition, and these differences are correlated with differences in food-plant functional traits. (2) The grazer-browser spectrum is the primary axis of dietary differentiation. (3) The LES is a second major axis of resource partitioning. (4) Larger-bodied herbivore species eat lower-quality diets on average (as suggested by the Jarman-Bell hypothesis), which contributes to dietary differentiation. (5) Taller herbivore species eat plant species that are taller on average, further contributing to dietary differentiation both within and between grazing and browsing guilds.

These latter two predictions draw on established explanations for differences in the consumption of particular parts within a plant and transpose them to explain differences in the consumption of different plant species. For example, many studies have shown that herbivore species differ in their preferred, typical, and maximum foraging heights (du Toit, 1990; Haschick & Kerley, 1996; O'Kane, Duffy, Page, & Macdonald, 2011; Renaud, Verheyden-Tixier, & Dumont, 2003; Stokke & du Toit, 2000), which should lead to height-structured differences in the accessibility of different plant species and the efficiency of harvesting them; thus, we expect short browsers to forage more heavily on prostrate forbs and low-growing shrubs than tall browsers, which should in turn eat larger proportions of canopy tree species than small browsers. In this way, plant height should serve as a functional trait differentiating the taxonomic composition of herbivores' diets, analogous to its role in enabling feeding-height stratification (du Toit, 1990). In addition to testing these predictions, we used a supervised classification algorithm to identify plant traits that contributed most to differentiating herbivore diets.

MATERIALS AND METHODS

Study site. Gorongosa National Park (4,000 km^2; 18°53'S, 34°26'E) has a tropical climate with a dry season from May-October and a wet season from November-April; mean ± SD annual rainfall from 1957–2019 was 892 ± 339 mm. The park encompasses the tip of the Great Rift Valley, which forms a wide alluvial plain bordered by wooded escarpments to the east and west (see **Fig. S1** in Supporting Information). Most large-herbivore biomass occurs within the Rift Valley in the south-central part of the park (Stalmans, Massad, Peel, Tarnita, & Pringle, 2019), which contains a gradient of habitats, from the Urema floodplain grassland to savanna-woodland (Tinley, 1977). These habitats broadly interface and interdigitate, and animals move between

them; we concentrated our sampling in a relatively narrow portion of this floodplain-savanna mosaic where all focal herbivore species overlap spatially (see **Fig. S1**). The large-herbivore community includes elephant and 18 ungulate species. Herbivore numbers crashed during the Mozambican Civil War (1977–1992) but have recovered since 2007; herbivore species composition remains largely intact, but community structure differs from the historical baseline (Pringle, 2017; Stalmans et al., 2019; Tinley, 1977). At the time of this study, medium-sized ungulates were abundant—notably waterbuck, reedbuck, impala, and warthog—while large-bodied species such as elephant, hippopotamus, buffalo, and zebra were less common than before the war (**Table 1**). Lion (*Panthera leo*) declined but persisted; leopard (*P. pardus*) and wild dog (*Lycaon pictus*) only returned to the park in mid-2018 (Bouley, Poulos, Branco, & Carter, 2018). Herbivore biomass in 2018 was comparable with prewar estimates, although relative abundances remained in flux (Stalmans et al., 2019). Fieldwork was conducted in accordance with permits from the Department of Scientific Services at Gorongosa National Park and the Republic of Mozambique (PNG/DSCi/C71/2017 and PNG/DSCi/C100/2018 to R.M.P.).

Analysis of herbivore diets. During the 2018 dry season (May-August), we collected 301 fecal samples from 14 large-herbivore species for DNA metabarcoding; 6 samples were removed during bioinformatic analysis and 9 more during quality-control filtering (see *Data processing,* below), leaving a final sample size of 286 (n = 7–30 per species, mean 20; **Table 1**). These 14 herbivore species accounted for 95% of Gorongosa's large-herbivore biomass in 2018 (Stalmans et al., 2019); the five species not included were too scarce in the study area to sample adequately [hippo (*Hippopotamus amphibius*), eland (*Tragelaphus oryx*), bushpig (*Potamochoerus larvatus*), grey duiker (*Sylvicapra grimmia*), and red duiker (*Cephalophus natalensis*)]. We

sampled from adults and subadults of both sexes. In most cases, fecal samples were obtained after visually observing defecation (see **Appendix 1**). We extracted DNA from finely homogenized fecal material (avoiding macroremains to mitigate bias towards indigestible parts) and amplified the P6-loop of the chloroplast *trn*L (UAA) intron (Taberlet et al., 2007), which is widely used in metabarcoding studies of herbivore diets and provides high taxonomic resolution (De Barba et al., 2014; Kartzinel et al., 2015). For each sample, we divided the number of sequence reads of each plant molecular operational taxonomic unit (mOTU) by the total read count to obtain relative read abundance (RRA). Our sampling and bioinformatic filtering protocols were largely as described in prior studies of herbivore diets in Gorongosa (Atkins et al., 2019; Branco et al., 2019; Guyton et al., 2020; Pansu et al., 2019); detailed methods and minor deviations from earlier protocols are in **Appendix 1**. Research was conducted in accordance with permits from the United States Department of Agriculture Animal and Plant Health Inspection Service (permit 130123 to R.M.P.).

Measurement of plant traits. We measured 27 physical and chemical functional traits of 204 plant species in Gorongosa during May–August of 2017 and 2018. Thus, our plant functional trait data and our herbivore diet data come from the same location and same season. Most plant species (~80%) were measured in 2018, concurrent with diet sampling. The 2017 seasonal year (Oct 2016–Sept 2017, 685 mm) was drier than that in 2018 (1113 mm), but both were well within 1 SD of the long-term average (892 ± 339 mm). This suite of 27 traits included nutrients of known importance to herbivores, structural attributes of probable importance, and properties linked to classical theories of herbivore resource partitioning. Complete lists of plants and traits are in **Tables S1, S2**. Plants were provisionally identified by A.B.P. using published keys

(Burrows, Burrows, Lötter, & Schmidt, 2018; Hyde, Wursten, Ballings, & Coates Palgrave, 2018), and all identifications were later confirmed or updated by botanist B.W. These 204 species included most of the locally common plants available to large herbivores in our study area.

Physical traits were measured using standard methods (Pérez-Harguindeguy et al., 2013) on 1–3 (mean 2.7) individuals per species; details are in **Appendix 2**. For chemical traits, we collected >5 g of the youngest fully unfurled leaves in approximately equal amounts from each of ≥3 individuals per species. Leaves were dried to constant weight (i.e., no additional mass loss after 24 h) at 55°C and analyzed by Dairy One Cooperative (Ithaca, NY, USA) using standard protocols from the Association of Official Agricultural Chemists (**Appendix 2**). We combined our plant-traits data into a 204-species × 27-trait matrix by averaging across replicates within species. In this matrix, 0.9% of cells were empty, typically because the amount of plant material was insufficient to perform all six chemical assays. To avoid biases associated with listwise deletion, we imputed missing values using predictive mean matching in *MICE* (van Buuren & Groothuis-Oudshoorn, 2011) in R version 4.1.0 (R Core Team, 2021).

Data processing. Plant species in the traits dataset were assigned to mOTUs using a systematic process (see **Appendix 3**). Briefly, any mOTU in the diet data that matched exactly one plant species in the trait dataset was assigned to that species, but some mOTUs could have belonged to any of a few closely related plant species with the same barcode. In those cases, the trait values of all applicable plant species were averaged to create a 'trait operational taxonomic unit' (TOTU); thus, the 34 plant species that shared barcodes with another species were reduced to 14 TOTUs, and the 117 species in the trait dataset that matched a dietary mOTU were reduced to 97

TOTUs. These 97 TOTUs collectively accounted for 93.6% of DNA sequence reads in the diet dataset. However, individual diets varied in the percentage of reads that corresponded to these 97 TOTUs. Thus, as a further quality-control step, we removed the 9 fecal samples for which <60% of reads matched a TOTU; in the remaining 286 samples, 95.4% of reads matched a TOTU (**Fig. S2**). Last, all mOTUs not matched to a TOTU were removed, and RRA was recalculated so that it summed to 1 for each sample. This process yielded identical sets of plant species in the diet and trait data.

To describe animal diets in terms of plant traits, we calculated the average plant-trait values for each animal diet, weighted by the proportional consumption (RRA) of each plant. The resulting dataset of diet-weighted trait averages (hereafter, **DT**) allowed us to position animal diets within plant-trait space. The nutritional profile of a physical mixture of plants (a diet) is closely approximated by weighted averages of the nutritional profiles of component species (Pearson, 1967), and diet-weighted nutritional averages are frequently used in studies of animal nutrition (Atkins et al., 2019; Branco et al., 2019; Vangilder, Torgerson, & Porath, 1982). We merely extended this approach to mixtures of nutritional and non-nutritional traits, which is analogous to the community-weighted trait-means approach used to link biodiversity and ecosystem functions (Lavorel & Garnier, 2002).

Statistical analyses. We used the median RRA of grasses in each species' diet to categorize grazers (≥60% grass RRA), browsers (≤10% grass RRA), and mixed feeders (intermediate; see **Table 1**); these arbitrary thresholds resulted in two arguable designations (reedbuck as grazer with 64% grass RRA, oribi as mixed feeder with 56% grass RRA), but classifying reedbuck as a mixed feeder does not qualitatively alter the few guild-specific results presented below. We

visualized compositional dissimilarity of fecal samples using non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarities between samples—first for all 14 herbivore species and then separately for grazers and non-grazers—and tested for significant differences among species in each of these groups using permutational multivariate analysis of variance (perMANOVA). To quantify pairwise dietary niche overlap between species, we calculated Pianka's niche-overlap index (Pianka, 1973) for each species pair based on population-level average diets using *EcoSimR* (Gotelli, Hart, & Ellison, 2015).

Our approach assumes that differential consumption of plants with different functional traits is a plausible mechanism of niche partitioning (operationally defined as differentiation in dietary species composition). However, diets with very different taxonomic composition are not necessarily very different in traits. We therefore explicitly tested the assumption that similarity in diet-weighted trait averages was indicative of overlap in plant species use by using a Mantel test to compare the pairwise Pianka niche-overlap indices against the pairwise Manhattan distances of diet-weighted trait averages (scaled to mean 0 and standard deviation 1) for all species pairs.

To evaluate the relationship between herbivore body size and diet quality (as per the Jarman-Bell hypothesis), we calculated dry-matter digestibility and digestible protein for each plant species using Robbins' summative equations (Robbins, Hanley, et al., 1987; Robbins, Mole, Hagerman, & Hanley, 1987). These two measures of diet quality are the cornerstone of many nutritional studies (Berry, Shipley, Long, & Loggers, 2019; Cook, Cook, Davis, & Irwin, 2016; Rowland et al., 2018; Wilson & Kerley, 2003). We then plotted the diet-weighted trait mean of each quality index against herbivore body mass (averaging male and female adult body masses from Kingdon et al., 2013) and fit the allometric equation $Q = aM^b$, where Q is diet quality, M is mass, and a and b are fitted constants (Kleynhans et al., 2011; Steuer et al., 2014).

Because the particular herbivore species included in this analysis could influence our results, we fit these equations both for all herbivore species (n = 14) and for ruminant species only (n = 11).

To test for differences in the mean height of food-plant taxa, we regressed the diet-weighted mean of plant height against herbivore shoulder height (Kingdon et al., 2013). Plant species' height was strongly positively correlated with all three measures of spinescence (density, length, width; $r \geq 0.73$), which were also highly correlated with each other ($r \geq 0.87$), making these traits too redundant for inclusion together in multivariate analyses (we retained height for the linear discriminant analysis described below). Nonetheless, we tested for a role of physical defenses in differentiating the diets of browsers and mixed feeders by regressing shoulder height against each spinescence metric and by plotting diet-weighted averages of two spinescence traits (density and width) in two-dimensional space.

To test whether the LES represented a dietary-niche axis, we first performed a principle component analysis (PCA) of leaf trait data (scaled to a unit variance) for all plant taxa (n = 97) detected in diets. We used data for all leaf traits except cellulose, hemicellulose, and remaining ash (n = 17), to minimize curvature induced by proportional data. We used the vectors representing the negative relationship between leaf nitrogen and leaf mass per area (see Results) as our operational approximation of the LES; these two traits are mechanistically linked to other canonical LES traits (photosynthetic and respiration rates, leaf longevity) and have the advantage of being easily measured. In line with other studies (Messier, McGill, Enquist, & Lechowicz, 2017; Onoda et al., 2017), we excluded leaf phosphorus from our LES proxy because its positive relationship with leaf nitrogen is partially decoupled by phylogeny and growth form (Kerkhoff, Fagan, Elser, & Enquist, 2006). The position of food plants in leaf-trait space is given by their scores on the first two principle components (PC1, PC2). We used these plant principle-

component scores to describe herbivore diets; each diet was positioned using the RRA-weighted average of the PC1 and PC2 values of constituent plants. This allowed us to analyze herbivore diets in terms of their positions along the two predominant axes of leaf-trait variation. To probe the robustness of our PCA-based inferences about the LES, we conducted a separate bivariate analysis in which we positioned plant species and herbivore diets in two-dimensional nitrogen–leaf mass per area space.

To quantify which plant traits were most important in influencing niche differentiation, we used linear discriminant analysis (LDA) of the **DT** matrix after scaling each trait to mean 0 and standard deviation 1 and removing traits with high correlations ($r > 0.7$), retaining 15 traits (**Fig. S3**). LDA identifies linear combinations of variables that maximize the separability of known classes, and has previously been used to identify axes of niche (Carnes & Slade, 1982; Harner & Whitmore, 1977) and trait differentiation (Hanane, 2015; McNaughton, 1990). We were thus able to quantify the degree to which these traits maximized the separability of herbivore species in plant-trait space, which we interpreted as a proxy for niche differentiation. We probed the ecological basis of the first two linear-discriminant axes by regressing them against herbivore grass consumption, body size, and location (floodplain versus savanna).

RESULTS

Herbivore diet composition and differentiation. The two dominant plant families in herbivore diets were Poaceae (grasses, 17 species, 16 TOTUs) and Fabaceae (legumes, 21 species, 17 TOTUs), which jointly accounted for 72% of RRA across all 286 samples; an additional 39 plant families accounted for the remaining 28%. Median grass RRA per species was 64–98% for the 8 grazers, 0–2% for the 3 browsers, and 12–56% for the 3 mixed feeders (**Table 1**, **Fig. 1**).

Community-wide NMDS ordination captured the grazer-browser spectrum (along the horizontal axis) and revealed interspecific dietary dissimilarities both within and between guilds (**Fig. 1a,d**). The within-guild patterns were more discernable when we plotted grazers and non-grazers separately (**Fig. 1b,c**). Dietary overlap was greater among grazers, in part because several abundant species (waterbuck, reedbuck, warthog) had high individual variability, reflecting their more generalized use of different habitat patches (e.g., floodplain, savanna, sodic sites, riparian zones, ecotones). Yet even among grazers, multiple species pairs segregated clearly in the ordination (**Fig. 1c**); the Pianka niche-overlap metric corroborated these visual differences (**Table S3**). The mean Manhattan distance in diet-weighted trait averages was strongly positively correlated with the degree of niche partitioning between pairs of species (**Fig. 1e**), validating our assumption that plant functional traits are a plausible mechanism of dietary differentiation at the plant species level. The same positive correlation emerged when we analyzed browsers and grazers separately, indicating that plant traits contribute to dietary differentiation within guilds (**Fig. S4**; grazers only: Mantel $r = 0.70$, $P = 0.001$; browsers only Mantel $r = 0.56$, $P = 0.006$). The few conspicuous outliers fell above the regression line (e.g., pairwise comparisons of impala and oribi with nyala and kudu), indicating that these pairs of species had taxonomically differentiated diets with convergent traits. (The opposite scenario of taxonomically convergent diets with differentiated traits is theoretically possible, if a minor dietary component differed massively in one or more traits, but we did not observe it.)

Do larger-bodied herbivores eat lower quality diets? We found negative correlations between herbivore body size and both dry-matter digestibility (**Fig. 2a**) and digestible protein content (**Fig. 2b**), as predicted by the Jarman-Bell hypothesis, although there was considerable noise in

these relationships. These negative correlations held when we restricted the analyses to ruminants only; indeed, these correlations were stronger, despite the reduced sample size (**Fig. 2**). Several grazing antelopes (hartebeest, wildebeest, sable) had lower diet quality, and one browsing antelope (bushbuck) had higher diet quality, than predicted by body mass alone (**Fig. 2**). This variability indicates that factors other than body size play a role in determining diet quality. Intraspecific variation in both quality metrics was also high across species (**Fig. S5**), most of which overlapped in the interquartile ranges for both quality metrics (**Fig. S5c,d**), indicating that species generally achieved nutritionally similar diets. Only a few species pairs did not overlap in the interquartile ranges for digestibility and protein (e.g. hartebeest/wildebeest with bushbuck/nyala/kudu), and these pairs occupy opposite ends of the grazer-browser spectrum, suggesting that the Jarman-Bell effect played little additional role in differentiating species' diets.

Do taller herbivores eat taller, more physically defended plant species? There was no significant correlation between shoulder height and diet-weighted mean of food-plant height across all 14 herbivore species, in part because grazers of all sizes ate shorter plant species than did browsers and mixed feeders (**Fig. 3a**). Among the six species of non-grazers, taller herbivores tended to eat taller plant species (**Fig. 3b**), although this correlation was not statistically significant. Taller non-grazers also ate more thorny plants; these correlations were statistically significant for each spinescence metric ($P \leq 0.013$) but heavily influenced by the exceptionally thorny diets of elephants, whereas the diets of the other five non-grazers overlapped heavily in spinescence (**Fig. S6**). Among the eight grazer species, there was a

significantly positive linear correlation between herbivore and food-plant heights (**Fig. 3c**), reflecting the large variation in mean height among grass species in Gorongosa (**Fig. S7**).

Is the leaf economic spectrum a dietary niche axis? The trait dataset encompassed several axes of leaf variation. The PCA captured 35.3% of variation on the first two axes (21.4% on PC1, 13.9% on PC2), indicating a low degree of redundancy in the traits measured. PC1 was positively related to leaf nitrogen and potassium and negatively to leaf mass per area. PC2 was positively related to calcium and lignin, and negatively to sodium, iron, and leaf tensile strength, which separated grasses from eudicots (**Fig. 4a**). As expected, leaf mass per area and leaf nitrogen were almost perfectly anticorrelated, reflecting the LES (Osnas et al., 2013; Wright et al., 2004). The LES was strongly aligned with the first principle component (**Fig. 4a,b**). Forbs were 'faster' and more nutrient-rich than woody plants; grasses and non-grasses separated along an axis orthogonal to the LES. For the most part, herbivore species' diets did not differ along the LES (**Fig. 4b**) and were instead distributed along PC2, corresponding to trait differences between monocots (represented by grasses, the palm *Hyphaene coriacea*, and two aquatic plants) and eudicots (i.e., the grazer-browser spectrum; **Fig. 4a**). Two species exhibited intraspecific variability along the LES: some elephants ate more 'slow' plants such as tough-leaved *Hyphaene*; conversely, some bushbuck—specifically those inhabiting the treeless Urema floodplain—ate more 'fast' plants, including nitrogen-rich forbs such as *Ludwigia adscendens*. These results were qualitatively recapitulated in a bivariate analysis based only on leaf nitrogen and leaf mass per area (**Fig. S8**). Thus, contrary to our prediction, the LES was not an independent axis of dietary differentiation among species, but rather an axis of individual variation within a few species.

Which plant traits distinguish the diets of large-herbivore species? The linear discriminant analysis classified most samples to the correct herbivore species, indicating consistent differences in diet-weighted trait averages among herbivore species. Model accuracy (median 62.9%) varied by herbivore species, ranging from 41.2% (sable) to 85.7% (zebra), but in all cases outperformed the expectation from random guessing (≤10.5%) (**Fig. S9**). The contribution of each trait to differentiating herbivore species is given by their weightings (coefficients) on each orthogonal linear discriminant function; we note that the traits that explain the major axes of leaf variation in plants (**Fig. 4a**) are not necessarily the same as those that best distinguish herbivore diets (**Fig. 5a**).

The first linear discriminant (LD1, accounting for 43.0% of the variation) was effectively the grazer-browser spectrum. LD1 was positively associated with hemicellulose, LMA, zinc, protein, and copper (consistent with the thin-yet-dense leaves of most grasses) and negatively associated with leaf-lamina thickness (characteristic of trees with thick leaves) (**Fig. 5a,b**). Accordingly, nearly all diets with positive values on LD1 belonged to grazers, nearly all those with negative values on LD1 belonged to browsers, and grass RRA explained 84.1% of the variance in LD1 (**Fig. 5a,d**).

The second linear discriminant (LD2, accounting for 18.3% of the variation) was negatively associated with sodium, stem dry-matter content, copper, and protein, and positively associated with leaf tensile strength, zinc, and stem-specific density (**Fig. 5a,c**). Small-bodied species such as oribi, bushbuck, and warthog tended to have negative values for LD2, as did individuals occurring in the Urema floodplain; large-bodied species and individuals in savanna habitat had more positive values for LD2. LD2 thus reflected the combined effects of body size

and habitat affiliation on dietary niche partitioning, and these two factors explained 42.4% of the variance in LD2 (**Fig. 5a,e**).

DISCUSSION

Our results show that sympatric large herbivore species in Gorongosa ate different suites of plant species, and that these differences in the taxonomic composition of diets have distinctive signatures of plant functional traits. Although we observed significant resource partitioning within both grazing and browsing guilds, the differences were weaker among grazers, in line with previous work from Gorongosa (Pansu et al., 2019). This discrepancy likely reflects, at least in part, the ongoing reassembly of the large-herbivore community, and specifically the fact that several grazer species were disproportionately abundant relative to pre-war conditions (Stalmans et al., 2019). The numerical dominance of waterbuck in particular has led to density-dependent spillover from the floodplain into savanna habitat and associated niche expansion (Becker et al., 2021), contributing to the high niche overlap we found among grazers. Yet, herbivore populations were increasing at the time of our study (Stalmans et al., 2019), suggesting that interspecific competition remained relatively weak as of 2018. We therefore hypothesize that our results are conservative in terms of the degree of dietary niche separation observed, both because of our methodology (which captures differences in taxonomic composition but not differences in plant tissues) and because weak interspecific competition should slacken pressure on species to differentiate their diets. We speculate that our results reflect the degree to which functional traits promote dietary differentiation even in the absence of such pressure, and we predict that future studies in Gorongosa will reveal even starker patterns of niche partitioning as interspecific competition intensifies. However, we also stress that Gorongosa's turbulent history and ongoing

reassembly may produce transient patterns in herbivores' use of particular plant species (and hence the plant-trait association in their diets) that do not reflect the stabler conditions in many African protected areas. These caveats and uncertainties underscore the need for comparative research to assess the generality of the patterns reported here.

Grazer-browser spectrum. Our results affirm the primacy of proportional grass consumption in differentiating herbivore diets in African savannas (Codron et al., 2007; Hofmann, 1989; Lamprey, 1963). Despite the prevalence of the grazer-browser spectrum, its mechanistic bases remain unclear. Although many studies have linked the morphological and physiological differences between grazers and browsers with chemical and structural differences between grasses and non-grasses (Hofmann & Stewart, 1972; Spencer, 1995), others have argued that the purported differences between grazers and browsers are overstated (Gordon, 2003; Robbins, Spalinger, & van Hoven, 1995). One review concluded that "there has been more hypothesis generation than testing" of ideas about which animal traits link mechanistically to which plant traits (Gordon 2003, page 14). Our study does not resolve this debate, but it does shed fresh light to guide future research. First, we identify which plant traits appear to be most important in creating separation along the grazer-browser spectrum (see **Fig. 5b**). Second, we document substantial trait variation among grasses and show that elements of this variation (such as mean height) contribute to within-guild differences in dietary species composition and deviations from guild-specific expectations. Grazers ate some non-grasses just as browsers ate some grasses; traits that vary both within and between grasses and non-grasses (e.g., leaf tensile strength) may help to explain how functional traits affect food choices independently of plant taxonomy.

Body size. The second major axis of diet differentiation in the LDA comprised a cluster of plant traits associated with dietary segregation among herbivores of different body size (shoulder height and body mass were highly correlated, $r = 0.84$). The seven most important traits on this axis were leaf tensile strength, zinc, sodium, stem dry matter content, stem density, copper, and protein—some of which are considered frequently (e.g., protein) and others infrequently (e.g., zinc) in studies of ungulate-plant interactions. Leaf tensile strength was the most important trait on LD2, perhaps because larger-bodied animals can harvest and process tough plants with their stronger facial muscles. Measures of spinescence distinguished elephant diets from those of smaller-bodied herbivores in this assemblage (**Fig. S6**). Thus, there is a cluster of leaf and stem traits associated with plants that are disproportionately eaten by the large-bodied herbivores (>170 kg, the size of a hartebeest and the approximate threshold between positive and negative values on LD2). This cluster of plant traits suggests the existence of a megafaunal herbivory syndrome, analogous to the megafaunal dispersal syndrome linking fruit traits to frugivores (Janzen & Martin, 1982), which might be conceptualized as extending the Jarman-Bell principle beyond conventional metrics of diet quality.

Despite broad consensus that larger-bodied mammalian herbivores tend to eat lower-quality diets, there are surprisingly few empirical demonstrations of the phenomenon (Clauss et al., 2013). Two studies in South Africa (Kleynhans et al., 2011; Owen-Smith, 1988) found that the diets of larger-bodied herbivores were lower in crude protein, and another in Kenya found an allometric decline in digestibility (Steuer et al., 2014). We found allometric declines in both crude protein and digestibility, both across all 14 herbivore species and for just the 11 ruminants, supporting the generality of these relationships. Indeed, our estimate of the Jarman-Bell effect may be conservative, because we calculated quality indices based solely on the composition of

leaves and not stems. The nutritional value of young stems often approaches that of leaves, whereas old stems tend to be considerably lower in quality; accordingly, our estimates of diet quality are probably most accurate for smaller herbivores (which are able to be more selective and eat fewer stems) than for larger species that are likely to eat more stem tissue (Owen-Smith, 1988). However, our approach also has an advantage: because we estimated diet quality using only the youngest fully unfurled leaves, our study compared all plants in a common currency. Thus, our study shows that large-bodied herbivores tend to eat more of lower-quality plant *species*, isolating the influence of food-plant identity—as opposed to leaf:stem ratio or phenology—on diet quality. Future studies could combine our trait-based approach with complementary measures of diet quality (e.g., metabolic fecal nitrogen) to further tease apart the determinants of diet quality.

Our results are consistent with the Jarman-Bell hypothesis and, at least among grazers, the idea that differences in herbivore height lead to differences in dietary plant height (**Figs. 2, 3**). The latter result differs from the classic formulation of height stratification, which emphasizes the proportion of time spent feeding at different heights (for browsers) and the relative use of stemmy grass vs. new shoots (for grazers) without explicit reference to plant species identity (du Toit 1990, du Toit & Olff 2014); our result is conceptually parallel and shows that interspecific differences in foraging height can translate into differences in the mean height of food-plant species. While the diet-quality and plant-height results are both rooted in herbivore body size (mass, shoulder height), our data suggest that these two mechanisms act independently of one another (**Fig. S7**). However, several lines of evidence also suggest that these two mechanisms played a relatively modest role in differentiating the taxonomic composition of herbivore diets. Protein and plant height were the 7th and 10th largest coefficients

on LD2 (5^{th} and 9^{th} on LD1), indicating that these traits did relatively little to separate species' diets. This inference is consistent with the high intraspecific variability and interspecific overlap in both diet-quality metrics (**Fig. S5**), notwithstanding their statistically significant correlations with body size. Similarly, most of the variation in the height of food-plant species appeared to be driven by the smallest-bodied herbivores, with limited differences among either large-bodied grazers (the 6 species ≥ 124-cm tall) or large-bodied non-grazers (the 3 species ≥ 104-cm tall), providing one explanation for the weakness of plant height in differentiating diet composition at the community level. Thus, our size-based hypotheses were mostly supported, but traits other than protein and height were more important in determining which plant species herbivores ate.

Leaf economic spectrum. That the LES failed to separate large-herbivore diets may appear to conflict with the support we found for the Jarman-Bell effect. We expected these results to align, as the degree of investment in cell walls (fiber) versus cell contents is a shared theme in leaf economics and animal nutrition: thicker cell walls increase leaf mass per area, and thus longevity (Onoda et al., 2017), but reduce leaf digestibility (Van Soest, 1994). However, high leaf mass per area can also be achieved by increasing leaf thickness, which is not a factor in digestibility. Variation in leaf thickness is evident in our data and was key in discriminating grazer and browser diets. Although grasses have thick cell walls and dense tissue, their leaves are thin (reducing leaf mass per area), rich in hemicellulose (a relatively digestible fiber), and low in lignin (which disproportionately reduces digestibility); most browse plants have the opposite traits. Thus, leaf mass per area is a composite trait that conflates several important leaf properties (e.g., cell wall composition, thickness, density) that differ systematically between grasses and non-grasses (Onoda et al., 2017; Shipley, 1999; Van Soest, 1994) and thus help to define the

grazer-browser spectrum. In this way, constituent traits of the LES—decoupled in the diets of selectively foraging herbivores (**Fig. S8**)—can contribute independently to diet differentiation. One caveat is that we quantified the LES using just two traits, leaf mass per area and leaf nitrogen; although these two traits represent a strong first approximation of leaf economics and are strongly correlated with the other LES traits (by definition of the LES), we did not measure leaf longevity or photosynthetic and respiration rates. Future work incorporating these traits could probe the robustness of our conclusion that the LES is not a basis of interspecific diet differentiation in large-herbivore assemblages.

Although the LES did not contribute to interspecific niche partitioning, we cannot evaluate the extent to which the LES shapes herbivore food *preferences* because we cannot infer herbivore selectivity in the absence of data on plant species' relative availability (which is difficult to quantify in a common currency for mixes of woody and herbaceous plants at large spatial scales). We posit two alternative hypotheses that might explain the distribution of diets down the middle of the LES (**Fig. 4b**). First, herbivores might indeed prefer 'fast' plants (as per the resource-availability hypothesis) but these species are rare (perhaps because they are preferred). Most support for this interpretation stems from work on the effects of insects on woody plants (Endara & Coley, 2011), although some studies have found that large mammals do prefer fast-growing species (Bryant et al., 1983; Bryant, Kuropat, Cooper, Frisby, & Owen-Smith, 1989). Future work could examine how dietary preferences interact with plant availability to shape diet composition and resource partitioning.

Alternatively, herbivores might be indifferent to the LES (or avoid the extremes) and achieve intermediate diets through the averaging effect of dietary diversity. Consistent with this second scenario, the plant species not detected in herbivore diets (n = 87) had nearly identical

distributions of leaf mass per area and nitrogen values to those present in diets (n = 117; **Fig. S10**). While some 'missing' plant species may be uncommon, inaccessible, or undetectable with our methods (e.g., owing to amplification biases in DNA metabarcoding), we know that at least some plants are missing because they are avoided. For example, the forb *Heliotropium indicum* is among the top-20 most abundant plants in the Gorongosa floodplain and is detectable with our methods (Pansu et al., 2019) but was not present in the diets analyzed here. *Heliotropium* spp. are very rich in protein (fast on the LES) but contain hepatotoxic pyrrolizidine alkaloids—one presumed example of how plant secondary metabolites might enable plants with otherwise desirable traits plants to escape herbivory. We consider it likely that plant chemical defenses account for some of the unexplained variance in our study, and the lack of secondary metabolites in our trait data is a caveat. We did not analyze secondary compounds because they are extremely diverse and their functional roles are often unknown; however, emerging metabolomic techniques (Li & Gaquerel, 2021; Sedio, 2017) offer a promising inroad and could be used in conjunction with a trait-centered framework such as ours.

Other caveats. DNA metabarcoding is a powerful method for diet analysis, and the available evidence suggests that the RRA of plant taxa in studies using the *trn*L-P6 marker performs well (Kartzinel et al., 2015; Willerslev et al., 2014), but the approach is not without limitations. One, mentioned in the previous paragraph, is taxon-specific amplification biases, which can skew RRA and result in false absences from diets; for example, sedges (Cyperaceae) are thought to be underrepresented in studies using this marker (De Barba et al., 2014). Differential digestibility is also a potential source of bias, although the magnitude and direction of this effect are uncertain; although indigestible plant parts are more likely to pass through the gut, we avoided such

remains, and highly digestible tissue may tend to have higher chloroplast densities and thus account for more of the plastid DNA present in feces (Craine, Towne, Miller, & Fierer, 2015).

Last, our study aimed to explore differentiation in the taxonomic composition of herbivore diets, which we see as an important complement to a long history of work focusing on the differential consumption of plant tissues such as leaves, stems, and fruits (Gwynne & Bell, 1968). Our methods cannot distinguish the plant part that was eaten, and we used standardized measurements of plant traits (e.g., sampling the youngest fully unfurled leaf for leaf traits) and mean trait values to characterize the trait composition of herbivore diets. Such standardized sampling was necessary to incorporate 204 plant species and 14 herbivore species in a common framework, but it means that we could not evaluate intraspecific trait variation among plants (e.g., grazed and ungrazed growth forms), within plants (e.g., sun-exposed vs. shaded leaves), or over time (e.g., seasonal variation in trait values). While we believe that trait variation among plant species is likely to overwhelm such intraspecific variability, explicit testing of this assumption would help to validate our results.

Conclusion. Our trait-based approach to diet analysis provided a common framework for testing both classic and novel hypotheses about resource partitioning in diverse large-herbivore assemblages. We found that herbivores differed in diet composition, that these differences were correlated with differences in plant functional traits, and that plant traits varied in their contribution to dietary differentiation. Plant traits that differed between grasses and eudicots created the primary axis of dietary differentiation, the grazer-browser spectrum. The second major axis of differentiation was a cluster of traits that was correlated with herbivore body size and the distinction between floodplain and savanna habitats. The Jarman-Bell hypothesis and

differences in the height of food-plant taxa were individually supported, but these mechanisms played subordinate roles in differentiating the taxonomic composition of herbivore species' diets. The LES was not a major axis of niche partitioning and failed to distinguish the diet composition of herbivore species. Together, these results reveal aspects of plant functional diversity that underpin dietary resource partitioning and help to stabilize species coexistence in savanna herbivores.

ACKNOWLEDGEMENTS

We thank Mozambique and the staff of Gorongosa National Park, especially M. Stalmans, J. Denlinger, M. Marchington, R. Branco, and rangers. M. Stahl, M. Dietrich, and B. Stankovikj helped in the field. M.P. Gaiarsa translated the abstract into Portuguese. This work was supported by the U.S. National Science Foundation (Graduate Research Fellowship to A.B.P., IOS-1656527 and DEB-1457697 to R.M.P., IOS-1656642 to R.A.L.). Additional support was provided by the High Meadows Environmental Institute's Grand Challenges Program, the Greg Carr Foundation, and the Cameron-Schrier Foundation.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

A.B.P. and R.M.P. conceived and designed the study; A.B.P. and M.C.H. collected and analyzed data; J.P. and J.M.L. assisted with methods and analyses; R.A.L. collected data and assisted with

analyses; B.W. assisted with taxonomic identification; A.B.P. and R.M.P. wrote the manuscript; all authors made revisions and approved the final draft.

DATA ACCESSIBILITY

Filtered herbivore diet data and the local Gorongosa plant-trait database are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4f4qrfjdk (Potter 2022), along with the unfiltered sequence data used for diet analysis: https://doi.org/10.5061/dryad.sxksn02zc (Guyton et al. 2020)

REFERENCES

Atkins, J. L., Long, R. A., Pansu, J., Daskin, J. H., Potter, A. B., Stalmans, M. E., … Pringle, R. M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*, *364*(6436), 173–177. doi: 10.1126/science.aau3561

Becker, J. A. L., Hutchinson, M. C., Potter, A. B., Park, S., Guyton, J. A., Abernathy, K., … Pringle, R. M. (2021). Ecological and behavioral mechanisms of density-dependent habitat expansion in a recovering African ungulate population. *Ecological Monographs*, e01476. doi: 10.1002/ecm.1476

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scientific American*, *225*, 86–93.

Berry, S. L., Shipley, L. A., Long, R. A., & Loggers, C. (2019). Differences in dietary niche and foraging behavior of sympatric mule and white-tailed deer. *Ecosphere*, *10*(7), e02815.

Bouley, P., Poulos, M., Branco, R., & Carter, N. H. (2018). Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation*, *227*, 233–242. doi: 10.1016/j.biocon.2018.08.024

Branco, P. S., Merkle, J. A., Pringle, R. M., Pansu, J., Potter, A. B., Reynolds, A., … Long, R. A. (2019). Determinants of elephant foraging behaviour in a coupled human-natural system: Is brown the new green? *Journal of Animal Ecology*, *88*(5), 780–792. doi: 10.1111/1365-2656.12971

Bryant, J. P., Chapin, F. S., & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, *40*(3), 357–368.

Bryant, J. P., Kuropat, P. J., Cooper, S. M., Frisby, K., & Owen-Smith, N. (1989). Resource availability hypothesis of plant antiherbivore defence tested in a South African savanna ecosystem. *Nature*, *340*(6230), 227–229. doi: 10.1038/340227a0

Burrows, J. E., Burrows, S. M., Lötter, M. C., & Schmidt, E. (2018). *Trees and Shrubs Mozambique* (Subscriber). Publishing Print Matters (Pty) Ltd.

Carnes, B. A., & Slade, N. A. (1982). Some comments on niche analysis in canonical space. *Ecology*, *63*(4), 888–893. doi: 10.2307/1937227

Cerling, T. E., Harris, J. M., & Passey, B. H. (2003). Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy*, *84*(2), 456–470.

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*(1), 343–366.

Christopherson, V., Tremblay, J.-P., Gagné, P. N., Bérubé, J., & St-Laurent, M.-H. (2019). Meeting caribou in the alpine: Do moose compete with caribou for food? *Global Ecology and Conservation*, *20*, e00733. doi: 10.1016/j.gecco.2019.e00733

Churski, M., Spitzer, R., Coissac, E., Taberlet, P., Lescinskaite, J., van Ginkel, H. A. L., …

Cromsigt, J. P. G. M. (2021). How do forest management and wolf space-use affect diet composition of the wolf's main prey, the red deer versus a non-prey species, the European bison? *Forest Ecology and Management*, *479*, 118620. doi: 10.1016/j.foreco.2020.118620

Clauss, M., Steuer, P., Müller, D. W. H., Codron, D., & Hummel, J. (2013). Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PLOS ONE*, *8*(10), e68714. doi: 10.1371/journal.pone.0068714

Codron, D., & Clauss, M. (2010). Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. *Canadian Journal of Zoology*, *88*(11), 1129–1138.

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., Ruiter, D. De, Sealy, J., … Fourie, N. (2007). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, *273*(1), 21–29. doi: 10.1111/j.1469-7998.2007.00292.x

Coley, P. D., Bryant, J. P., & Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, *230*(4728), 895–899.

Cook, J. G., Cook, R. C., Davis, R. W., & Irwin, L. L. (2016). Nutritional ecology of elk during summer and autumn in the Pacific Northwest. *Wildlife Monographs*, *195*(1), 1–81.

Craine, J. M., Towne, E. G., Miller, M., & Fierer, N. (2015). Climatic warming and the future of bison as grazers. *Scientific Reports*, *5*, 16738.

Cromsigt, J. P. G. M., & Olff, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. *Ecology*, *87*(6), 1532–1541.

De Barba, M., Miquel, C., Boyer, F., Mercier, C., Rioux, D., Coissac, E., & Taberlet, P. (2014). DNA metabarcoding multiplexing and validation of data accuracy for diet assessment:

application to omnivorous diet. *Molecular Ecology Resources*, *14*(2), 306–323. doi: 10.1111/1755-0998.12188

du Toit, J. T. (1990). Feeding-height stratification among African browsing ruminants. *African Journal of Ecology*, *28*(1), 55–61.

du Toit, J. T., & Olff, H. (2014). Generalities in grazing and browsing ecology: using across-guild comparisons to control contingencies. *Oecologia*, *174*(4), 1075–1083.

Endara, M. J., & Coley, P. D. (2011). The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology*, *25*(2), 389–398. doi: 10.1111/j.1365-2435.2010.01803.x

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C 3 plants. *Oecologia*, *78*(1), 9–19.

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., … Coley, P. D. (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, *87*(7), S150–S162.

Gordon, I. J. (2003). Browsing and grazing ruminants: are they different beasts? *Forest Ecology and Management*, *181*(1–2), 13–21. doi: 10.1016/S0378-1127(03)00124-5

Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015). *EcoSimR: Null model analysis for ecological data*. doi: 10.5281/zenodo.16522

Guyton, J. A., Pansu, J., Hutchinson, M. C., Kartzinel, T. R., Potter, A. B., Coverdale, T. C. T. C., … Pringle, R. M. (2020). Trophic rewilding revives biotic resistance to shrub invasion. *Nature Ecology & Evolution*, *4*(5), 712–724. doi: 10.1038/s41559-019-1068-y

Guyton, J.A., (2020). DRYAD REFERENCE TO BE COMPLETED

Gwynne, M. D., & Bell, R. H. V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature*, *220*(5165), 390–393.

Hanane, S. (2015). Nest-niche differentiation in two sympatric Streptopelia species from a North African agricultural area: the role of human presence. *Ecological Research*, *30*(4), 573–580.

Harner, E. J., & Whitmore, R. C. (1977). Multivariate measures of niche overlap using discriminant analysis. *Theoretical Population Biology*, *12*(1), 21–36. doi: 10.1016/0040-5809(77)90033-8

Haschick, S. L., & Kerley, G. I. H. (1996). Experimentally determined foraging heights of bush buck Tragelaphus scriptus and boergoats Capra hircus. *South African Journal of Wildlife Research*, *26*(2), 64–65. doi: 10.10520/EJC116993

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, *78*(4), 443–457. doi: 10.1007/BF00378733

Hofmann, R. R., & Stewart, D. R. M. (1972). Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia*, *36*(2), 226–240.

Hyde, M. A., Wursten, B. T., Ballings, P., & Coates Palgrave, M. (2018). Flora of Mozambique. Retrieved September 26, 2018, from https://www.mozambiqueflora.com/index.php

Janis, C. M., & Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, *92*(3), 267–284.

Janzen, D. H., & Martin, P. S. (1982). Neotropical anachronisms: the fruits the gomphotheres ate. *Science*, *215*(4528), 19–27.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, *48*(3), 215–267.

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., … Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences*, *112*(26), 8019–8024. doi: 10.1073/pnas.1503283112

Kerkhoff, A. J., Fagan, W. F., Elser, J. J., & Enquist, B. J. (2006). Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist*, *168*(4), E103--E122.

Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. (Eds.). (2013). *Mammals of Africa* (Vol. 1–6). Bloomsbury.

Kleynhans, E. J., Jolles, A. E., Bos, M. R. E., & Olff, H. (2011). Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos*, *120*(4), 591–600. doi: 10.1111/j.1600-0706.2010.18712.x

Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, *112*(3), 797–802.

Lamprey, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *African Journal of Ecology*, *1*(1), 63–92.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits : *Functional Ecology*, *16*, 545–556.

Li, D., & Gaquerel, E. (2021). Next-generation mass spectrometry metabolomics revives the functional analysis of plant metabolic diversity. *Annual Review of Plant Biology*, *72*(1), 867–891. doi: 10.1146/annurev-arplant-071720-114836

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology

from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185.

McNaughton, S. J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature*, *345*(6276), 613.

McNaughton, S. J., & Georgiadis, N. J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, *17*(57), 39–65. doi: 10.1146/annurev.es.17.110186.000351

Messier, J., McGill, B. J., Enquist, B. J., & Lechowicz, M. J. (2017). Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography*, *40*(6), 685–697.

Müller, D. W. H., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J., & Clauss, M. (2013). Assessing the Jarman--Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *164*(1), 129–140.

Nichols, R. V, Cromsigt, J. P. G. M., & Spong, G. (2015). DNA left on browsed twigs uncovers bite-scale resource use patterns in European ungulates. *Oecologia*, *178*(1), 275–284.

O'Kane, C. A. J., Duffy, K. J., Page, B. R., & Macdonald, D. W. (2011). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, *27*(3), 249–258. doi: 10.1017/S0266467410000817

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., … Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, *214*(4), 1447–1463. doi: 10.1111/nph.14496

Osnas, J. L. D., Lichstein, J. W., Reich, P. B., & Pacala, S. W. (2013). Global leaf trait relationships: mass, area, and the leaf economics spectrum. *Science*, *340*(6133), 741–744.

doi: 10.1126/science.1231574

Owen-Smith, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press.

Pansu, J., Guyton, J. A., Potter, A. B., Atkins, J. L., Daskin, J. H., Wursten, B., … Pringle, R. M. (2019). Trophic ecology of large herbivores in a reassembling African ecosystem. *Journal of Ecology*, *107*(3), 1355–1376. doi: 10.1111/1365-2745.13113

Pearson, H. A. (1967). Cattle diet digestibilities determined from components. *Journal of Range Management*, *20*(6), 405–406. doi: 10.2307/3896417

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., … others. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, *4*(1), 53–74.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, *182*(3), 565–588.

Pringle, R. M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature*, *546*(7656), 91–99. doi: 10.1038/nature22902

Pringle, R. M., & Hutchinson, M. C. (2020). Resolving food-web structure. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 55–80. doi: 10.1146/annurev-ecolsys-110218-024908

Pringle, R. M., Kartzinel, T. R., Palmer, T. M., Thurman, T. J., Fox-Dobbs, K., Xu, C. C. Y., … others. (2019). Predator-induced collapse of niche structure and species coexistence.

Nature, *570*(7759), 58–64.

Potter DRYAD REFERENCE TO BE COMPLETED

R Core Team. (2021). *R: A Language and Environment for Statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Renaud, P. C., Verheyden-Tixier, H., & Dumont, B. (2003). Damage to saplings by red deer (Cervus elaphus): effect of foliage height and structure. *Forest Ecology and Management*, *181*(1), 31–37. doi: https://doi.org/10.1016/S0378-1127(03)00126-9

Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C., & Mautz, W. W. (1987). Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, *68*(1), 98–107.

Robbins, C. T., Mole, S., Hagerman, A. E., & Hanley, T. A. (1987). Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology*, *68*(6), 1606–1615.

Robbins, C. T., Spalinger, D. E., & van Hoven, W. (1995). Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia*, *103*(2), 208–213. doi: 10.1007/BF00329082

Rowland, M. M., Wisdom, M. J., Nielson, R. M., Cook, J. G., Cook, R. C., Johnson, B. K., … others. (2018). Modeling elk nutrition and habitat use in western Oregon and Washington. *Wildlife Monographs*, *199*(1), 1–102.

Schmitt, M. H., Shuttleworth, A., Shrader, A. M., & Ward, D. (2020). The role of volatile plant secondary metabolites as pre-ingestive cues and potential toxins dictating diet selection by African elephants. *Oikos*, *129*(1), 24–34. doi: 10.1111/oik.06665

Scogings, P. F., Hjältén, J., & Skarpe, C. (2011). Secondary metabolites and nutrients of woody plants in relation to browsing intensity in African savannas. *Oecologia*, *167*(4), 1063–1073.

doi: 10.1007/s00442-011-2042-9

Searle, K. R., & Shipley, L. A. (2008). The comparative feeding behaviour of large browsing and grazing herbivores. In *The ecology of browsing and grazing* (pp. 117–148). Springer.

Sedio, B. E. (2017). Recent breakthroughs in metabolomics promise to reveal the cryptic chemical traits that mediate plant community composition, character evolution and lineage diversification. *New Phytologist*, *214*(3), 952–958. doi: 10.1111/nph.14438

Shipley, L. A. (1999). Grazers and browsers: how digestive morphology affects diet selection. *Grazing Behavior of Livestock and Wildlife*, *70*, 20–27.

Spencer, L. M. (1995). Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy*, *76*(2), 448–471.

Stalmans, M. E., Massad, T. J., Peel, M. J. S., Tarnita, C. E., & Pringle, R. M. (2019). War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. *PLOS ONE*, *14*(3), e0212864. doi: 10.1371/journal.pone.0212864

Steuer, P., Südekum, K.-H., Tütken, T., Müller, D. W. H., Kaandorp, J., Bucher, M., … Hummel, J. (2014). Does body mass convey a digestive advantage for large herbivores? *Functional Ecology*, *28*(5), 1127–1134.

Stokke, S., & du Toit, J. T. (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, *23*(1), 70–80. doi: https://doi.org/10.1111/j.1600-0587.2000.tb00262.x

Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., … Willerslev, E. (2007). Power and limitations of the chloroplast trn L (UAA) intron for plant DNA barcoding. *Nucleic Acids Research*, *35*(3), e14.

Tinley, K. L. (1977). *Framework of the Gorongosa Ecosystem*. University of Pretoria.

van Buuren, S., & Groothuis-Oudshoorn, K. (2011). {mice}: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software*, *45*(3), 1–67.

Van Soest, P. J. (1994). *Nutritional ecology of the ruminant* (2nd ed.). Cornell University Press.

Vangilder, L. D., Torgerson, O., & Porath, W. R. (1982). Factors influencing diet selection by white-tailed deer. *The Journal of Wildlife Management*, *46*(3), 711–718.

Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E., Edwards, M. E., … others. (2014). Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature*, *506*(7486), 47–51.

Wilmshurst, J. F., Fryxell, J. M., & Bergman, C. M. (2000). The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*(1441), 345–349.

Wilson, S. L., & Kerley, G. I. H. (2003). Bite diameter selection by thicket browsers: the effect of body size and plant morphology on forage intake and quality. *Forest Ecology and Management*, *181*(1), 51–65.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … others. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827.

Table 1. Attributes of the 14 large-herbivore species analyzed in this study, listed in order of increasing grass consumption

Common Name	Latin Name	Body size (kg)	Pop. density in 2018 (indiv./km^2)	Fecal samples (*n*)	Median Poaceae RRA (IQR)	Median Fabaceae RRA (IQR)	Median other families RRA (IQR)
Kudu	*Tragelaphus strepsiceros*	205	1.11	20	0.00 (0)	0.06 (0.00–0.13)	0.94 (0.86–1.00)
Bushbuck	*Tragelaphus sylvaticus*	35	0.96	15	0.00 (0.00–0.02)	0.07 (0.00–0.25)	0.93 (0.72–0.99)
Nyala	*Tragelaphus angasii*	85	1.07	13	0.02 (0.00–0.04)	0.05 (0.04–0.07)	0.92 (0.88–0.94)
Elephant	*Loxodonta africana*	4640	0.32	18	0.12 (0.01–0.26)	0.21 (0.05–0.38)	0.55 (0.35–0.75)
Impala	*Aepyceros melampus*	42	3.50	30	0.25 (0.13–0.40)	0.38 (0.16–0.59)	0.15 (0.07–0.53)
Oribi	*Ourebia ourebi*	18	2.30	30	0.56 (0.32–0.66)	0.30 (0.06–0.45)	0.09 (0.01–0.29)
Reedbuck	*Redunca arundinum*	45	5.96	28	0.64 (0.42–0.86)	0.18 (0.04–0.48)	0.00 (0.00–0.04)
Buffalo	*Syncerus caffer*	504	0.56	17	0.78 (0.71–0.92)	0.04 (0.02–0.18)	0.06 (0.03–0.22)
Waterbuck	*Kobus ellipsiprymnus*	204	32.23	30	0.78 (0.50–0.93)	0.06 (0.02–0.28)	0.05 (0.00–0.16)
Zebra	*Equus quagga*	323	0.01	7	0.90 (0.82–0.92)	0.08 (0.07–0.10)	0.00 (0.00–0.06)
Sable	*Hippotragus niger*	226	0.45	17	0.95 (0.82–0.97)	0.03 (0.02–0.04)	0.00 (0.00–0.09)
Wildebeest	*Connochaetes taurinus*	214	0.33	18	0.97 (0.87–1.00)	0.03 (0.00–0.11)	0.00 (0.00–0.02)
Warthog	*Phacochoerus africanus*	68	6.23	27	0.97 (0.94–1.00)	0.01 (0.00–0.03)	0.00 (0.00–0.03)
Hartebeest	*Alcelaphus buselaphus*	172	0.31	16	0.98 (0.94–0.99)	0.01 (0.00–0.03)	0.01 (0.00–0.03)

FIGURE CAPTIONS

Figure 1—Dietary dissimilarity among large-herbivore species. (a) NMDS of the diets of 14 sympatric large herbivore species. Each point represents a fecal sample (n = 286); colors indicate species, shapes indicate feeding guilds (squares, browsers; triangles, mixed-feeders; circles, grazers; legend key lists species top-bottom in order of increasing grass RRA). Distances between points reflect Bray-Curtis compositional dissimilarity. **(b, c)** NMDS of 6 browsers and mixed feeders (b) and 8 grazers (c); 10 extreme outliers (samples with <50% grass for hartebeest, sable, and buffalo and <10% grass for waterbuck and reedbuck) are not shown in (c) to facilitate visualization, but are shown in (a). **(d)** The grazer-browser spectrum. Centerlines show median, boxes show interquartile range, whiskers show 1.5 × interquartile range, and dots show outliers; dashed lines show the thresholds used to distinguish feeding guilds. **(e)** Correlation between dietary niche separation (1 – Pianka niche-overlap index) and dietary trait separation (Manhattan distance of diet-weighted trait averages) for each species pair (Mantel r = 0.89, p = 0.001, n = 91 pairs; trendline is an ordinary least-squares regression).

Figure 2—Allometric relationships between herbivore body mass and diet quality. (a) Percentage dry-matter digestibility = 60.53 × $\text{Mass}^{-0.029}$ (adj. R^2 = 0.20, t = -2.09, df = 12, P = 0.059). **(b)** Percentage digestible protein = 16.84 × $\text{Mass}^{-0.076}$ (adj. R^2 = 0.26, t = -2.34, df = 12, P = 0.038). Data points (colored by species; squares, browsers; triangles, mixed feeders; circles, grazers) correspond to the mean of male and female body masses (Kingdon et al., 2013) and the diet-weighted mean of each quality metric. Fitted regressions for all 14 species are indicated with solid lines. Dotted lines are the regressions when restricted to ruminant species only (n = 11); the relationships hold for both digestibility (adj. R^2 = 0.32, t = -2.39, df = 9, P = 0.040) and protein

(adj. R^2 = 0.45, t = -3.04, df = 9, P = 0.014). Note log scale on both axes; corresponding data are presented on linear axes in Fig. S5.

Figure 3—Relationships between herbivore height and height of food-plant species. (a) Data for all 14 herbivore species show an increasing overall trend but a statistically non-significant correlation (adj. R^2 = 0.11, t = 1.67 df = 12, P = 0.12), reflecting marked differences in plant height between grazers and non-grazers. **(b)** Data for just the 6 species of browser and mixed feeder (adj. R^2 = 0.41, t = 2.11, df = 4, P = 0.10; dashed trendline). Dashed horizontal line shows the 75th quantile of plant species' heights in the traits dataset. **(c)** Data for just the 8 species of grazer (adj. R^2 = 0.67, t = 3.96, df = 6, P = 0.007). Error bars show ± 1 SEM of the diet-weighted mean height of plant species in each herbivore species' diet.

Figure 4—Position of herbivore diets along two major axes of variation in plant functional traits. Axes in both panels are identical and represent the first two principle components of plant-trait variation. The LES, approximated here by two key traits, leaf mass per area and leaf nitrogen (crude protein), spans left to right of the PCA (corresponding to PC1), while the orthogonal axis corresponds to traits such as calcium and hemicellulose that distinguish monocots from eudicots. Food-plant species are represented by diamonds in both panels. **(a)** All plants recorded in herbivore diets (n = 97); vectors illustrate (by direction and relative length) the contributions of 17 leaf traits to both principle components. Colors indicate plant growth form, with 'Other' used for miscellaneous growth forms, such as herbaceous vines and plants intermediate between woody and herbaceous (e.g., subshrubs); plants with extreme values in each corner of the plot are shown (labeled only by genus for visual clarity; see Table S1 for

species identities). LMA is leaf mass per area and LDMC is leaf dry matter content. **(b)** The same ordination with the same plants (in gray) and herbivore diets superimposed (points are 286 individual fecal samples, colored by species and with markers corresponding to guild as in Figs. 1–3), indicating the position of herbivore diets in plant leaf-trait space. Vectors show the orientation of leaf mass per area and leaf nitrogen, major traits of the LES.

Figure 5—Plant traits that separate herbivore diets. (a) Positioning of herbivore diets (colored symbols) along the first two linear discriminant axes. Each linear discriminant function is a linear combination of 15 uncorrelated plant traits, the coefficients of which are illustrated by the vectors (here multiplied by 2.2 for visual clarity); vector length indicates the relative importance of each trait in separating the diets of herbivore species, and vector orientation indicates the degree to which each trait is associated with LD1 or LD2. LMA is leaf mass per area, SDMC is stem dry matter content, and protein is nitrogen × 6.25. **(b, c)** The same coefficients (unscaled) showing the weighting and direction of each trait on LD1 (b) and LD2 (c). **(d)** Regression of LD1 values for each herbivore diet (points) against the proportional grass content of the diet (adj. $R^2 = 0.84$, $F_{1,284} = 1515$, $P < 0.0001$). **(e)** Linear model of LD2 values as a function of log-transformed body mass and habitat affiliation (whole model adj. $R^2 = 0.42$, $F_{2,283} = 104.7$, $P < 0.0001$; $\log_{10}$ body mass $F_{1,283} = 165.0$, $P < 0.0001$; habitat $F_{1,283} = 44.3$, $P < 0.0001$).

Figure 1

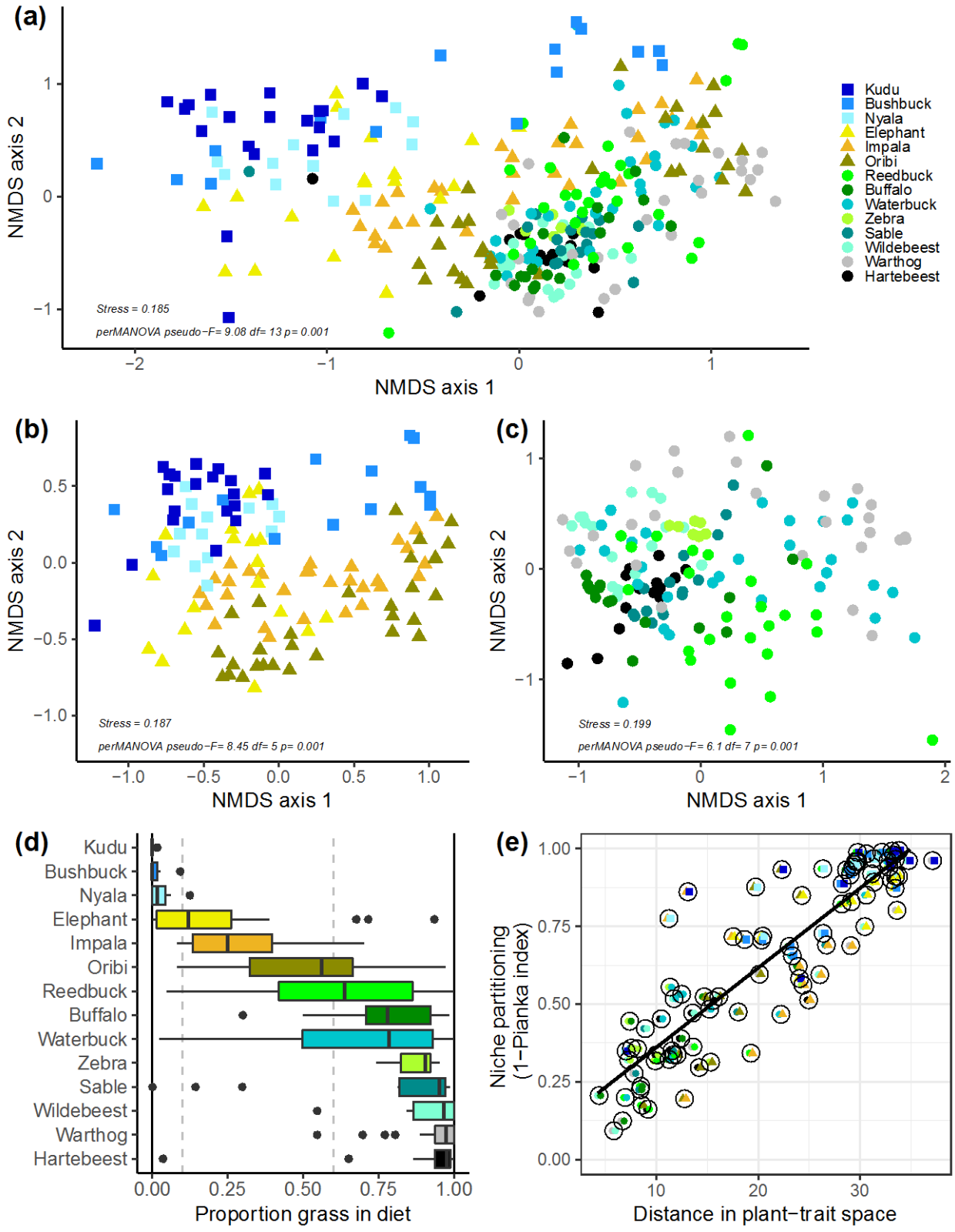

Figure 2

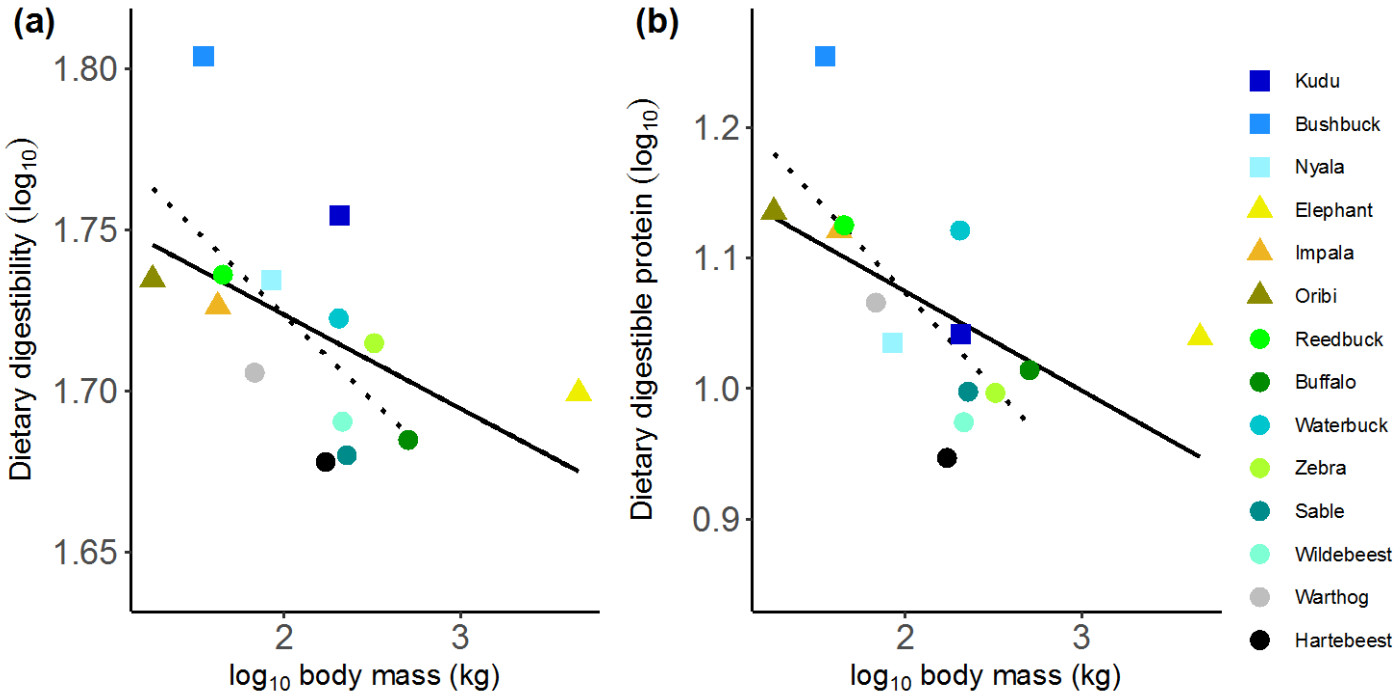

Figure 3:

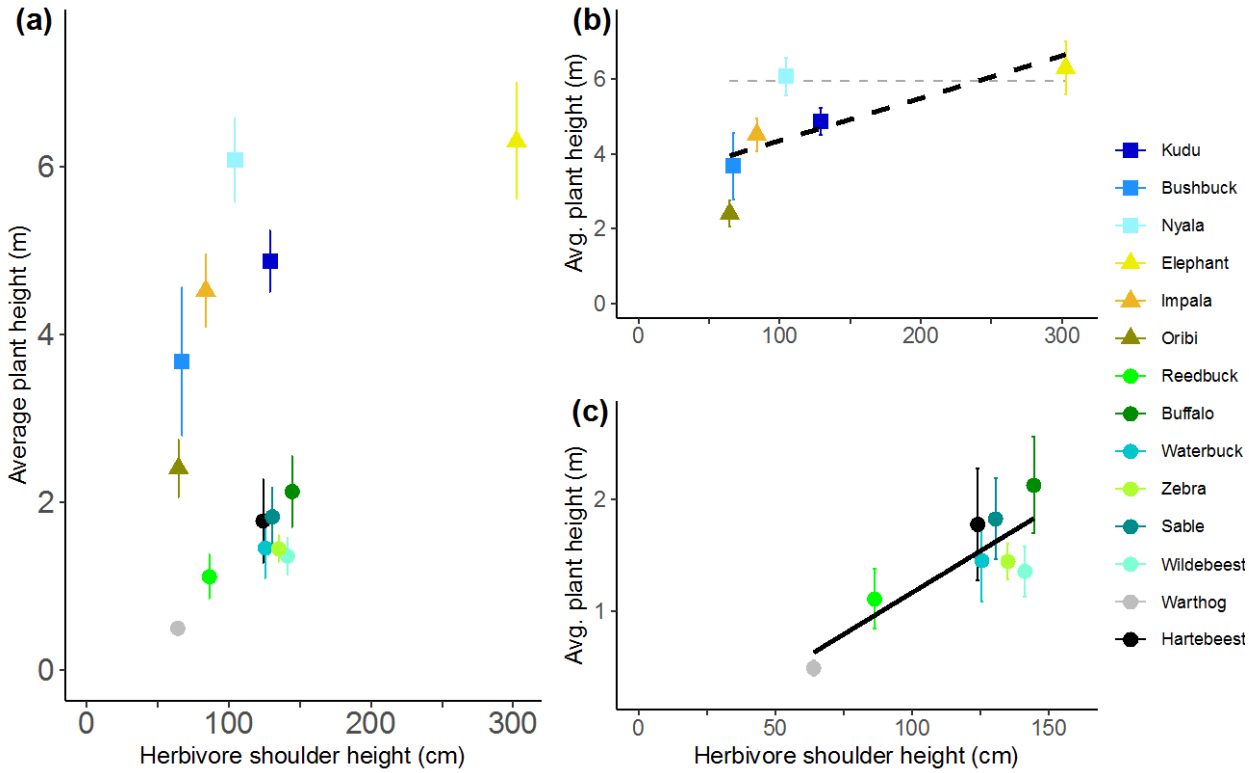

Figure 4:

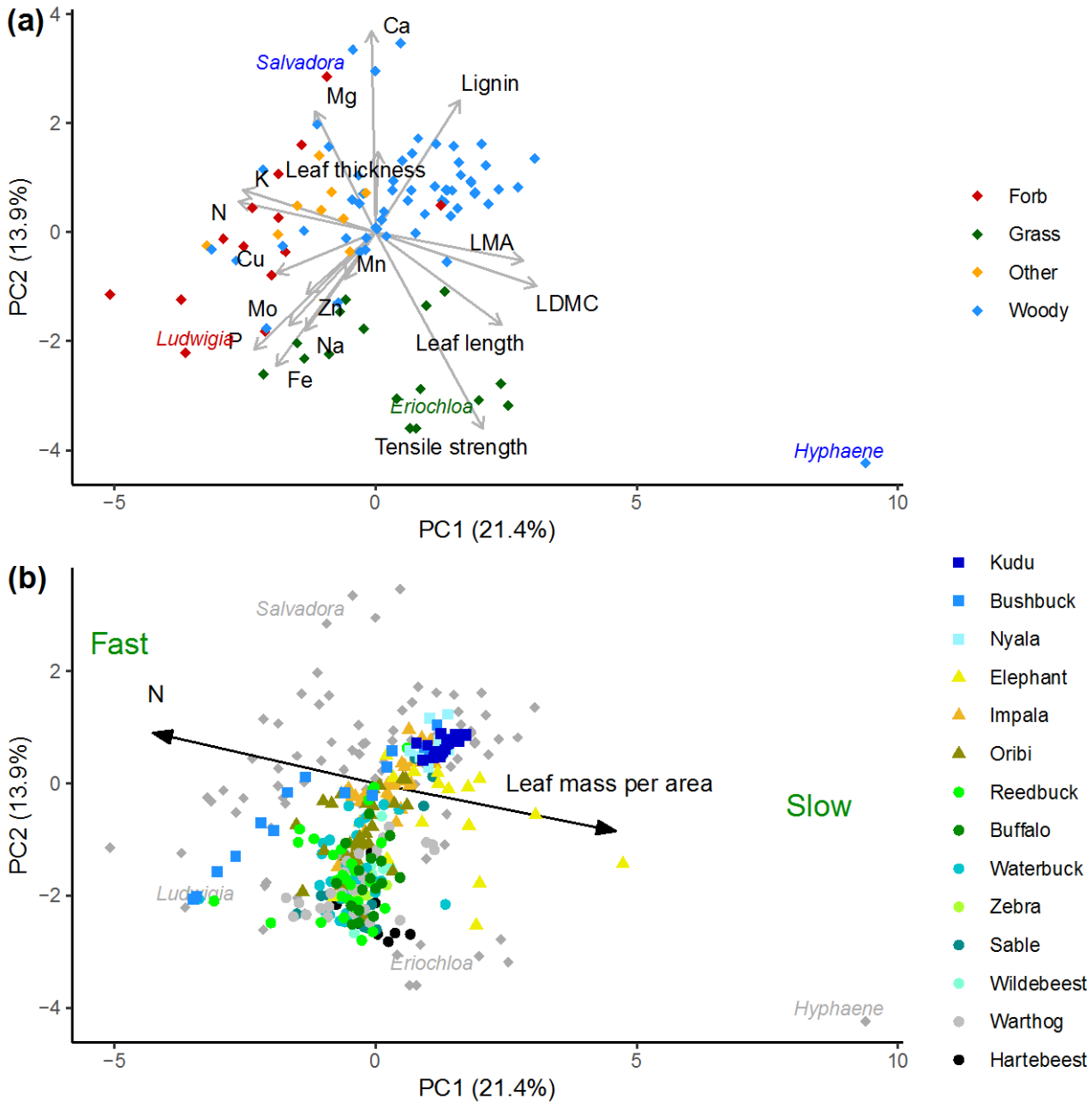

Figure 5: