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Trophic ecology of large herbivores in a reassembling African ecosystem

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SUMMARY

1. Diverse megafauna assemblages have declined or disappeared throughout much of the world, and many efforts are underway to restore them. Understanding the trophic ecology of such reassembling systems is necessary for predicting recovery dynamics, guiding management, and testing general theory. Yet there are few studies of recovering large-mammal communities, and fewer still that have characterized food-web structure with high taxonomic resolution.

2. In Gorongosa National Park, large herbivores have rebounded from near-extirpation following the Mozambican Civil War (1977-1992). However, contemporary community structure differs radically from the pre-war baseline: medium-sized ungulates now outnumber larger-bodied species, and several apex carnivores remain locally extinct.

3. We used DNA metabarcoding to quantify diet composition of Gorongosa's 14 most abundant large-mammal populations. We tested five hypotheses: *(i)* the most abundant populations exhibit greatest individual-level dietary variability; *(ii)* these populations also have the greatest total niche width (dietary diversity); *(iii)* interspecific niche overlap is high, with the diets of less-abundant species nested within those of more-abundant species; *(iv)* partitioning of forage species is stronger in more structurally heterogeneous habitats; and *(v)* selectivity for plant taxa converges within guilds and digestive types, but diverges across them.

4. Abundant (and narrow-mouthed) populations exhibited higher among-individual dietary variation, but not necessarily the greatest dietary diversity. Interspecific dietary overlap was high, especially among grazers and in structurally homogenous habitat, whereas niche separation was more

pronounced among browsers and in heterogeneous habitat. Patterns of selectivity were similar for ruminants—grazers and browsers alike—but differed between ruminants and non-ruminants.

5. *Synthesis.* The structure of this recovering food web was consistent with several hypotheses predicated on competition, habitat complexity, and herbivore traits, but it differed from patterns observed in more-intact assemblages. We propose that intraspecific competition in the fastest-recovering populations has promoted individual variation and a more nested food web, wherein rare species use subsets of foods eaten by abundant species, and that this scenario is reinforced by weak top-down control. Future work should test these conjectures and analyze how the taxonomic dietary niche axis studied here interacts with other mechanisms of diet partitioning to affect community reassembly following wildlife declines.

Keywords: African savannas, community assembly, defaunation, herbivory, individual specialization, intraspecific niche variation, molecular diet analysis, restoration ecology, species coexistence, trophic cascades

SUMMARY IN FRENCH

1. Les communautés de grands mammifères ont décliné, voire disparu, en de nombreux endroits du globe, et d'importants efforts sont actuellement en cours pour les restaurer. Comprendre l'écologie trophique de ces espèces dans les écosystèmes en restauration est nécessaire afin d'anticiper leurs dynamiques de rétablissement, d'orienter leur gestion, et de tester la généralité des théories dérivées de systèmes considérés comme préservés. Néanmoins, les études sur le rétablissement des

communautés de grands mammifères restent rares à ce jour, et peu d'entre elles ont caractérisé, à haute résolution taxonomique, la structure du réseau trophique.

2. Dans le Parc National de Gorongosa (Mozambique), les populations de grands herbivores se sont redressées après avoir été quasiment exterminées suite à la guerre civile (1977-1992). Cependant, la structure actuelle de la communauté diffère radicalement de celle observée avant-guerre : les ongulés de taille moyenne dépassent aujourd'hui en nombre les espèces les plus volumineuses, et de nombreuses espèces de carnivores supérieurs sont toujours localement éteintes.

3. Dans cette étude, une approche de metabarcoding ADN a été employée sur des échantillons fécaux afin de déterminer la composition taxonomique du régime alimentaire des 14 populations de grands mammifères les plus abondantes. Nous avons ainsi testé cinq hypothèses relatives à leur écologie trophique: (i) la variabilité de la niche alimentaire au niveau individuel est plus importante chez les populations les plus abondantes; (ii) ces dernières ont également une niche trophique plus large au niveau populationnel; (iii) le chevauchement des niches entre espèces est important, et les régimes alimentaires des espèces les plus rares sont imbriqués dans ceux des espèces les plus abondantes ; (iv) la ségrégation des niches trophiques est plus importante dans les habitats structurellement plus hétérogènes ; (v) la sélectivité des taxons de plantes par les herbivores tend à converger au sein d'une même guildes alimentaire et entre espèces partageant le même type de système digestif, mais divergent entre ces groupes.

4. Les populations abondantes, et à museau étroit, présentent une variabilité interindividuelle du régime alimentaire plus importante que les autres, mais n'ont pas nécessairement une niche trophique plus large. Le chevauchement des niches trophiques au niveau interspécifique est important, en particulier parmi les pousseurs et dans les habitats structurellement homogènes, alors que la différenciation des niches est plus prononcée chez les brouteurs et dans les habitats hétérogènes. Les différentes espèces de ruminants exhibent des patrons de sélectivité similaires,

indépendamment de leur guildes alimentaire, mais ceux-ci diffèrent entre ruminants et non-ruminants.

5. *Synthèse*. La structure de ce réseau trophique en restauration est cohérente avec plusieurs hypothèses basées sur la compétition, la complexité de l'habitat et les traits des herbivores, mais elle diffère des patrons observés dans les communautés peu ou pas perturbées. Nous proposons ici l'idée que la compétition intraspécifique a favorisé la variabilité interindividuelle du régime alimentaire chez les populations qui se sont rapidement rétablies, et a mené à un réseau trophique plus imbriqué, dans lequel les espèces d'herbivores les plus rares utilisent un sous-ensemble des ressources mangées par les espèces les plus abondantes ; ce scénario étant renforcé par un faible contrôle des populations par les prédateurs. Les travaux à venir devront tester ces conjectures et analyser la manière dont la composante 'taxonomique' de la niche trophique, étudiée ici, interagit avec les autres mécanismes de partition des ressources, et affecte le réassemblage des communautés suite au déclin des populations.

INTRODUCTION

Large mammalian herbivore (LMH) populations have declined throughout much of Africa in recent decades (Craigie et al. 2010; Ripple et al. 2015; Daskin & Pringle 2018), and the rehabilitation of these degraded assemblages has emerged as a central conservation goal (Corlett 2016). Due to their enormous consumption of biomass, LMH exert strong effects on plant architecture, population dynamics, and community structure in savannas, which in turn shapes many ecosystem properties and processes (Sinclair 1975; McNaughton 1985; Owen-Smith 1988; Pringle et al. 2016). The nature and strength of these effects—and how they change when ecosystems are de- or re-faunated—hinge upon food-web structure (Dobson 2009). Consequently, understanding LMH trophic networks is crucial for both basic understanding and effective management of savanna ecosystems (Eby et al. 2014; Burkepile & Parker 2017).

The trophic ecology of LMH has been studied extensively in African savannas, but knowledge is greatest for protected areas with relatively stable histories, such as South Africa's Kruger and Hluhluwe-iMfolozi Parks, Botswana's Chobe National Park, Tanzania's Serengeti ecosystem, and Kenya's Laikipia highlands (e.g., Bell 1971; Sinclair 1985; Codron et al. 2007a; Kleynhans et al. 2011; Owen-Smith, Le Roux & Macandza 2013; du Toit & Olff 2014; O'Shaughnessy, Cain & Owen-Smith 2014; Kartzinel et al. 2015; Owen-Smith, Cromsigt & Arsenault 2017). By contrast, few studies have investigated LMH food webs in communities that are reassembling after severe perturbations (e.g. defaunation, habitat conversion, resource overexploitation). Such perturbations, along with asymmetries in population-recovery rates, can create 'no-analog' scenarios in which species composition and relative abundances differ radically from prior configurations. Recovering systems thus present opportunities both to investigate the factors that regulate community reassembly (which may inform restoration and rewilding efforts) and to test the generality of LMH trophic ecology patterns observed in more intact systems.

LMH assemblages are classically understood to be structured by resource competition and niche separation, yet the dietary niche has multiple dimensions that emerge at different scales (Sinclair 1985; Kleynhans et al. 2011). From coarsest to finest scale, LMH populations may separate in time and space across habitats, in the utilization of plant functional groups (e.g, grasses vs. browse), in the particular suite of plant species consumed, and in the selection of tissues that differ in nutritional quality, chemistry, bite size, or height within plants (Gwynne & Bell 1968; Bell 1971; Jarman 1974; Sinclair 1985; Duncan et al. 1990; Belovsky 1997; du Toit 2003; Shipley 2007; du Toit & Olff 2014; Kartzinel et al. 2015; Owen-Smith, Martin & Yoganand 2015). Interspecific separation at each of these levels has been invoked to explain LMH community structure, but the evidence is murkiest with respect to partitioning at the meso-scale level of plant species (Jarman 1971; Field 1972; Sinclair 1985; Makhabu 2005; Kleynhans et al. 2011; Macandza, Owen-Smith & Cain 2012; Owen-Smith, le Roux, & Macandza 2013; Kartzinel et al. 2015). Theory shows that different-sized herbivores can coexist on a single forage type if they partition plant height (Farnsworth, Focardi, &

Beecham 2002), and African LMH clearly separate according to the proportion of grass vs. browse in the diet (McNaughton & Georgiadis 1986; Codron et al. 2007a). Yet partitioning along these axes does not preclude differences in taxonomic diet composition, nor does it rule out the possibility that such distinctions are important in governing competition and community structure. Historically, the difficulty of identifying food items to genus or species level has been a major obstacle to resolving the taxonomic dimension of trophic niches (Paine 1988). However, molecular methods for diet analysis (Pompanon et al. 2012) now enable trophic interactions to be characterized at the individual, population, and community levels with high coverage and taxonomic resolution (Newmaster et al. 2013; Craine et al. 2015; Kartzinel et al. 2015).

Multiple factors can influence the utilization of different plant taxa by sympatric large-herbivore populations. These include herbivore traits such as body mass, craniofacial anatomy, and gut architecture (Vesey-Fitzgerald 1960; Jarman 1974; Stokke & du Toit 2000; Codron & Clauss 2010; du Toit & Olf 2014); herbivore distribution and vegetation heterogeneity (du Toit 1990, 2003; Cromsigt & Olf 2006); plant species traits such as height, nutritional content, and defenses (Janzen 1979; Cingolani, Posse & Collantes 2005; Arsenault & Owen-Smith 2008; Kleynhans *et al.* 2011); and species interactions such as competition and predation (Sinclair 1985; Ford et al. 2014; du Toit & Olf 2014). Less is known about the degree and determinants of intraspecific variation in LMH diet composition. Within populations of apparently generalist consumers, individuals can be relatively specialized, utilizing narrow and distinct subsets of the population-level diet (Bolnick et al. 2003, 2007, 2011; Codron et al. 2016; Maldonado et al. 2017). Together, the extent of among-individual differentiation and the breadth of individual diets shape the population niche (Van Valen 1965; Roughgarden 1972). Thus, decomposing population-level diets into their individual-level constituents and identifying factors that influence the degree of among-individual variation will enable fuller understanding of how community-level patterns of diet overlap and partitioning emerge (Roughgarden 1972; Bolnick 2011). Yet few studies have simultaneously investigated community-wide patterns of intra- and interspecific diet variation (Bison et al. 2015).

The linkage between individual variation and population niche width suggests that they might share a similar range of ecological determinants. For example, populations that are broadly distributed across a wide diversity of habitats will have greater potential for individual differentiation, because individuals collectively encounter a greater range of food types. Smaller species, and those with narrower muzzles (and thus greater ability to finely select food items: Gordon & Illius 1988; Arsenault & Owen-Smith 2008), might be expected to have high inter-individual diet variation than large-bodied and/or wide-mouthed species (Bell 1970; Jarman 1974). Similarly, solitary species might exhibit greater among-individual variation than herd-forming species that forage synchronously in time and space (Bison et al. 2015). Species interactions likely also play a role. Intraspecific competition is an important structuring force in savanna LMH assemblages (Jarman & Sinclair 1979; Owen-Smith 1982; Sinclair, Dublin & Borner 1985; Fritz & Garine-Wichatitsky 1996; Dunham, Robertson & Grant 2004) and may force individuals to exploit resources not used by conspecifics, expanding population niche (Svanback & Bolnick 2007). Predation pressure can modulate the strength of intraspecific competition, and can also constrain individual variation directly by confining risk-averse herbivores to a subset of safer habitats (le Roux, Kerley & Croomsigt 2018).

The restoration of Mozambique's Gorongosa National Park (**Appendix S1**) provides a unique opportunity to test hypotheses about LMH trophic ecology in a system that is reassembling following severe defaunation (Pringle 2012; Daskin, Stalmans & Pringle 2016; Correia et al. 2017). Intensive hunting during and after the Mozambican civil war (1977-1992) caused >90% declines in all LMH populations for which pre-war data exist (Tinley 1977). Several apex-predator species were extirpated, including leopards, wild dogs, and hyenas; lions persisted, but at greatly reduced abundance (Pringle 2017). Since 2004, total LMH biomass has rebounded to rival pre-war levels, but community structure remains heavily skewed relative to the pre-war baseline due to differences in population-recovery rates (Stalmans & Peel 2016). Mid-sized ungulates have increased most rapidly and supplanted formerly dominant larger-bodied species in abundance and biomass (see Methods;

Appendix S2a).

We used fecal DNA metabarcoding to characterize individual- and population-level diet composition for the 14 most abundant large-mammal species in this reassembling ecosystem. We then tested predictions derived from five general hypotheses about LMH trophic ecology, at nested levels of biological organization from individuals to the landscape. These hypotheses, presented in **Table 1**, were predicated on the following overarching theory. In a community characterized by strong asymmetries in population recovery and weak top-down pressure, the most abundant populations experience strong intraspecific competition, which forces individuals to differentiate their resource use (Hypothesis 1). This individual-level differentiation has population- and community-level ramifications, leading to broader population-level niches in abundant species (Hypothesis 2), and also to greater interspecific dietary overlap, with the diets of rare species nested within those of abundant species (Hypothesis 3). Because the recovering nature of this system should not eliminate the influence of other factors generally thought to influence LMH diets, we further tested for effects of landscape structure (Hypothesis 4) and herbivore species' traits (Hypothesis 5) on patterns of diet composition and selectivity; we likewise incorporated herbivore traits into our analyses of among-individual variation, population niche width, and interspecific niche overlap (Hypotheses 1–3).

METHODS

Study site

Gorongosa is a 4000-km² national park in central Mozambique (18.96° S, 34.36° E). The Great Rift Valley runs through the center of the park, encompassing Lake Urema and its surrounding floodplain, along with *Acacia*, palm, and broadleaf savanna woodlands (Tinley 1977; Stalmans & Beilfuss 2008). The outlying eastern and western escarpments comprise a heterogeneous mix of Miombo woodlands. Our study was conducted within the southern Rift Valley (**Appendix S1a**), which supports

the vast majority of LMH and receives 700–900 mm rainfall annually. The dry season spans May to October; most rainfall occurs between November and February, with up to 60% of the Rift Valley flooding during this period (Tinley 1977; Stalmans & Beilfuss 2008).

The pre-war LMH assemblage was dominated by large-bodied grazers, including buffalo (*Syncerus caffer*), hippo (*Hippopotamus amphibius*), zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), and wildebeest (*Connochaetes taurinus*). Since 2004, the Gorongosa Project has facilitated the recovery of the park's wildlife (Pringle 2017), and mid-sized ungulates have proliferated rapidly. Most strikingly, waterbuck numbers have increased by an order of magnitude relative to the pre-war baseline, with >45,000 individuals accounting for >60% of total LMH biomass in 2016 (Stalmans & Peel 2016). Other now-abundant mid-size ungulates include reedbuck (*Redunca arundinum*, >10,500), warthog (*Phacochoerus africanus*, >5,400) and impala (*Aepyceros melampus*, >4700) (**Appendix S2a**). In contrast, the formerly dominant large-bodied grazers remain at <20% of their pre-war numbers (Stalmans & Peel 2016). Lions (*Panthera leo*), the only apex carnivore that persisted throughout war and recovery, occurred at roughly a third of pre-war abundance at the time of this study (Pringle 2017).

Collection of fecal samples for DNA metabarcoding

We used DNA metabarcoding (Taberlet et al. 2007; Valentini et al. 2009; Taberlet et al. 2012) to characterize herbivore diets by sequencing, identifying, and quantifying plant-DNA fragments in fecal samples (each derived from a single individual, generally reflecting consumption over the preceding 24–72 h: Steuer et al. 2011) (**Appendix S2b**). Although all methods of diet analysis have blind spots, DNA metabarcoding has been shown to outperform multiple alternative methods for producing taxonomically well resolved diet profiles for mammalian herbivores (Soininen et al. 2009; Newmaster et al. 2013). We collected samples across a 540 km² area (~14% of the park) spanning four habitat types, distinguished by vegetation structure and hydrology: (i) Urema floodplain and (ii) seasonally flooded riverine grasslands, both dominated by grasses with small shrubs and almost no

trees; (iii) floodplain-savanna transition, subject to intermittent short-duration flooding, with patches of trees (*Faidherbia albida*, *Vachellia xanthophloea*, *Hyphaene petersiana*) interspersed in an otherwise open understory; and (iv) savanna woodland, infrequently flooded with a diverse overstory (including *Senegalia*, *Vachellia*, *Combretum*, and palm species).

In total, we obtained 338 fresh fecal samples from adult individuals of 20 different mammal species; of these, 311 provided usable results after quality-control filtering, including 293 from the 14 most abundant species (**Table 2**). These 14 species included eight classified by Tinley (1977) as grazers, along with two browsers, three mixed-feeders, and one omnivore (baboon, *Papio cynocephalus*). Although baboons are not conventionally considered LMH, they are an abundant and important component of Gorongosa's plant-animal interaction networks (Correia et al. 2017; Timóteo et al. 2018) and may compete for food with ungulates and elephants. Samples from six additional species—zebra (*Equus quagga*), red duiker (*Cephalophus natalensis*), bushpig (*Potamochoerus larvatus*), vervet monkey (*Chlorocebus pygerythrus*), civet (*Civettictis civetta*), and serval (*Leptailurus serval*)—were excluded from our analyses due to low sample sizes ($n = 2-7$); however, we present descriptive data from these samples in **Appendix S3**. All samples were collected from June–August 2016, the mid-dry season. For each sample, we recorded GPS coordinates and the surrounding habitat type (**Appendix S1a,b**). Sample collection and processing followed protocols described by Kartzinel et al. (2015). Samples were collected in unused plastic bags, immediately placed on ice in a cooler, and processed the same day as follows: we homogenized samples within the collection bag and transferred pea-sized portions into tubes containing silica beads and buffer (Zymo Xpedition™ Stabilization/Lysis Solution, Zymo Research, California USA), which were frozen (-20°C) until transport to the United States and then stored at -80°C. All samples were subjected to a standard antiviral heat treatment (30 min at 72°C) before importation into the United States.

Fecal DNA analyses

DNA was extracted from each sample individually using the Zymo Xpedition™ Soil/Fecal DNA MiniPrep kit, per manufacturer instructions. We included one extraction control per extraction series of 25 samples. Standard PCR methods were used to amplify the P6-loop of the *trnL* intron (Taberlet et al. 2007), a widely used metabarcode marker for vascular plants (Valentini et al. 2009; Taberlet et al. 2012; Kartzinel et al. 2015; Pansu et al. 2015a). We conducted multiple PCR replicates per sample, along with extraction and PCR controls. PCR products were purified using MinElute™ purification kits (Qiagen, Maryland USA). Sequencing libraries were prepared using a PCR-free approach and sequenced on an Illumina HiSeq 2500 (2×150 bp paired-end reads).

Sequence data were curated using the OBITOOLS package (Boyer et al. 2016) to (i) assemble paired-end reads, (ii) assign sequences to their original samples, (iii) remove low-quality sequences and those putatively resulting from amplification/PCR errors, (iv) discard singletons represented only once in the dataset, and (v) assign remaining sequences to plant taxa (**Appendix S2c**). To facilitate taxonomic identification of plant sequences, we built a local DNA reference database from 507 plant specimens, representing 244 species (212 genera, 63 families) and including the most abundant and widespread taxa in the study area (**Appendix S2d**). Taxonomic assignments were made by comparison to this local database, as well as a reference set from the European Molecular Biology Laboratory database (Ficetola et al. 2010). Plant sequences from samples with low similarity (<80% identity) to the closest reference sequence were considered putative contaminants and discarded (Pansu et al. 2015b), as were outlying PCR replicates. Remaining sequences were designated as molecular Operational Taxonomic Units (mOTUs). For each sample, we averaged the number of reads across all retained PCR replicates and removed sequences representing <1% of averaged reads. Full methodological details about PCR amplification and sequencing, processing of DNA-metabarcoding data, and the local reference database are provided in the Supporting Information (**Appendices S2, S4**).

The mOTUs-by-samples matrix was rarefied to 4000 reads per sample (the minimum number of reads per sample was 4605) and converted into proportions to yield relative read abundance (RRA)—the proportional representation of each plant mOTU in each fecal sample. After filtering, the rarefied dataset contained a total of 176 unique plant mOTUs from the 293 fecal samples (**Appendices S3, S4**). RRA is widely used as a semi-quantitative proxy of the proportional biomass of foods eaten (Pompanon et al. 2012; De Barba et al. 2014; Bison et al. 2015; Craine et al. 2015; McClenaghan et al. 2015; Deagle et al. 2018), and this relationship has been validated in studies of LMH using the *trnL* approach, at least for family-level taxonomic groupings (e.g., grasses vs. non-grasses: Willerslev et al. 2014; Kartzinel et al. 2015). Moreover, previous studies using this approach have found that conclusions based on RRA are often qualitatively similar to those based on presence/absence data (Willerslev et al. 2014; Kartzinel et al. 2015; Gebremedhin et al. 2016), but are less sensitive to inclusion of low-abundance reads resulting from incidental ingestion, contamination, or PCR/sequencing errors (Deagle et al. 2018). All analyses presented in the main text were performed on RRA data using the *vegan* package (Oksanen et al. 2017) in R v.3.3.2 (R Core Team 2016); for completeness, we also present corresponding analyses of presence-absence data in the Supporting Information. To assess the spatial distribution of samples and the effect of spatial proximity on diet composition, we evaluated correlations between dietary dissimilarity (Bray-Curtis index) and geographic distance between samples for each species, using Mantel tests with 999 permutations.

Hypothesis testing

Determinants of among-individual variation, V (Hypothesis 1). We quantified among-individual dietary variation using a modified version of Schoener's (1968) proportional-similarity index (PS_i), which estimates the compositional overlap (here, in plant mOTUs) between an individual sample and the population-wide average diet (Bolnick et al. 2002; Bison et al. 2015). Low PS_i values indicate low

overlap and thus high intraspecific variability. We calculated the mean PS_i for each species and measured among-individual variation as $V = 1 - \overline{PS_i}$ (Bolnick et al. 2002, 2007; Araújo et al. 2009). Thus, $V = 0$ indicates that all individuals utilize the same suite of resources, and V approaching 1 indicates greater among-individual variation (Bolnick et al. 2007). We computed V using the *RInSp* package (Zaccarelli, Bolnick & Mancinelli 2013).

We initially used linear regression to assess how V varied as a function of population density, habitat-use diversity, body size, muzzle width, and social-group size. We included only ungulates in this analysis, excluding baboons and elephants because (i) we lacked population-density estimates for baboons, (ii) we quantified only the plant component of baboons' omnivorous diet and thus could not fully estimate among-individual variation, and (iii) both of these species forage using appendages rather than their mouths and thus confound the hypothesized effect of muzzle width (**Table 1**). Population densities for the year of the study were obtained from Stalmans & Peel (2016). We calculated a Shannon index of habitat-use diversity for each species based on the proportion of samples collected within each of the four habitats defined above. Muzzle-width data were obtained from Janis & Ehrhardt (1988), and data on the typical body mass and social-group size for each species across its range were extracted from the PanTHERIA database (Jones et al. 2009).

We then used model selection to identify the best set of predictors for V . To assess collinearity among predictor variables, we used a variance-inflation-factor analysis in the *car* package (Fox & Weisberg 2011), assuming values < 4 to represent an acceptable level of independence (Fox 1991). Body mass and muzzle width were highly correlated ($r = 0.96$, variance inflation factors > 15), making it inappropriate to include both in the same model; all other variables had variance inflation factors ≤ 2 . We retained muzzle width in lieu of body mass because bite size is thought to be the proximate determinant of fine-grain forage selection (Arsenault & Owen-Smith 2008). Our candidate set of models comprised all possible additive combinations of the four retained predictor variables, along with a null intercept-only model. Using the *MuMin* package (Bartoń 2016),

we ranked models based on Akaike's Information Criterion (AIC_c) and calculated Akaike weights (w_i , the likelihood of a model's being the best in the candidate set) and relative variable importance (RVI, the summed w_i for all models containing a given variable) (Anderson 2008).

Population-level total niche width, TNW (Hypothesis 2). We calculated TNW of each population as the Shannon diversity of diet composition (Roughgarden 1972; Bolnick et al. 2007), using the *RInSp* package. TNW accounts for the taxonomic richness and evenness of the population diet, with 0 indicating a diet comprising just one taxon. We repeated the regression and model-selection analyses described above for this variable. To test whether more generalized populations exhibit greater inter-individual variation, we evaluated the correlation between V and TNW across species (Araújo et al. 2009; Bison et al. 2015; Maldonado et al. 2017). Population niche width hinges on the interplay between V and individual dietary richness (**Appendix S5**; Roughgarden 1972; Bolnick et al. 2003); and the V -TNW relationship is used at the intraspecific level to test the niche-variation hypothesis (Van Valen 1965), which holds that expansions in population-level niche width occur via differentiation of individual-level resource use rather than expansion of individuals' niches. In this type of analysis, samples should ideally represent a reasonable approximation of each individual's overall diet through time (Araújo, Bolnick & Layman 2011). If there are substantially fewer items in the sampled diet (e.g., because of limited gut capacity), then V will tend to be overestimated, and this effect becomes more severe as TNW increases (Bolnick et al. 2007). Thus, when individual diets are quantified at a single time point, sampling artifacts can drive positive correlations between V and TNW. For this reason, it is necessary to use null models to test whether the slope of the observed V -TNW relationship is greater than expected based on random subsampling of the population diet (Bolnick et al. 2007). We therefore also regressed TNW against simulated V values, averaged for each species (\pm 95% CI) from 1000 iterations of the null model developed by Bison et al. (2015) for use with proportional diet data derived from DNA metabarcoding. If the V -TNW correlation is more

than just a sampling artifact, then the slope of the observed regression should be steeper than that produced by the null model (Bolnick et al. 2007). To test for a difference between the slopes of the observed and simulated V values against TNW, we used a factorial linear model ($V \sim \text{TNW} \times \text{Data Type}$), where the interaction term signifies whether the slope of $V \sim \text{TNW}$ differs for observed vs. simulated diet data (Bolnick et al. 2007; Bison et al. 2015).

Community- and guild-level patterns of dietary overlap (Hypothesis 3). We calculated the Bray-Curtis index of compositional dissimilarity between each pair of fecal samples (i.e., individual diets) and ordinated these values using non-metric multidimensional scaling (NMDS) to visualize patterns of dietary dissimilarity (both within and among species) in two dimensions (Borcard, Gillet & Legendre 2011; Kartzinel et al. 2015). We did this first for the whole community, and then separately for grazers and non-grazers (per **Table 2**). We analyzed dietary differences among species using permutational analysis of variance (perMANOVA) in the *vegan* package (Oksanen et al. 2017). As descriptive measures of interspecific dietary dissimilarity and overlap, we present both (i) the mean of the pairwise Bray-Curtis distances between individual samples for each species pair and (ii) the complementary niche-overlap index of Pianka (1973), based on the average diet for each species (i.e., the mean proportion of each mOTU across all samples from the population). Pianka's index, calculated using the *EcoSimR* package (Gotelli, Hart & Ellison 2015), is a symmetric pairwise measure of niche overlap that ranges from 0 (no overlap) to 1 (identical diets) (see also Arsenault & Owen-Smith 2008; de longh et al. 2011; Kleyhans et al. 2011). Statistical significance of the Pianka index for each species pair was evaluated with reference to 1000 iterations of a null model in which diet items for each species were drawn randomly and independently of one another while maintaining the observed total dietary species richness (Gotelli, Hart & Ellison 2015).

Landscape-level correlates of interspecific dietary overlap (Hypothesis 4). To validate our *a priori* assumption that savanna-woodland is more structurally heterogeneous than floodplain-grassland, we quantified the proportional woody cover within a 100-m radius around each fecal-sample location (0.39 ± 0.02 in savanna; 0.06 ± 0.01 in floodplain). This analysis was based on a supervised classification of woody vs. herbaceous vegetation cover (accuracy, 87%; sensitivity to woody cover, 79%; specificity, 92%) in high-resolution 2010 satellite imagery (WorldView-2, Digital Globe, Longmont, CO, USA) using ArcMap 10.4.1 (ESRI, Redlands, CA, USA). We then compared patterns of resource overlap among samples collected from floodplain and savanna. Because inferred dietary overlap is likely to be affected by the number and identity of species included in the analysis (irrespective of habitat attributes), we restricted this comparison to the seven species that routinely occur in both habitats ($n = 56$ and 59 in savanna and floodplain, respectively). We calculated the average diet for each species in each habitat and analyzed mean interspecific dietary dissimilarity/overlap between each species pair using the Pianka and Bray-Curtis indices, as described above.

Dietary utilization and selection relative to environmental availability (Hypothesis 5). We analyzed selectivity for the seven floodplain species—waterbuck, reedbuck, and oribi (all ruminant grazers), impala (ruminant mixed-feeder), bushbuck (ruminant browser), warthog (non-ruminant grazer), and baboon (omnivore)—using Jacobs' (1974) *D* index, which measures utilization of plant taxa relative to their availability. This index ranges from -1 to 1 , with negative values indicating avoidance (low consumption relative to availability), positive values indicating selection (high consumption relative to availability), and values ≈ 0 indicating utilization in proportion to availability. To improve taxonomic resolution in this analysis, we reran the taxonomic assignment of plant mOTUs, this time restricting the DNA reference library to plant species known to occur on the floodplain. Floodplain vegetation surveys were conducted in August 2016 (coinciding with fecal-sample collection) within 18 one-hectare plots (six along each of three parallel 3-km transects stretching from Lake Urema to the

floodplain-savanna boundary). Within each plot, we randomly placed fifteen 1-m² quadrats and estimated the areal cover of each plant species using the Braun-Blanquet (1932) method, which bins each species according to its percent cover (1 = <5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–95%; 6 = 96–100%; see also Westhoff & Van Der Maarel 1978). These bins were converted into relative-abundance estimates using the median value of each bin (2.5, 15, 37.5, 62.5, 85, 98). Relative abundances of each species were averaged within, and then among, plots to estimate overall availability of each potential food taxon. For the 14 most common plant taxa (those representing at least 1% of total cover and collectively accounting for > 96% of cover), we calculated *D* using the mean RRA of each taxon in each LMH species' diet (Soininen et al. 2013).

For preliminary insight into how herbivore selectivity might reflect variation in plant nutritional quality, we measured the crude-protein content of five common floodplain plants representing each major life-form: the two most abundant grasses (*Cynodon dactylon* and *Digitaria swazilandensis*), the most abundant forbs (*Heliotropium indicum* and *H. ovalifolium*) and the lone woody shrub (*Mimosa pigra*). These measurements are part of a more comprehensive plant-traits dataset that is still under development. For each species, > 5 g of young leaves from ≥ 3 different individuals were collected, pooled together, and oven-dried at 60°C. Nitrogen concentration was determined via combustion by Dairy One Cooperative, Inc. (Ithaca, New York, USA), and crude-protein content was estimated as 6.25×N.

RESULTS

Overview of LMH diet composition

The mean relative read abundance (RRA) of plant families in each species' diet was broadly consistent with Tinley's (1977) pre-war guild categorization of Gorongosa LMH (**Table 2**), but also encompassed considerable within-guild variability. Grass was dominant in the diets of most putative

grazers, with 31 Poaceae mOTUs accounting for $\geq 50\%$ RRA in all but two species, oribi (42%, vs. 50% Fabaceae) and buffalo (34%, vs. 44% Malvaceae) (**Table 2; Appendices S3, S6**). Fabaceae was the second-most-consumed family, on average, across all grazers (16–50% of RRA for buffalo, waterbuck, reedbuck, and oribi; $\leq 3\%$ for all others). Mean grass RRA was 10–20% for mixed-feeders (impala, nyala, elephant) and $<0.1\%$ for browsers (bushbuck, kudu). The most abundant families in the diets of these five non-grazers were Fabaceae (45 mOTUs, 27%–49% RRA, except for kudu, 4%); Rhamnaceae (7 mOTUs, 9%–23% RRA); Annonaceae (1 mOTU, *Cleistochlamys kirkii*, 50% RRA for kudu, 1–6% for all others); Ebenaceae (2 mOTUs, 9–13% RRA for nyala and bushbuck, $<2\%$ all others); Malvaceae (10 mOTUs, 1–12% RRA); and Sapindaceae (2 mOTUs, 2–6% RRA) (**Appendices S3, S6**). The plant component of baboon diets comprised substantial quantities of Fabaceae (28%), Malvaceae (24%), Moraceae (13%), and Arecaceae (12%).

Intraspecific dietary dissimilarity increased significantly with distance between samples for all species (Mantel tests, $r = 0.15\text{--}0.89$, $P < 0.03$ for all species; **Appendix S1c**). Waterbuck and elephant samples were the most widely and evenly distributed across the study area, and their composition was relatively weakly correlated with geographic distance ($r = 0.15\text{--}0.28$); wildebeest, buffalo, and hartebeest samples had a more spatially discrete distribution and exhibited stronger correlations with distance ($r = 0.60\text{--}0.89$; **Appendix S1c**).

Individual dietary richness was greatest for the three mixed-feeders (9.8–10.8 mOTUs sample⁻¹) and two large grazers (buffalo and hartebeest, 9.5 mOTUs sample⁻¹) and least for the abundant mid-size grazers (warthog, oribi, reedbuck, waterbuck, 4.9–6.8 mOTUs sample⁻¹) (**Table 2**). The mixed-feeders also had the largest population niche widths (TNW = 3.11–3.14), followed by waterbuck and bushbuck; wildebeest and kudu had the lowest population niche widths (**Table 2**).

Determinants of among-individual variation, V (Hypothesis 1)

The greatest among-individual dietary variability was observed in two of the most abundant species, waterbuck ($V = 0.74$) and impala ($V = 0.72$), whereas the lowest V values occurred in species at the bottom of the population-density spectrum: buffalo (0.43), kudu (0.45), wildebeest (0.48), hartebeest (0.46), and sable (0.49) (**Fig. 1**). The top model for V , which was by far the best in the candidate set ($w_i = 0.67$; $r^2 = 0.69$, $F_{2,9} = 13.25$, $P = 0.002$), included two predictors: a positive effect of population density (RVI = 0.81; $t_9 = 3.16$, $P = 0.01$) and a negative effect of muzzle width (RVI = 0.95; $t_9 = -3.92$, $P < 0.004$) (**Appendix S7a**). These factors were also correlated with V in univariate regressions (albeit marginally for population density) (**Fig. 1a,b**). The remaining two variables had limited explanatory power: habitat-use diversity (RVI = 0.17) was positively but non-significantly correlated with V in univariate regression (**Fig. 1c**), while sociality (RVI = 0.06) exhibited no univariate correlation with V (**Fig. 1d**). Full model-selection results are given in **Appendix S7a**.

Population-level total niche width, TNW (Hypothesis 2)

TNW was strongly and positively correlated with both observed and simulated V values (**Fig. 2a**); however, the slopes of these relationships were identical (0.17; TNW \times Data Type interaction $t_{22} = 0.05$, $P = 0.96$). Observed V values were systematically higher than those produced by the null model (**Fig 2a**). Contrary to expectation, the factors that predicted V (population density and muzzle width) were not significantly correlated with TNW (**Fig. 2b-e**), and no combination of predictor variables had substantial explanatory power (the top model included only an intercept: **Appendix S7b**). The greatest population niche widths were instead observed in the three moderately abundant mixed-feeders, which also had the highest mean individual-level dietary species richness, while grazer and browser species were interspersed across the remainder of the TNW spectrum (**Table 2, Appendix S5**).

Community- and guild-level patterns of dietary overlap (Hypothesis 3)

As hypothesized, the Gorongosa LMH community exhibited a high degree of interspecific overlap in the RRA of plant taxa utilized (**Fig. 3a–c; Appendix S8a–c**). Diet composition differed significantly across feeding guilds, although this separation manifested as a gradient in ordination space, rather than as discrete clusters, reflecting considerable cross-guild overlap.

Within guilds, we found especially high dietary overlap among the grazers (**Fig. 3d; Appendix S8d**). The most abundant species—waterbuck, reedbuck, warthog, oribi—accounted for much of this overlap, and the minimum convex polygon for waterbuck encompassed nearly all other grazer samples in the NMDS ordination (**Fig. 3d**). This pattern persisted when we employed a re-sampling procedure to homogenize the number of samples per species. These results are consistent with the greater among-individual differentiation observed in abundant grazers (**Fig. 1a**), which produces greater spread in two-dimensional niche space, and they are corroborated by the pairwise Pianka niche-overlap index (**Table 3; Appendix S9**). The mean of the pairwise Pianka indices across all grazers was 0.44 ± 0.05 SE. Overlap was statistically significant between waterbuck and all other grazers except buffalo, and was particularly high among waterbuck, reedbuck, and oribi (mean 0.89 ± 0.02 SE). Warthog, sable, wildebeest, and hartebeest formed another cluster in which all pairwise niche-overlap values were significant (mean 0.60 ± 0.05 SE). In contrast to grazers, mixed-feeders and browsers showed greater niche separation (**Fig. 3e**). The overall mean of the pairwise Pianka indices for non-grazers was 0.28 ± 0.05 SE, with values < 0.5 for all species pairs except impala–bushbuck (0.82) (**Table 3**). Although overlap was generally low between grazers and non-grazers (mean 0.15 ± 0.3 SE), the five most abundant antelope species were an exception: the grazers waterbuck, reedbuck, and oribi each overlapped significantly with both impala (a mixed-feeder) and bushbuck (a browser).

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These results based on the Pianka niche-overlap index were highly correlated with mean Bray-Curtis dissimilarity values ($r = -0.85$, $F_{1,89} = 250.6$, $P < 0.0001$). Likewise, results based on presence-absence data (**Appendices S8-S10**) were broadly consistent with our primary analyses based on RRA (**Table 3, Figs. 3, 4**).

Landscape-level correlates of interspecific dietary overlap (Hypothesis 4)

As hypothesized, dietary niche overlap was high in structurally homogeneous floodplain-grassland (mean of the pairwise Pianka indices 0.48 ± 0.08 SE), whereas niche segregation was greater in heterogeneous savanna (0.25 ± 0.05 SE; $t_{34.5} = 2.54$, $P = 0.02$; **Fig. 4; Appendix S10**). The NMDS plot for the floodplain (**Fig. 4a**) broadly recapitulated that for grazer guild at large (cf. **Fig. 3d**), with the minimum convex polygon for waterbuck encompassing nearly all other samples irrespective of guild (warthog being the lone exception). By contrast, species separated by guild in savanna (**Fig. 4b**), and waterbuck dominated a smaller fraction of grazer niche space.

Dietary utilization and selection relative to environmental availability (Hypothesis 5)

Among floodplain plant taxa, the grass *Cynodon dactylon* was by far the most abundant (42.8%), followed by forbs of the Boraginaceae, Asteraceae, and Euphorbiaceae, and two other grass taxa (*Digitaria swazilandensis*, *Echinochloa* spp.) (**Fig. 5a**). Patterns of utilization (**Fig. 5b**) and selection relative to availability (**Fig. 5c**) exhibited similarities across all seven floodplain LMH species, irrespective of feeding guild and digestive type. However, there were several exceptions to this broad trend. The most heavily consumed and selected plant overall was the leguminous shrub *Mimosa pigra*, which accounted for <3% cover but 35–74% of dietary RRA for all five ruminant species across the grazer-browser spectrum; only warthog avoided it. *Cynodon* was rare in all antelope diets and selected only by warthog (47.3% RRA). The most heavily consumed grass, *D.*

swazilandensis (4% cover), was strongly selected by all grazers, weakly avoided by impala (mixed-feeder), and strongly avoided by bushbuck (browser) and baboon. Grazers differed in their selectivity for *Echinochloa* spp., with waterbuck and warthog selecting it and reedbuck and oribi avoiding it. Baboons selected a lumped asteraceous taxon (*Vernonia-Ambrosia*) that was avoided by all ungulates, and disproportionately selected the malvaceous forb *Abutilon* spp. The forbs *Corchorus fascicularis*, *Glinus lotoides*, *Tephrosia* spp., *Sida* sp., and *Heliotropium* spp. (here comprising two lumped species, *H. ovalifolium* and *H. indicum*) were lightly utilized and universally avoided by all herbivores.

The crude-protein content of *M. pigra* (26.0%) was the second-highest among floodplain plants for which we currently have data), perhaps explaining why grazers and browsers alike selected it. The universally avoided dominant forb taxon, *Heliotropium* spp., had similarly high protein content (33.4% for *H. indicum*, 19.6% for *H. ovalifolium*), but this genus is associated with high concentrations of hepatotoxic pyrrolizidine alkaloids. Among grasses, *D. swazilandensis* had slightly higher crude-protein content than *C. dactylon* (18.7% vs. 15.5%).

DISCUSSION

We assembled a comprehensive and high-resolution account of a diverse LMH-plant food web, enabled by the power of DNA-based methods to characterize the taxonomic diet composition of generalist consumers that are difficult to observe at close range. Our results were consistent with several predictions of the five general hypotheses that guided the research (**Table 1**), but inconsistent with others (and in some cases with conventional wisdom about LMH foraging preferences). Because our study represents one of the first detailed analyses of consumer-resource interactions in a community that is recovering from near-extirpation, we are able to identify patterns

that diverge from those observed in more intact systems and suggest approaches to test their generality and mechanistic basis. Below, we discuss our results in the context of each hypothesis in turn and outline a series of next steps for future research.

Individual variation was greatest in abundant, narrow-muzzled species (Hypothesis 1)

The combination of population density and muzzle width explained 69% of the variance in V . Although this has not to our knowledge previously been documented for LMH communities, the effects of both variables are consistent with theoretical expectations. Increasing population density should generally intensify intraspecific competition, which can in turn increase V by forcing individuals to exploit resources that are less utilized by conspecifics (Svanbäck & Bolnick 2005, 2007; Araújo, Bolnick & Leyman 2011). Such a pattern is expected if individuals have shared forage preferences but are capable of diversifying onto different resource types as preferred ones become scarce (Svanbäck & Bolnick 2005, 2007; Jones & Post 2016)—for example, by expanding into novel habitats that support different resource assemblages (Mobæk et al. 2009; Soininen et al. 2014). Waterbuck, which had the highest V , population density, and habitat-use diversity of any species, provide the strongest case in support of this interpretation. Historically, Gorongosa's waterbuck were confined to floodplain and riverine habitats (Tinley 1977); during the post-war exponential growth in waterbuck numbers, however, the proportion of individuals occupying wooded areas has steadily increased (Stalmans & Peel 2016). More generally, **Appendix S1c** shows that diet dissimilarity increased with distance between samples (a rough proxy for species' distributions), such that more widely distributed species encompass a wider range of between-sample differentiation. Species with greater V also tended to have higher habitat-use diversity, although this correlation was weakened by the outlying high V and low habitat-diversity values for nyala (**Fig. 1c**; $r = 0.48$, $P = 0.11$ with nyala; $r = 0.78$, $P < 0.005$ without). Nyala are mixed-feeders that, in Gorongosa, occur within a band of habitat comprising several savanna and sand-forest vegetation types (**Appendix S1**), all of

which classified as 'savanna' in our study; it is possible that a more nuanced habitat classification would have bolstered the community-wide correlation between V and habitat-use diversity.

The other predictor in the best-fitting model of V , muzzle width, is also consistent with general expectations. Narrow-mouthed species are able to discriminate among foods at a finer spatial grain than wide-mouthed species, and can therefore be more selective (Jarman 1974; Gordon & Illius 1988; Janis & Ehrhardt 1988; Arsenault & Owen-Smith 2008). This argument has been invoked to explain the selection of high-quality plant parts (new shoots, fruits), and our data indicate that it can also apply to the selection of particular plant taxa growing within multispecies clumps. In contrast, wide-mouthed species take larger bites, ingesting more homogeneously across the plant taxa available at a particular location, and therefore have less capacity for individual-level differentiation. One caveat to this interpretation is that muzzle width was so highly correlated with body mass as to make them statistically indistinguishable ($r = 0.96$), and other physiological mechanisms are thought to link body size with diet selection (Bell 1970; Jarman 1974; Owen-Smith 1988). For example, smaller species have higher mass-specific metabolic rates and should therefore be more selective for higher-quality food, whereas larger species require greater total forage biomass for maintenance and cannot afford to be as selective. This might promote a negative correlation between V and body size if there are a limited number of forage types with sufficient biomass to meet the requirements of the largest-bodied herbivores. However, equally enticing logic suggests an opposing intuition: populations of larger species should encompass a larger range of body sizes (even among the adults sampled in this study) and hence perhaps greater among-individual variation. Given the importance of bite size in forage selection by ungulates (Gordon & Illius 1988; Arsenault & Owen-Smith 2008), we consider muzzle width to be a more likely proximate determinant of V than body size *per se*, but these possibilities are not mutually exclusive and further work will be required to tease them apart.

The lack of support for social-group size as a determinant of V echoes the findings of a recent study on Alpine ungulates (Bison et al. 2015). We note that there can be considerable intraspecific variation in this trait, as well as in other traits that might structure intraspecific dietary variation in LMH assemblages (see Clutton-Brock, Iason & Guinness 1987; du Toit et al. 2005; Bolnick et al. 2011), which is not reflected in the global species-level values that we used. For instance, sex-linked differences in size and reproductive condition may influence individual diets and hence population V (Clutton-Brock, Iason & Guinness 1987). We did not explore these possibilities here because our sample sizes for individuals of known sex were insufficient for most species, and because system-specific data on traits and intraspecific variation are not yet available. Future work should explicitly investigate the roles of sex, age, size, condition, social status, and other axes of intraspecific trait variation in governing V .

No clear evidence for greater individual variation in generalized species (Hypothesis 2)

The slope of the positive correlation between V and TNW did not differ from that of a null model in which individual diets were drawn randomly from the population-level diet (**Fig. 2a**). Thus, we cannot exclude the possibility that the observed correlation was a sampling artifact, nor conclude that dietary generalists exhibit greater individual variation than specialists. Support for this idea has been mixed in the literature. Bison et al. (2015) found support for it in alpine ungulates using a DNA-metabarcoding dataset similar to ours, as did Maldonado et al. (2017) using $\delta^{15}\text{N}$ in passerine birds. Araújo et al. (2009) and Cachera et al. (2017), in studies of Brazilian frogs and marine fish, respectively, found as we did that observed positive V -TNW correlations were no steeper than the null expectations. The equivocal support for this idea across taxa suggests the need for more mechanistic approaches.

All of these studies, including ours, found greater V than predicted by null models. In general, high V is expected when there is ample ecological opportunity—‘empty’ or incompletely filled niche space offering a diversity of available resources (Van Valen 1965; Araújo et al. 2009). This has been the case in post-war Gorongosa. The largest-bodied LMH species remain at fractions of their prior abundances, several species of large grazer (roan, tsessebe, white rhinoceros) and browser (black rhinoceros) known from 19th-century records are locally extinct, and three large carnivores present in 1972 have yet to recover. All of these factors have likely contributed to ecological release of the remaining mid-sized ungulate species. However, another possible explanation for the high V observed in studies based on temporal snapshots of individual diets relates to spatial heterogeneity in resource availability. Null models that sample randomly from population-level diets implicitly assume that all individuals have access to the entire suite of resources used by the population (Araújo, Bolnick & Layman 2011). In most natural settings, however, individuals are distributed throughout heterogeneous environments, and their stomach contents at any given time will reflect the resource types available in the patch they occupy, which will promote greater variation among samples than if all individuals could exploit all resources simultaneously. Yet, if individuals move between patches through time, their overall niche breadths through time will be broader and likely more overlapping—and V will be lower—than can be inferred from a temporally static series of fecal samples. Stable-isotope approaches, which integrate diet over longer time periods, will be less susceptible to this issue, but cannot resolve the identity of forage taxa. We therefore recommend that future metabarcoding studies strive to characterize diets of known individuals using repeated fecal sampling through time.

Although V was strongly correlated with TNW, the strongest population-level predictors of V —population density and muzzle width—had negligible explanatory power for TNW, either singly or in combination (**Fig. 2b,c, Appendix S7b**). The three mixed-feeders had the greatest population niche widths, and these were also the species with the greatest individual dietary richness (**Table 2; Appendix S5**). The lack of concordance in the predictors of V and TNW can arise because TNW

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depends on both among-individual variation and individual niche breadth (Roughgarden 1972); in our data, these components explained 92% of the variance in TNW together, but only 21–44% individually, and their relative contribution to TNW varied among populations (**Appendix S5**; see also Bolnick et al. 2003; Jones & Post 2016). Our results are consistent with the idea that mixed-feeders have wider fundamental niches (comprising both grasses and non-grasses) but are less able to specialize on subsets of resources within these types (and hence differ less among individuals). In this way, functional trade-offs in foraging abilities could dampen the community-wide correlation between V and TNW by modulating the relative contributions of individual variation and individual niche breadth to population niche width.

Interspecific niche overlap was high, especially among grazers (Hypothesis 3)

As predicted, Gorongosa's recovering large-herbivore assemblage exhibited pronounced interspecific overlap in the suite of plant species consumed—especially within guilds, but in some cases also across them. Waterbuck in particular, and to a lesser extent other abundant grazers, exhibited high dietary niche overlap with other grazers (**Table 3, Fig. 3d**). In addition, the most abundant mixed-feeder, impala, overlapped significantly with the most abundant grazer and browser species (**Table 3**). The waterbuck and impala populations both increased considerably over the two years preceding our study (**Appendix S2a**), and they had among the highest habitat-use diversity scores (**Fig. 1c, Appendix S1b**), perhaps contributing to the surprising degree of cross-guild overlap. In general, niche overlap was weaker among the non-grazers, although these species were also fewer and less abundant, making it difficult to isolate the relative effects of population density and feeding guild.

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These results are consistent with the interpretation that intraspecific competition among abundant species leads to greater individual variation in these species, and hence to a community in which interspecific dietary overlap is high and the niches of rare species are nested within those of abundant ones. They further suggest that waterbuck, reedbuck, warthog, impala, and oribi—which have recovered most rapidly and become numerically dominant—may be competing for resources with less-abundant grazers such as wildebeest and hartebeest, perhaps impeding their recovery. Cross-species overlap in the use of forage taxa, such as documented here, indicates the potential for interspecific competition, but not its strength or even its existence. Herbivores can ameliorate competition by using different parts of the same plant species, or via fine-grained spatiotemporal partitioning (Farnsworth, Focardi & Beecham 2002); these mechanisms are even thought to generate facilitative interactions in LMH assemblages under some conditions (Bell 1971). However, recent work has concluded that interspecific competition is the prevailing force when resources are limiting (du Toit & Olff 2014). Along these lines, herbivore exclosures erected in the Gorongosa floodplain as part of a different study provide evidence that palatable forage becomes severely depleted during the dry season (**Appendix S11**). The aforementioned post-war expansion of waterbuck out of the floodplain and into savanna (Stalmans & Peel 2016) may be a response to resource limitation in the floodplain. And the depleted predator guild of Gorongosa may exacerbate this scenario by relaxing top-down control of mid-sized ungulates (which are generally predator-limited; Sinclair, Mduma & Brashares 2003) and by dissipating the landscape of fear (which constrains antelope foraging behavior; Ford et al. 2014), allowing species to occupy habitats that would otherwise be prohibitively risky.

Despite an immense amount of research on the diet, nutrition, and coexistence mechanisms of ungulates, the generality of dietary niche partitioning at the level of plant species in LMH guilds remains unclear. In principle, LMH species should differ in the taxonomic composition of their diets for the same reasons that they diverge in their selectivity/acceptance of plant tissues with higher or lower nutritional quality (Jarman 1974), along with factors such as differential tolerance of plant

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defenses and secondary metabolites (Owen-Smith & Cooper 1987). And indeed, most studies that have achieved fine-grained taxonomic resolution of diet composition have reported differential within-guild utilization of forage taxa during at least some seasons (Lamprey 1963; Hansen, Muganbi & Bauni 1985; Owen-Smith & Cooper 1987; Prins et al. 2006; Arsenault & Owen-Smith 2011; Kleynhans et al. 2011; Macandza, Owen-Smith & Cain 2012; Owen-Smith, Le Roux & Macandza 2013). Other studies, however, have emphasized high within-guild similarity in forage species utilized (Sinclair 1985; de longh et al. 2011; O’Shaughnessy et al. 2014). Because different investigators have quantified diets in different ways, direct quantitative comparisons across studies are unlikely to be informative. For example, Kleynhans et al. (2011) found, as we did, that buffalo exhibited the lowest average pairwise dietary overlap with other grazers, with a mean Pianka overlap index of 0.38 in dry-season contrasts between warthog, wildebeest, and impala; however, these authors analyzed only the grass component of diets. In our study, the mean of the same three pairwise contrasts was 0.15—in part because grasses contributed only 10–34% of the estimated diets of impala and buffalo, compared with 95–97% for wildebeest and warthog (**Table 2**). Which of these communities exhibited greater overall interspecific dietary overlap cannot be inferred. DNA metabarcoding using the *trnL* approach represents a promising standardized path towards understanding the extent and generality of species-level diet partitioning/overlap in LMH communities. To date, however, there are few available studies for comparison. Our conclusion that interspecific dietary niche overlap is ‘high’ in this system is based on qualitative comparison with a prior study that used the same metabarcoding approach for seven LMH species in Kenya (Kartzinel et al. 2015), which found high interspecific dissimilarity in diet composition—even between congeneric grazers (plains and Grevy’s zebras, *Equus quagga* and *E. grevyi*). That system differs from Gorongosa in being historically intact and having a complete large-carnivore assemblage.

We hypothesize that interspecific dietary niche overlap is anomalously high in post-war Gorongosa for two inter-related reasons. First, the asymmetric recovery rates of different LMH populations have enabled the most abundant species to expand into dietary niche space ordinarily

occupied by heterospecific competitors; and second, the absence of several top-carnivore species has enabled these abundant populations to expand into habitats where they would not otherwise occur. We plan to test this hypothesis in two ways. First, we are assembling a multi-site comparative diet dataset, using standardized metabarcoding methods, from savanna LMH assemblages across Africa; this will enable us to determine whether strong interspecific segregation in plant-species utilization is indeed the norm in intact assemblages, and whether certain community properties tend to be associated with stronger or weaker partitioning (e.g., numerical dominance of one or a few species, as with waterbuck in Gorongosa). Second, longer-term dietary monitoring in Gorongosa will reveal whether the patterns documented here persist as the community continues to recover. Wild dogs were reintroduced to Gorongosa in 2018, and leopard reintroductions are planned (Pringle 2017, Angier 2018), which should enable a test of whether the return of top carnivores shrinks the dietary niches of mid-sized ungulate populations.

Niche overlap was greater in structurally homogeneous habitat (Hypothesis 4)

We found greater interspecific niche overlap in floodplain-grassland than in nearby savanna. The floodplain comprises a stratum of grasses, forbs, and subshrubs that is generally < 50-cm tall, such that the vast majority of primary production is accessible to even the smallest LMH (oribi, warthog). In savanna, by contrast, greater heterogeneity in vegetation structure creates resources that are exclusively available to taller species such as waterbuck and climbers such as baboon (du Toit & Olf 2014). Thus, our results are consistent with the hypothesis that structural habitat heterogeneity promotes separation in the taxonomic composition of LMH diets (see also Jarman 1974; du Toit 2003; du Toit & Olf 2014). However, we cannot rule out one plausible (and not mutually exclusive) explanation for this result—that greater plant species diversity in savanna creates a larger total niche space to partition. Testing this possibility would require comparable data on the alpha and beta diversity of plants in both habitats.

Similar patterns of selectivity across floodplain grazers, especially antelopes (Hypothesis 5)

We found mixed support for our prediction that patterns of selectivity would be similar for ruminant grazers and diverge as a function of feeding guild (grazers vs. non-grazers) and digestive system (ruminant versus non-ruminant). Broad similarities in selectivity were evident across all seven floodplain LMH species. Although no plant taxon was universally selected, six of the most abundant 14 taxa were universally avoided. Moreover, the most heavily selected plant species overall—the woody legume *M. pigra*—was strongly selected by all five antelope species, grazers and non-grazers alike. The grass *D. swazilandensis* was the only plant taxon that conformed to expectations based on conventional LMH feeding guilds, being selected by all grazers and avoided by mixed-feeders, browsers, and baboons.

The lawn-forming grass *C. dactylon* was lightly utilized (**Fig. 5b**) and strongly avoided relative to its availability (**Fig. 5c**) by all antelopes. It was heavily consumed and selected only by warthog (a non-ruminant), comprising roughly half of estimated diet; this preference has been observed elsewhere and attributed to *C. dactylon*'s short growth form and underground rhizomes, which warthogs are able to excavate (Roodt 2015). However, *C. dactylon* is widely considered to be highly palatable, nutritious, and selected by grazers of all types throughout Africa (Grzimek & Grzimek 1960; Lamprey 1963; Dougall & Glover 1964; Stewart & Stewart 1970; Sinclair 1977); Tinley (1977) found it to be the most frequently grazed plant overall in pre-war Gorongosa. One potential explanation for our results relates to the continued scarcity of large-bodied and/or herd-forming grazers—hippo, buffalo, zebra, wildebeest—that formerly dominated the Urema floodplain. *Cynodon* is most palatable and intensely grazed when kept short and fertilized (McNaughton 1984), and it can accumulate toxic hydrocyanic acid when it wilts (Roodt 2015). It is therefore possible that the largest herbivores maintained *Cynodon* lawns in a state more palatable to other grazers by removing rank growth and stimulating production of new shoots.

Differences in nutritional quality might help to explain some of the variation in selectivity for different plant species: the most heavily selected species, *M. pigra*, was high in protein, and *D. swazilandensis* was more protein-rich than *C. dactylon*. It is clear, however, that protein content is not the only factor governing selectivity, because the dominant forb taxon, *Heliotropium* spp., had high crude protein but was universally avoided. This genus produces hepatotoxic pyrrolizidine alkaloids, which cause severe liver damage and can be lethal to adults of a variety of mammal species (Freeland & Janzen 1974; Stegelmeier, Gardner & Davis 2009). Such chemical defenses might explain why forbs such as *Heliotropium* were consumed only rarely, despite their abundance. Ultimately, a mechanistic understanding of LMH forage selection will require analyzing diet-composition data in light of multiple plant functional traits (Cingolani, Posse & Collantes 2005; Codron et al. 2007b; Mládek *et al.* 2013). Prior work in African savannas has focused heavily on intraspecific and phenological variation in the nutritional value of different plant tissues. This perspective has been instrumental to our understanding of LMH trophic ecology, but it also reflects the longstanding difficulty of identifying the full range of plant species eaten. We believe that community-level, trait-based analyses of LMH diets will yield a fresh wave of insights about the factors governing forage selection, in addition to reinforcing principles already gleaned from the study of intraspecific trait variation.

CONCLUSION

In evaluating five broad hypotheses within the context of this recovering ecosystem, we have addressed both general ecological questions about diet differentiation and specific questions about the circumstances attending large-scale ecological rehabilitation in Gorongosa. However, important questions remain unanswered about the mechanisms underlying these patterns, the extent to which they represent departures from the norm in more-intact systems, and how they will shift as wildlife populations continue to recover and carnivore populations are reestablished. Our hypotheses were

predicated largely upon expectations about resource competition, but the depleted carnivore guild has undoubtedly contributed to the current spatial distribution and relative abundance of LMH species—and the intensity of competition within and between them—and hence to patterns of dietary differentiation and overlap. The ongoing restoration of the historical predator community offers a valuable opportunity to understand how top carnivores influence the behavior, diet composition, and niche structure of their large-herbivore prey.

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Author contributions

JP, TRK, and RMP conceived and designed the study. JP, ABP, JLA, and RMP collected fecal samples. JAG and BW collected and identified plant specimens for the local reference database. JHD created the tree-cover map and contributed to spatial analysis. JP and ABP conducted DNA analyses. JP performed bioinformatic analyses and analyzed the data. JP and

RMP drafted the manuscript. All co-authors contributed manuscript revisions and approved the submitted version.

Data accessibility

Sample information, unfiltered/filtered sequencing data, and the Gorongosa reference database have been deposited (under fasta and table formats) in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.63tj806> (Pansu, 2018). Local reference database sequences have also been deposited in BOLD (process ID's: PNG001-18 to PNG575-18).

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Table 1—Hypotheses and predictions tested in this study

	Hypothesis	Specific predictions	Support for prediction	Data
Hypothesis 1: Individual-level dietary variation	Among-individual dietary variation (<i>V</i>) is predicted by population-level traits—notably abundance, along with distribution, morphology, and behaviour.	a. Abundant species exhibit greater <i>V</i> , because individuals differentiate resource use to mitigate intraspecific competition.	Strong	Fig. 1a; Appendix S6
		b. <i>V</i> decreases with muzzle width, because narrow-mouthed individuals can select food items more precisely.	Strong	Fig. 1b; Appendix S6
		c. Species that are widely distributed across diverse habitats exhibit greater <i>V</i> , because individuals encounter a wider range of plants.	Mixed	Fig. 1c; Appendices S1 and S6
		d. <i>V</i> decreases with social-group size, because more social individuals tend to synchronize foraging in time and space.	None	Fig. 1d; Appendix S6
Hypothesis 2: Population-level diet breadth	More generalized species, with greater total niche width (TNW), exhibit greater among-individual variation.	a. TNW is positively correlated with <i>V</i> across species, with greater slope than predicted by random sampling from the population diet.	Mixed	Fig. 2a; Appendix S7
		b. TNW and <i>V</i> share the same suite of ecological and anatomical predictors, such that abundant species also have the greatest TNW.	None	Figs. 2b-e
Hypothesis 3: Community- and guild-level niche structure	Intraspecific competition forces individuals of abundant populations to diversify the range of resource types used, leading to high interspecific niche overlap, especially among grazers.	a. Community-wide interspecific overlap in diet composition is high.	Strong	Fig. 3a-c; Table 3; Appendices S8a-c and S9
		b. The dietary niche space occupied by rare species is nested within that of abundant species.	Strong	Fig. 3c-e; Table 3; Appendices S8c-e and S9
		c. Grazers exhibit the greatest within-guild dietary overlap, because this guild includes the most abundant species, and because limited stratification in the herbaceous layer allows less partitioning.	Strong	Fig. 3d-e; Table 3; Appendices S8d-e and S9
Hypothesis 4: Landscape-level influences on interspecific dietary overlap	Habitat heterogeneity facilitates resource partitioning.	a. Interspecific niche separation in structurally heterogeneous savanna-woodland habitat is greater than that observed among the same species in more homogeneous floodplain-grassland	Strong	Fig. 4; Appendix 10
Hypothesis 5: Dietary utilization relative to environmental availability	Variation in the taxonomic composition of LMH diets arises from the availability, nutritional content, and defensive properties of plant species; herbivores that are members of the same guild and share similar digestive physiology should share similar patterns of selectivity for different plant taxa.	a. Grazers predominantly select for grasses, browsers for forbs and shrubs, and mixed-feeders for a combination.	Weak	Fig. 5
		b. Grazing ruminants exhibit concordant selectivity patterns, which differ from those of non-ruminant grazers, ruminant non-grazers, and baboons.	None	Fig. 5
		c. Herbivores generally, and ruminants especially, select for plant taxa with high protein content.	Weak	Fig. 5

Table 2—Species investigated in this study and their characteristics. Species are listed in order of population density within each feeding guild (numbers in parentheses after species' names indicate the overall rank abundance). Because baboon troops rather than individuals are counted in aerial surveys, we do not have a density estimate for this species. Summary data for species that were too infrequently sampled for inclusion in our analyses (zebra, red duiker, bushpig, vervet monkey, civet, and serval) are presented in **Appendix S3**.

Common name	Latin name	Population density (No. individuals per km ²)	Body size (kg)	No. samples	<i>A priori</i> guild assignment	Mean percent grass RRA (± SE)	Population dietary niche width (TNW)	Individual niche breadth (mean no. mOTUs per sample ± SE)
Waterbuck ⁽¹⁾	<i>Kobus ellipsiprymnus</i>	12.1	210	42	Grazer	50 (± 6)	2.86	6.8 (± 0.4)
Reedbuck ⁽²⁾	<i>Redunca arundinum</i>	2.84	44	12	Grazer	56 (± 10)	2.34	6.7 (± 1.0)
Warthog ⁽³⁾	<i>Phacochoerus africanus</i>	1.47	82	18	Grazer	97 (± 2)	2.10	4.9 (± 0.3)
Oribi ⁽⁵⁾	<i>Ourebia ourebi</i>	1.06	17	16	Grazer	42 (± 7)	2.30	6.4 (± 0.9)
Sable ⁽⁹⁾	<i>Hippotragus niger</i>	0.22	228	18	Grazer	86 (± 5)	2.17	8.2 (± 0.6)
Buffalo ⁽¹⁰⁾	<i>Syncerus caffer</i>	0.18	580	23	Grazer	34 (± 4)	2.18	9.5 (± 0.5)
Hartebeest ⁽¹²⁾	<i>Alcelaphus buselaphus</i>	0.15	171	15	Grazer	91 (± 4)	2.55	9.5 (± 0.7)
Wildebeest ⁽¹³⁾	<i>Connochaetes taurinus</i>	0.10	180	25	Grazer	95 (± 1)	1.64	7.0 (± 0.6)
Impala ⁽⁴⁾	<i>Aepyceros melampus</i>	1.28	53	23	Mixed-feeder	10 (± 2)	3.11	9.8 (± 1.0)
Nyala ⁽⁸⁾	<i>Tragelaphus angasii</i>	0.35	43	13	Mixed-feeder	12 (± 5)	3.08	10.8 (± 0.8)
Elephant ⁽¹¹⁾	<i>Loxodonta africana</i>	0.15	3940	21	Mixed-feeder	20 (± 4)	3.14	10.2 (± 0.7)
Bushbuck ⁽⁶⁾	<i>Tragelaphus sylvaticus</i>	0.55	43	25	Browser	0 (± 0)	2.68	7.7 (± 0.6)
Kudu ⁽⁷⁾	<i>Tragelaphus strepsiceros</i>	0.40	214	12	Browser	0 (± 0)	1.97	7.8 (± 1.2)
Chacma baboon ^(na)	<i>Papio ursinus</i>	NA	18	30	Omnivore	4 (± 1)	2.57	5.3 (± 0.4)

Table 3—Pairwise measures of interspecific dietary niche overlap and dissimilarity. Numbers in parentheses after species' names indicate the rank abundance of that species. *Below diagonal*: Pianka's index of dietary niche overlap, ranging from 0 (no overlap) to 1 (complete overlap). Asterisks indicate statistically significant niche overlap (i.e., greater than expected by chance based on comparison with 1000 null models, $\alpha = 0.05$). *Above diagonal*: Mean pairwise Bray–Curtis dissimilarities, ranging from 0 (complete overlap) to 1 (no overlap). Upper-left quadrant reflects overlap between grazers; lower-left quadrant reflects overlap between non-grazers; lower-left and upper-right quadrants both reflect cross-guild overlap. Analogous results based on presence-absence data are provided in **Appendix S9**.

	Grazer								Non-grazer					
	Waterbuck	Reedbuck	Warthog	Oribi	Sable	Buffalo	Hartebeest	Wildebeest	Impala	Nyala	Elephant	Bushbuck	Kudu	Baboon
Waterbuck ⁽¹⁾		0.818	0.877	0.834	0.883	0.916	0.856	0.841	0.887	0.958	0.945	0.942	0.996	0.970
Reedbuck ⁽²⁾	0.887*		0.841	0.760	0.877	0.923	0.837	0.782	0.862	0.970	0.960	0.924	0.999	0.974
Warthog ⁽³⁾	0.558*	0.512*		0.869	0.766	0.912	0.789	0.756	0.947	0.954	0.962	0.993	0.996	0.981
Oribi ⁽⁵⁾	0.858*	0.922*	0.374		0.929	0.938	0.872	0.841	0.842	0.966	0.962	0.904	0.993	0.946
Sable ⁽⁹⁾	0.335*	0.223	0.721*	0.112		0.820	0.753	0.796	0.953	0.950	0.930	0.996	0.997	0.979
Buffalo ⁽¹⁰⁾	0.159	0.109	0.194	0.104	0.273		0.864	0.897	0.946	0.957	0.935	0.990	0.990	0.986
Hartebeest ⁽¹²⁾	0.507*	0.390	0.605*	0.304	0.566*	0.193		0.736	0.926	0.912	0.918	0.991	0.994	0.974
Wildebeest ⁽¹³⁾	0.596*	0.628*	0.697*	0.467	0.371*	0.101	0.667*		0.936	0.932	0.953	0.997	0.995	0.988
Impala ⁽⁴⁾	0.708*	0.684*	0.157	0.776*	0.084	0.082	0.158	0.159		0.912	0.949	0.855	0.940	0.953
Nyala ⁽⁸⁾	0.198	0.08	0.169	0.087	0.155	0.057	0.266	0.228	0.282		0.892	0.892	0.863	0.955
Elephant ⁽¹¹⁾	0.2	0.069	0.107	0.105	0.16	0.091	0.197	0.061	0.144	0.492*		0.947	0.916	0.930
Bushbuck ⁽⁶⁾	0.435*	0.438*	0.029	0.525*	0.005	0.036	0.03	0.004	0.819*	0.389*	0.182		0.937	0.953
Kudu ⁽⁷⁾	0.01	0	0.004	0.011	0.001	0.004	0.005	0.001	0.121	0.396*	0.229	0.129		0.984
Baboon ^(na)	0.125	0.078	0.047	0.184	0.05	0.017	0.057	0.013	0.193	0.208	0.394*	0.183	0.026	

Figure 1. Among-individual diet variation (V) as functions of species' attributes. (a) Population density; (b) muzzle width; (c) habitat diversity (Shannon index of habitat types from which dung samples were collected); and (d) social group size. Lines show linear regressions (solid, $P < 0.05$; dashed, $P < 0.10$), and regression statistics are included at the bottom of each panel. Downward triangles represent grazers, upward triangles represent non-grazers, and colors correspond to herbivore species.

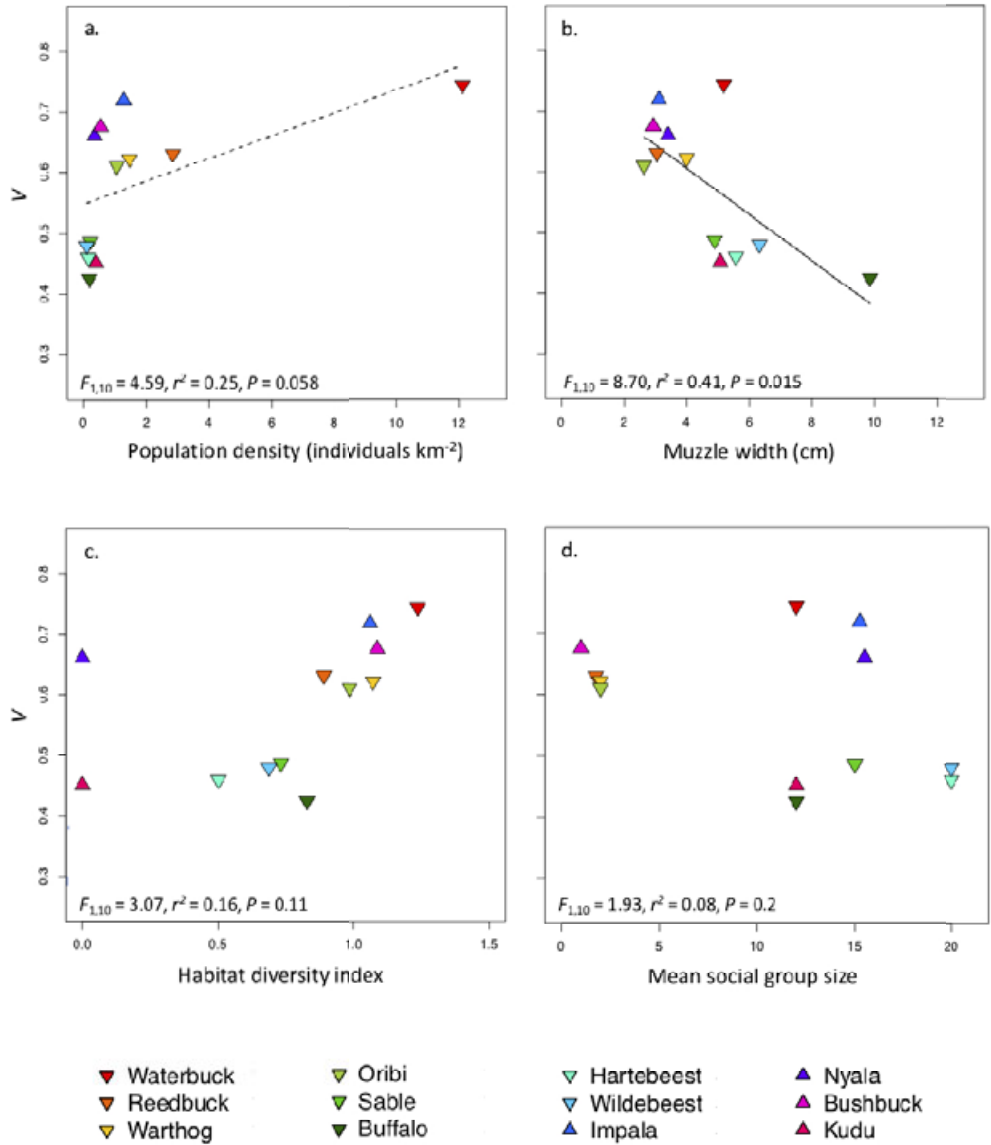


Figure 2—Total niche width (TNW) as functions of among-individual variation (V) and species' attributes. (a) Observed and simulated V values; (b) population density; (c) muzzle width; (d) habitat diversity; and (e) social group size. In panel a, triangles represent observed values for each species, and squares show mean simulated V values (\pm 95% confidence intervals) from the null model; lines show linear regressions (solid, observed values; dashed, simulated values). Downward triangles represent grazers, upward triangles represent non-grazers, and colors correspond to herbivore species. Elephants are included in panel a only (thus $n = 13$); in panels b-e, $n = 12$ ungulate species, as in Fig. 1. Regression statistics are included in each panel.

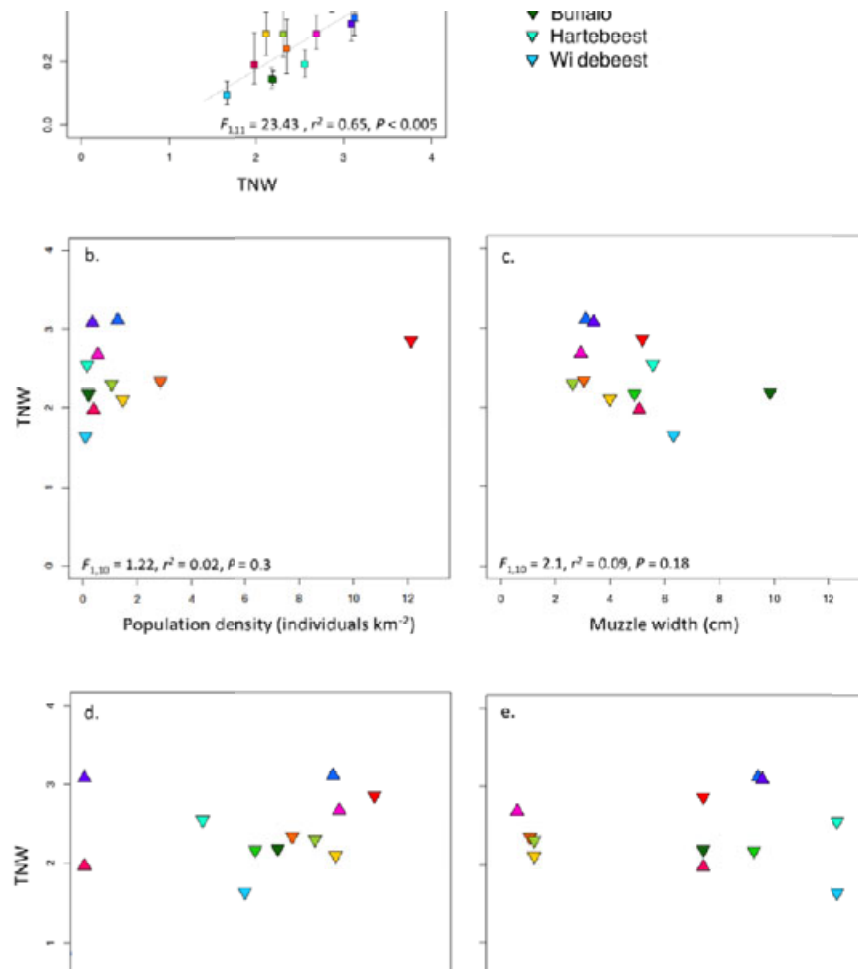


Figure 3—Dietary niche overlap among large-herbivore species and feeding guilds. (a) Bipartite plant-herbivore interaction network. Lines connect the 14 herbivore species (top) to dietary plant mOTUs (bottom, colored by plant family). Widths of upper boxes reflect the number of samples analyzed for each species; widths of lower boxes reflect the relative abundance of each plant mOTU across all samples in the dataset; and widths of connecting lines reflect the relative read abundance of each mOTU within the diet of each species. We show only connections representing $\geq 1\%$ of each species' diet (total $n = 74$). (b) Non-metric dimensional scaling (NMDS) ordination of Bray-Curtis dietary dissimilarity among the *a priori* feeding guilds listed in **Table 1** (stress=0.16; perMANOVA, pseudo- $F_{3,289} = 12.91$, $r^2 = 0.12$, $P < 0.001$). (c) NMDS ordination of Bray-Curtis dissimilarity among species (same ordination as in panel b, but colored by species to show community-wide inter-specific diet dissimilarity; perMANOVA, pseudo- $F_{13,279} = 9.09$, $r^2 = 0.30$, $P < 0.001$). (d) NMDS ordination of Bray-Curtis dissimilarity among just the eight grazer species (stress=0.19; perMANOVA, pseudo- $F_{7,161} = 7.90$, $r^2 = 0.26$, $P < 0.001$). (e) NMDS ordination of Bray-Curtis dissimilarity among just the six non-grazer species (stress=0.14; perMANOVA, pseudo- $F_{5,118} = 6.38$, $r^2 = 0.21$, $P < 0.001$). Each point in (b–e) corresponds to one fecal sample; minimum convex polygons are shown for each species. Analogous results based on presence-absence of plant mOTUs are shown in **Appendix S8**.

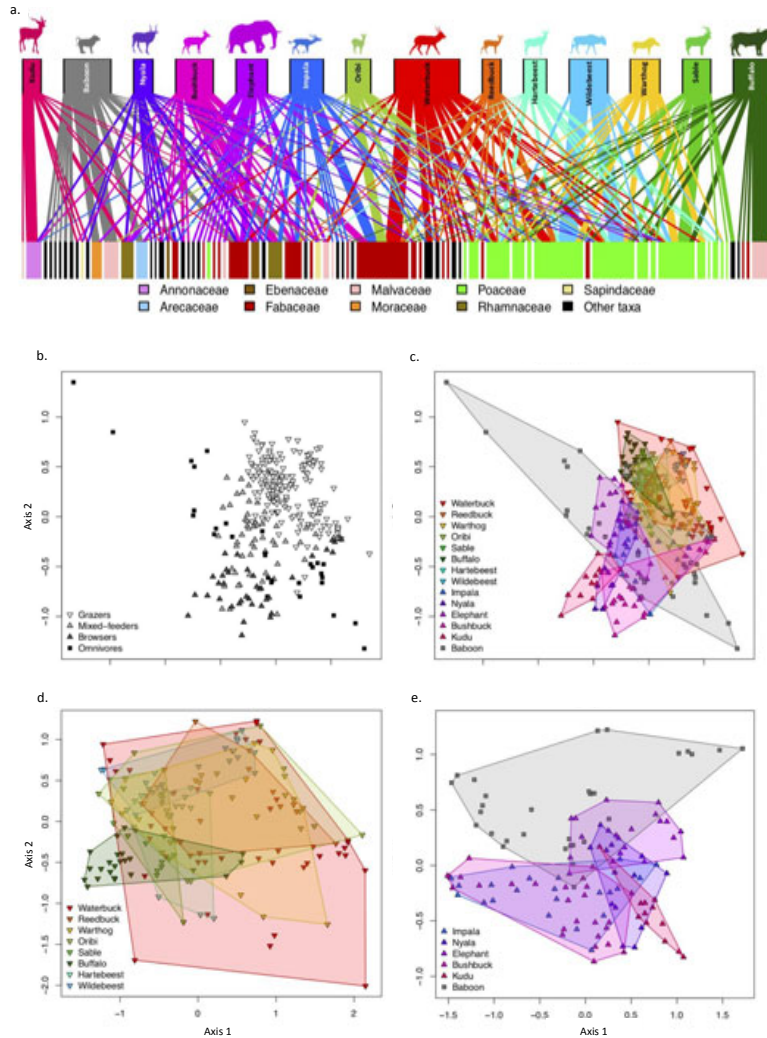


Figure 4—Niche partitioning as a function of habitat type. Non-metric dimensional scaling (NMDS) ordinations of Bray-Curtis dissimilarities for fecal samples retrieved from (a) floodplain-grassland (stress=0.19; perMANOVA, pseudo- $F_{6,52} = 5.02$, $r^2 = 0.37$, $P < 0.001$) and (b) savanna-woodland (stress=0.16; perMANOVA, pseudo- $F_{6,49} = 6.03$, $r^2 = 0.42$, $P < 0.001$). This analysis was restricted to the subset of seven species that regularly occur in both habitat types. Downward triangles represent grazers, upward triangles represent non-grazers, squares represent baboons, and colors correspond to species. Analogous results based on presence-absence data are presented in **Appendix S10**.

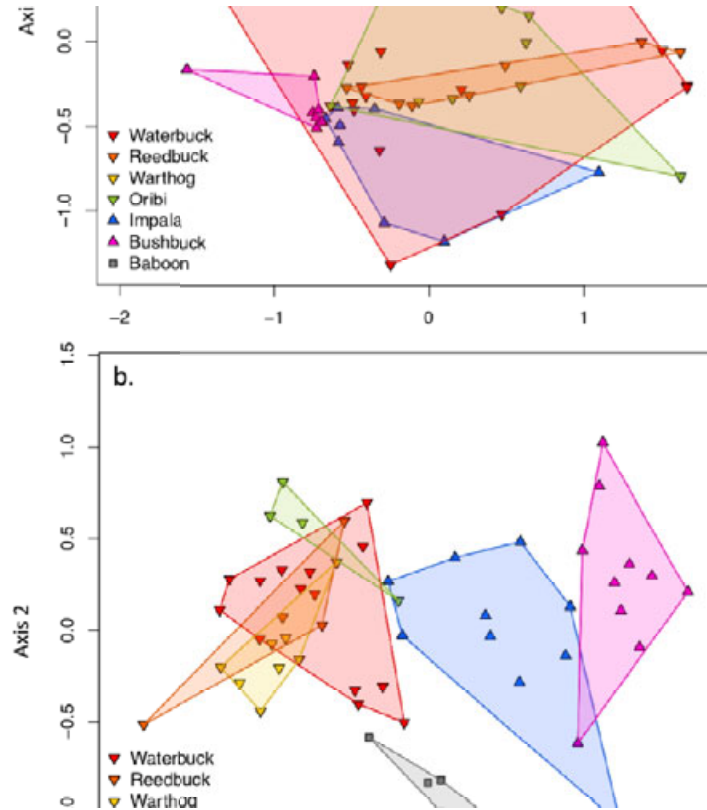
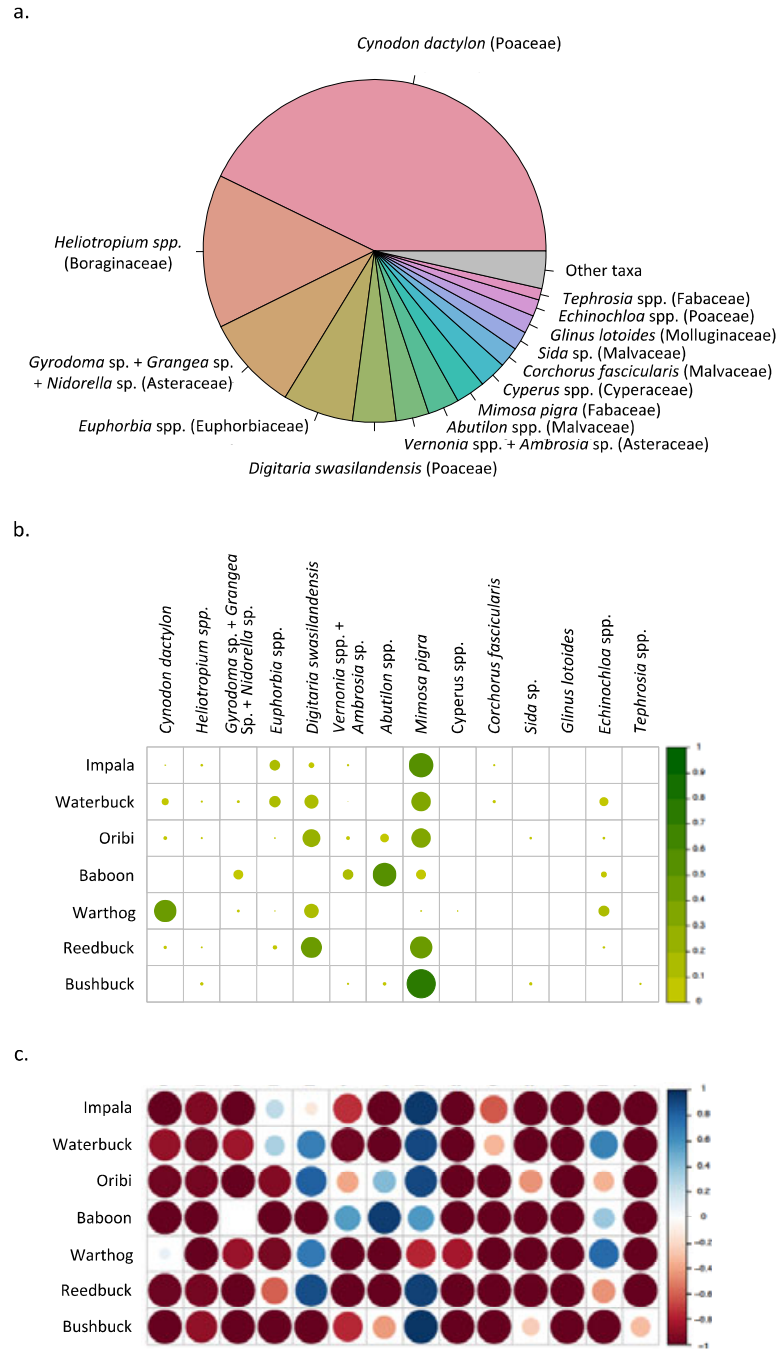


Figure. 5—Availability, utilization, and selectivity of common floodplain plant taxa. (a) Relative availability (proportional areal cover) of the 14 plant taxa representing at least 1% of total plant cover (collectively accounting for >96% of cover). (b) Proportional contribution of each plant mOTU to the diet of each ungulate species; circle size and color reflect relative read abundance. (c) Jacob's *D* selectivity index for each plant taxon, ranging from -1 (strongest avoidance, red) to 1 (strongest selection, blue). Plant taxa sharing the same barcode in the local reference database were combined for the purposes of this analysis.



Supporting Information

Appendix S1—Map of Gorongosa National Park and spatial distribution of samples.

Appendix S2—Supplementary materials and methods.

Appendix S3—Mean relative read abundance (RRA) of plant mOTUs in mammal diets.

Appendix S4—Supplementary information for DNA-metabarcoding results

Appendix S5—Total niche width (TNW) in relation to among-individual variation (V) and individual dietary species richness.

Appendix S6—Relative read abundance (RRA) of the 15 top dietary plant families.

Appendix S7—Full model-selection results for among-individual diet variability (V) and total niche width (TNW).

Appendix S8—Dietary niche overlap among large-herbivore species and feeding guilds, based on presence-absence data.

Appendix S9—Pairwise measures of interspecific dietary niche overlap and dissimilarity, based on presence-absence data.

Appendix S10—Niche partitioning as a function of habitat type, based on presence-absence data.

Appendix S11—Photographs illustrating herbivore-induced resource depletion in the Gorongosa floodplain.