



## RESEARCH ARTICLE

# Trophic ecology of large herbivores in a reassembling African ecosystem

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## Abstract

1. 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 prewar 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 homogeneous 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

predation pressure. Future work should test these conjectures and analyse how the taxonomic dietary niche axis studied here interacts with other mechanisms of diet partitioning to affect community reassembly following wildlife declines.

#### KEYWORDS

community assembly, herbivory, individual specialization, intraspecific niche variation, molecular diet analysis, restoration ecology, species coexistence, trophic rewilding

## 1 | INTRODUCTION

Large mammalian herbivore (LMH) populations have declined throughout much of Africa in recent decades (Craigie et al., 2010; Daskin & Pringle, 2018; Ripple et al., 2015), 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 (McNaughton, 1985; Owen-Smith, 1988; Pringle, Prior, Palmer, Young, & Goheen, 2016; Sinclair, 1975). The nature and strength of these effects—and how they change when ecosystems are defaunated or refaunated—hinge upon food-web structure (Dobson, 2009). Understanding LMH trophic networks is therefore crucial for both basic understanding and effective management of savanna ecosystems (Burkepile & Parker, 2017; Eby et al., 2014).

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 National Park, Botswana's Chobe National Park, Tanzania's Serengeti ecosystem, and Kenya's Laikipia highlands (e.g., Bell, 1971; Codron et al., 2007; du Toit & Olff, 2014; Kartzinzel et al., 2015; Kleynhans, Jolles, Bos, & Olff, 2011; O'Shaughnessy, Cain, & Owen-Smith, 2014; Owen-Smith, Croomsigt, & Arsenault, 2017; Owen-Smith, Le Roux, & Macandza, 2013; Sinclair, 1985). 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 differential 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 patterns observed in more intact systems.

Large mammalian herbivore 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 (Kleynhans et al., 2011; Sinclair, 1985). 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 (Bell, 1971; Belovsky, 1997; du Toit, 2003; du Toit & Olff, 2014; Duncan, Foote, Gordon, Gakahu, & Lloyd, 1990; Gwynne & Bell, 1968; Jarman, 1974; Kartzinzel et al., 2015; Owen-Smith, Martin, & Yoganand, 2015; Shipley, 2007; Sinclair, 1985). 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 mesoscale level of plant species (Field, 1972; Jarman, 1971; Kartzinzel et al., 2015; Kleynhans et al., 2011; Macandza, Owen-Smith, & Cain, 2012; Makhabu, 2005; Owen-Smith et al., 2013; Sinclair, 1985). 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 versus browse in the diet (Codron et al., 2007; McNaughton & Georgiadis, 1986). 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) have made it easier to characterize trophic interactions with high coverage and taxonomic resolution (Craine, Towne, Miller, & Fierer, 2015; Kartzinzel et al., 2015; Newmaster et al., 2013).

Multiple factors can influence the utilization of different forage taxa by sympatric LMH species. These include herbivore traits such as body mass, craniofacial anatomy, and gut architecture (Codron & Clauss, 2010; du Toit & Olff, 2014; Jarman, 1974; Stokke & du Toit, 2000; Vesey-Fitzgerald, 1960); herbivore distribution and vegetation heterogeneity (Croomsigt & Olff, 2006; du Toit, 1990, 2003); plant traits such as height, nutritional content, and defences (Arsenault & Owen-Smith, 2008; Cingolani, Posse, & Collantes, 2005; Janzen, 1979; Kleynhans et al., 2011); and species interactions such as competition and predation (du Toit & Olff, 2014; Ford et al., 2014; Sinclair, 1985). 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, 2011; Bolnick, Svanbäck, Araújo, & Persson, 2007; Codron, Codron, Sponheimer, & Clauss, 2016; Maldonado, Bozinovic, Newsome, & Sabat, 2017). Together, the extent of among-individual differentiation and the breadth of

individual diets shape the population niche (Roughgarden, 1972; Van Valen, 1965). 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 (Bolnick et al., 2011; Roughgarden, 1972). 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 similar 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: Arsenault & Owen-Smith, 2008; Gordon & Illius, 1988), might be expected to have higher among-individual 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 (Dunham, Robertson, & Grant, 2004; Fritz & Garine-Wichatitsky, 1996; Jarman & Sinclair, 1979; Owen-Smith, 1982; Sinclair, Dublin, & Borner, 1985) and may force individuals to exploit resources not used by conspecifics (Svanbäck & 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 (Ford et al., 2014; le Roux, Kerley, & Crooms, 2018).

The restoration of Mozambique's Gorongosa National Park (Supporting Information Appendix S1) provides a unique opportunity to test hypotheses about LMH trophic ecology in a system that is reassembling following severe defaunation (Correia, Timóteo, Rodríguez-Echeverría, Mazars-Simon, & Heleno, 2017; Daskin, Stalmans, & Pringle, 2016; Pringle, 2012). Intensive hunting during and after the Mozambican Civil War (1977–1992) caused >90% declines in all LMH populations for which prewar 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). Total LMH biomass has since rebounded to rival prewar levels, but community structure remains heavily skewed relative to the prewar 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 Section 2; Supporting Information Appendix S2a).

We used faecal 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 predation 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). We further tested for effects of landscape structure (Hypothesis 4) and herbivore traits (Hypothesis 5) on patterns of diet composition and selectivity, and we incorporated herbivore traits into our analyses of among-individual variation, population niche width, and interspecific niche overlap (Hypotheses 1–3).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

Gorongosa is a 4,000-km<sup>2</sup> national park in central Mozambique (18.96°S, 34.36°E). The Great Rift Valley runs through the centre of the park, encompassing Lake Urema and its surrounding floodplain, along with *Acacia*, palm, and broadleaf savanna woodlands (Stalmans & Beilfuss, 2008; Tinley, 1977). Our study was conducted within the southern Rift Valley (Supporting Information 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 (Stalmans & Beilfuss, 2008; Tinley, 1977).

The prewar 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. Most strikingly, waterbuck numbers have increased by an order of magnitude relative to the prewar baseline, with >45,000 individuals accounting for >60% of total LMH biomass in 2016 (Stalmans & Peel, 2016). Other now-abundant mid-sized ungulates include reedbuck (*Redunca arundinum*, >10,500), warthog (*Phacochoerus africanus*, >5,400), and impala (*Aepyceros melampus*, >4,700) (Supporting Information Appendix S2a). In contrast, the formerly dominant large-bodied grazers remain at <20% of their prewar numbers (Stalmans & Peel, 2016). Lions (*Panthera leo*), the only apex carnivore that persisted throughout war and recovery, occurred at roughly a third of prewar abundance at the time of this study (Pringle, 2017).

### 2.2 | Collection of faecal samples for DNA metabarcoding

We used DNA metabarcoding (Taberlet et al., 2007, 2012; Valentini et al., 2009) to characterize herbivore diets by sequencing,

**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 (V) is predicted by population-level traits—notably abundance, along with distribution, morphology, and behaviour	a. Abundant species exhibit greater V, because individuals differentiate resource use to mitigate intraspecific competition	Strong	Figure 1a; Supporting Information Appendix S7a
		b. V decreases with muzzle width, because narrow-mouthed individuals can select food items more precisely	Strong	Figure 1b; Supporting Information Appendix S7a
		c. Species that are widely distributed across different habitats exhibit greater V, because individuals encounter a wider range of plants	Mixed	Figure 1c; Supporting Information Appendices S1 and S7a
		d. V decreases with social-group size, because more social individuals tend to synchronize foraging	None	Figure 1d; Supporting Information Appendix S7a
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 V across species, with greater slope than predicted by random sampling from the population diet	Mixed	Figure 2a; Supporting Information Appendices S5 and S7b
		b. TNW and V share the same suite of ecological and anatomical predictors, such that abundant species also have the greatest TNW	None	Figure 2b–e; Supporting Information Appendix S7b
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	Figure 3a–c; Table 3; Supporting Information Appendices S8a–c and S9
		b. The dietary niche space occupied by rare species is nested within that of abundant species	Strong	Figure 3c–e; Table 3; Supporting Information 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	Figure 3d,e; Table 3; Supporting Information 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 among the same species in more homogeneous floodplain-grassland	Strong	Figure 4; Supporting Information Appendix S10
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 forage selectivity	a. Grazers predominantly select for grasses, browsers for forbs and shrubs, and mixed-feeders for a combination	Weak	Figure 5
		b. Grazing ruminants exhibit concordant selectivity patterns, which differ from those of non-ruminants and non-grazers	None	Figure 5
		c. Herbivores generally, and ruminants especially, select for plant taxa with high protein content	Weak	Figure 5

identifying, and quantifying plant-DNA fragments in faecal samples (each derived from a single individual, generally reflecting consumption over the preceding 24–72 hr: Steuer et al., 2011) (Supporting Information 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 (Newmaster et al., 2013; Soininen et al., 2009). We collected samples across a 540 km<sup>2</sup>

area (~14% of the park) spanning four habitat types distinguished by vegetation structure and hydrology: (a) Urema floodplain and (b) seasonally flooded riverine grasslands, both dominated by grasses with small shrubs and very few trees; (c) 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 (d) savanna woodland, infrequently flooded with a diverse overstorey (including *Senegalia*, *Vachellia*, *Combretum*, and palm species).

In total, we obtained 338 fresh faecal 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 ursinus*). 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, Correia, Rodríguez-Echeverría, Freitas, & Heleno, 2018) and may compete for food with ungulates. 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 ( $n = 2\text{--}7$ ); however, we present descriptive data from these samples in Supporting Information Appendix S3. All samples were collected from June to August 2016, the mid-dry season. For each sample, we recorded GPS coordinates and the surrounding habitat type (Supporting Information Appendix S1a,b). Sample collection and processing followed protocols described by Kartzin 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, CA, USA), which were frozen ( $-20^{\circ}\text{C}$ ) until transport to the United States and then stored at  $-80^{\circ}\text{C}$ . All samples were subjected to a standard antiviral heat treatment (30 min at  $72^{\circ}\text{C}$ ) before importation into the United States.

### 2.3 | Faecal 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 (Kartzin et al., 2015; Pansu, Giguët-Covex et al., 2015; Taberlet et al., 2012; Valentini et al., 2009). We conducted multiple PCR replicates per sample, along with extraction and PCR controls. PCR products were purified using MinElute™ purification kits (Qiagen, MD, USA). Sequencing libraries were prepared using a PCR-free approach and sequenced on an Illumina HiSeq 2500 ( $2 \times 150$  bp paired-end reads).

Sequence data were curated using the OBITOOLS package (Boyer et al., 2016) to (a) assemble paired-end reads, (b) assign sequences to their original samples, (c) remove low-quality sequences and those putatively resulting from PCR amplification/sequencing errors, (d) discard singletons represented only once in the dataset, and (e) assign remaining sequences to plant taxa (Supporting Information 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 (Supporting Information Appendix S2d). Taxonomic assignments were made by comparison to this local database as well as a reference set generated 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, Winkworth et al., 2015), 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 of PCR amplification and sequencing, processing of DNA-metabarcoding data, and the local reference database are provided in the Supporting Information Appendices S2 and S4.

The mOTUs-by-samples matrix was rarefied to 4,000 reads per sample (the minimum number of reads per sample was 4,605) and converted into proportions to yield relative read abundance (RRA)—the proportional representation of each plant mOTU in each faecal sample. After filtering, the rarefied dataset contained a total of 176 unique plant mOTUs from the 293 faecal samples (Supporting Information Appendices S3 and S4). RRA is widely used as a proxy of the proportional quantity of foods eaten (Bison et al., 2015; Craine et al., 2015; De Barba et al., 2014; Deagle et al., 2018; McClenaghan, Gibson, Shokralla, & Hajibabaei, 2015; Pompanon et al., 2012), 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: Kartzin et al., 2015; Willerslev et al., 2014). Moreover, previous studies using this approach have found that conclusions based on RRA are often qualitatively similar to those based on presence/absence data (Gebremedhin et al., 2016; Kartzin et al., 2015; Willerslev et al., 2014), 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); 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.

**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 Supporting Information Appendix S3

Common name	Latin name	Population density (no. individuals per km <sup>2</sup> ) in 2016	Body size (kg)	No. of samples	A priori guild assignment	Mean percent grass RRA (±SE)	Population dietary niche width (TNW)	Individual niche breadth (mean no. mOTUs per sample ± SE)
Waterbuck <sup>(1)</sup>	<i>Kobus ellipsiprymnus</i>	12.1	210	42	Grazer	50 (±6)	2.86	6.8 (±0.4)
Reedbuck <sup>(2)</sup>	<i>Redunca arundinum</i>	2.84	44	12	Grazer	56 (±10)	2.34	6.7 (±1.0)
Warthog <sup>(3)</sup>	<i>Phacochoerus africanus</i>	1.47	82	18	Grazer	97 (±2)	2.10	4.9 (±0.3)
Oribi <sup>(5)</sup>	<i>Ourebia ourebi</i>	1.06	17	16	Grazer	42 (±7)	2.30	6.4 (±0.9)
Sable <sup>(9)</sup>	<i>Hippotragus niger</i>	0.22	228	18	Grazer	86 (±5)	2.17	8.2 (±0.6)
Buffalo <sup>(10)</sup>	<i>Syncerus caffer</i>	0.18	580	23	Grazer	34 (±4)	2.18	9.5 (±0.5)
Hartebeest <sup>(12)</sup>	<i>Alcelaphus buselaphus</i>	0.15	171	15	Grazer	91 (±4)	2.55	9.5 (±0.7)
Wildebeest <sup>(13)</sup>	<i>Connochaetes taurinus</i>	0.10	180	25	Grazer	95 (±1)	1.64	7.0 (±0.6)
Impala <sup>(4)</sup>	<i>Aepyceros melampus</i>	1.28	53	23	Mixed-feeder	10 (±2)	3.11	9.8 (±1.0)
Nyala <sup>(8)</sup>	<i>Tragelaphus angasii</i>	0.35	43	13	Mixed-feeder	12 (±5)	3.08	10.8 (±0.8)
Elephant <sup>(11)</sup>	<i>Loxodonta africana</i>	0.15	3,940	21	Mixed-feeder	20 (±4)	3.14	10.2 (±0.7)
Bushbuck <sup>(6)</sup>	<i>Tragelaphus sylvaticus</i>	0.55	43	25	Browser	0 (±0)	2.68	7.7 (±0.6)
Kudu <sup>(7)</sup>	<i>Tragelaphus strepsiceros</i>	0.40	214	12	Browser	0 (±0)	1.97	7.8 (±1.2)
Baboon	<i>Papio ursinus</i>		18	30	Omnivore	4 (±1)	2.57	5.3 (±0.4)



## 2.4 | Hypothesis testing

### 2.4.1 | 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 (Bison et al., 2015; Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002). 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  $V = 1 - PS_i$  (Araújo, Bolnick, Martinelli, Giaretta, & Reis, 2009; Bolnick et al., 2007, 2002). 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 (a) we lacked population-density estimates for baboons, (b) we quantified only the plant component of baboons' omnivorous diet and thus could not fully estimate among-individual variation, and (c) 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 and 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 (Supporting Information Appendix S1b). Muzzle-width data were obtained from Janis and 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  $\leq 2$ . 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).

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

We calculated TNW of each population as the Shannon diversity of diet composition (Bolnick et al., 2007; Roughgarden, 1972), 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 among-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 (Supporting Information Appendix S5; Bolnick et al., 2003; Roughgarden, 1972); and the  $V \sim$  TNW relationship is used at the intraspecific level to test the niche-variation hypothesis (Van Valen, 1965), which holds that expansions in population 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 artefacts 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  $V \sim$  TNW relationship is greater than expected based on random subsampling of the population diet (Bolnick et al., 2007). Therefore, we also regressed TNW against simulated  $V$  values, averaged for each species ( $\pm 95\%$  CI) from 1,000 iterations of the null model developed by Bison et al. (2015) for use with proportional diet data derived from DNA metabarcoding. If the  $V \sim$  TNW correlation is more than just a sampling artefact, 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 ( $V \sim$  TNW  $\times$  data type), where the interaction term signifies whether the slope of  $V \sim$  TNW differs for observed versus simulated diet data (Bison et al., 2015; Bolnick et al., 2007).

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

We calculated the Bray-Curtis index of compositional dissimilarity between each pair of faecal samples (i.e., individual diets) and ordinated these values using non-metric multidimensional scaling (NMDS) to visualize the patterns of dietary dissimilarity (both within and among species) in two dimensions (Borcard, Gillet, & Legendre, 2011; Kartzinell et al., 2015). We did this first for the whole community, and then separately for grazers and non-grazers (per Table 2). We analysed 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 (a) the mean of the pairwise Bray–Curtis distances between individual samples for each species pair and (b) 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; Kleynhans et al., 2011). Statistical significance of the Pianka index for each species pair was evaluated with reference to 1,000 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 et al., 2015).

#### 2.4.4 | 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 faecal-sample location ( $0.39 \pm 0.02$  in savanna;  $0.06 \pm 0.01$  in floodplain). This analysis was based on a supervised classification of woody versus 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 the 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 analysed mean interspecific dietary dissimilarity/overlap between each species pair using the Pianka and Bray–Curtis indices, as described above.

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

We analysed 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  $\approx 0$  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 faecal-sample collection) within 18 1-ha 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 15 1-m<sup>2</sup> 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  $\geq 3$  different individuals were collected, pooled together, and oven-dried at 60°C. Nitrogen concentration was determined via combustion by Dairy One Cooperative, Inc. (Ithaca, NY, USA), and crude-protein content was estimated as  $6.25 \times N$ .

### 3 | RESULTS

#### 3.1 | Overview of LMH diet composition

The mean RRA of plant families in each species' diet was broadly consistent with Tinley's (1977) prewar 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; Supporting Information Appendices S3 and 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 (one mOTU, *Cleistochlamys kirkii*, 50% RRA for kudu, 1%–6% for all others); Ebenaceae (two mOTUs, 9%–13% RRA for nyala and bushbuck, <2% all others); Malvaceae (10 mOTUs, 1%–12% RRA); and Sapindaceae (two mOTUs, 2%–6% RRA) (Supporting Information Appendices S3 and



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,  $r = 0.15$ – $0.89$ ,  $p < 0.03$  for all species; Supporting Information 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 ( $r = 0.15$ – $0.28$ ); wildebeest, buffalo, and hartebeest samples had more spatially discontinuous distributions and exhibited stronger correlations with distance ( $r = 0.60$ – $0.89$ ; Supporting Information Appendix S1c).

Individual dietary richness was greatest for the three mixed-feeders (9.8–10.8 mOTUs per sample) and two large grazers (buffalo and hartebeest, 9.5 mOTUs per sample) and least for the abundant mid-sized grazers (warthog, oribi, reedbuck, waterbuck, 4.9–6.8 mOTUs per sample) (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).

### 3.2 | 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) (Figure 1). The top model for  $V$ , which was by far the best in the candidate set ( $w_1 = 0.67$ ;  $r^2 = 0.69$ ,  $F_{2,9} = 13.25$ ,  $p = 0.002$ ), 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 ( $RVI = 0.95$ ;  $t_9 = -3.92$ ,  $p < 0.004$ ) (Supporting Information Appendix S7a). These factors were also correlated with  $V$  in univariate regressions (albeit marginally for population density) (Figure 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 (Figure 1c), while sociality ( $RVI = 0.06$ ) exhibited no univariate correlation with  $V$  (Figure 1d). Full model-selection results are given in Supporting Information Appendix S7a.

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

Total niche width was strongly and positively correlated with both observed and simulated  $V$  values (Figure 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 (Figure 2a). Contrary to expectation, the factors that predicted  $V$  (population

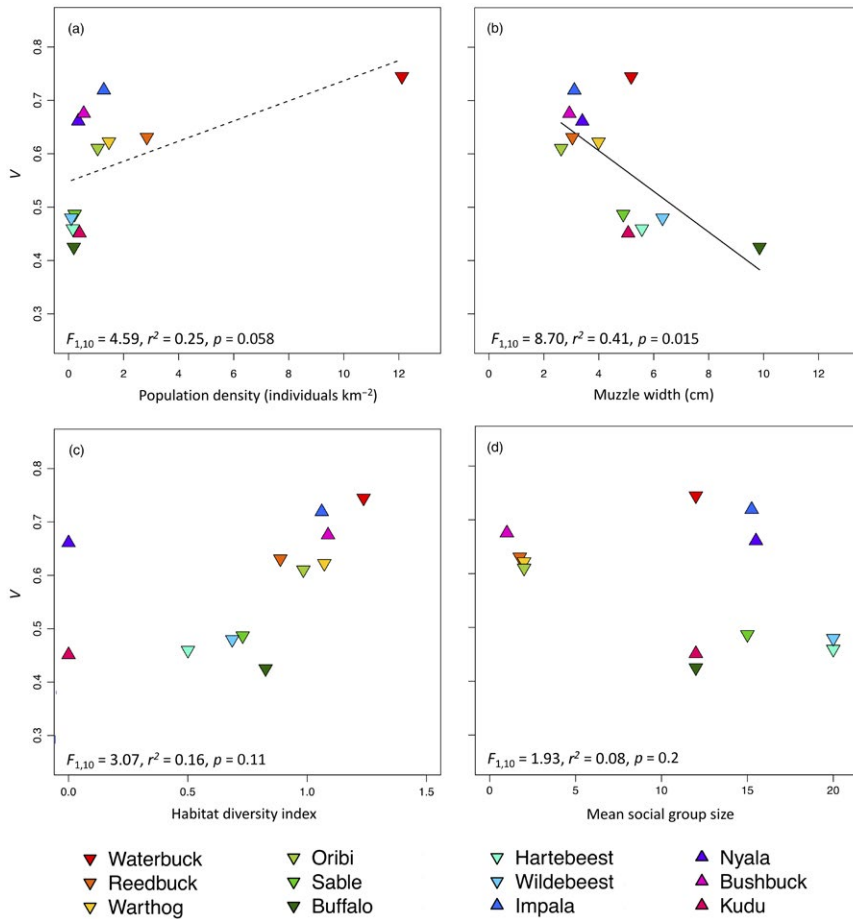
density and muzzle width) were not significantly correlated with TNW (Figure 2b–e), and no combination of predictor variables had substantial explanatory power (the top model included only an intercept: Supporting Information Appendix S7b). The greatest population niche widths were instead observed in 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, Supporting Information Appendix S5).

### 3.4 | 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 (Figure 3a–c; Supporting Information 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 (Figure 3d; Supporting Information 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 (Figure 3d). This pattern persisted when we employed a resampling procedure to homogenize the number of samples per species. These results are consistent with the greater among-individual differentiation observed in abundant grazers (Figure 1a), which produces greater spread in two-dimensional niche space, and they are corroborated by the pairwise Pianka niche-overlap index (Table 3; Supporting Information Appendix S9). The mean of the pairwise Pianka indices across all grazers was  $0.44 \pm 0.05$  SE. Overlap was statistically significant between waterbuck and all other grazers except buffalo, and was particularly high among waterbuck, reedbuck, and oribi (mean  $0.89 \pm 0.02$  SE). Warthog, sable, wildebeest, and hartebeest formed another cluster in which all pairwise niche-overlap values were significant (mean  $0.60 \pm 0.05$  SE). In contrast to grazers, mixed-feeders and browsers showed greater niche separation (Figure 3e). The overall mean of the pairwise Pianka indices for non-grazers was  $0.28 \pm 0.05$  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  $0.15 \pm 0.3$  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).

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 (Supporting Information Appendices S8–S10) were broadly consistent with our primary analyses based on RRA (Table 3, Figures 3 and 4).



**FIGURE 1** Among-individual diet variation ( $V$ ) as functions of species' attributes. (a) Population density; (b) muzzle width; (c) habitat diversity; 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 colours correspond to herbivore species

### 3.5 | 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  $0.48 \pm 0.08$  SE), whereas niche segregation was greater in savanna ( $0.25 \pm 0.05$  SE;  $t_{34.5} = 2.54, p = 0.02$ ; Figure 4; Supporting Information Appendix S10). The NMDS plot for the floodplain (Figure 4a) broadly recapitulated that for grazer guild at large (cf. Figure 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 (Figure 4b), and waterbuck dominated a smaller fraction of grazer niche space.

### 3.6 | 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.) (Figure 5a). Patterns of utilization (Figure 5b) and selection relative to availability (Figure 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%).

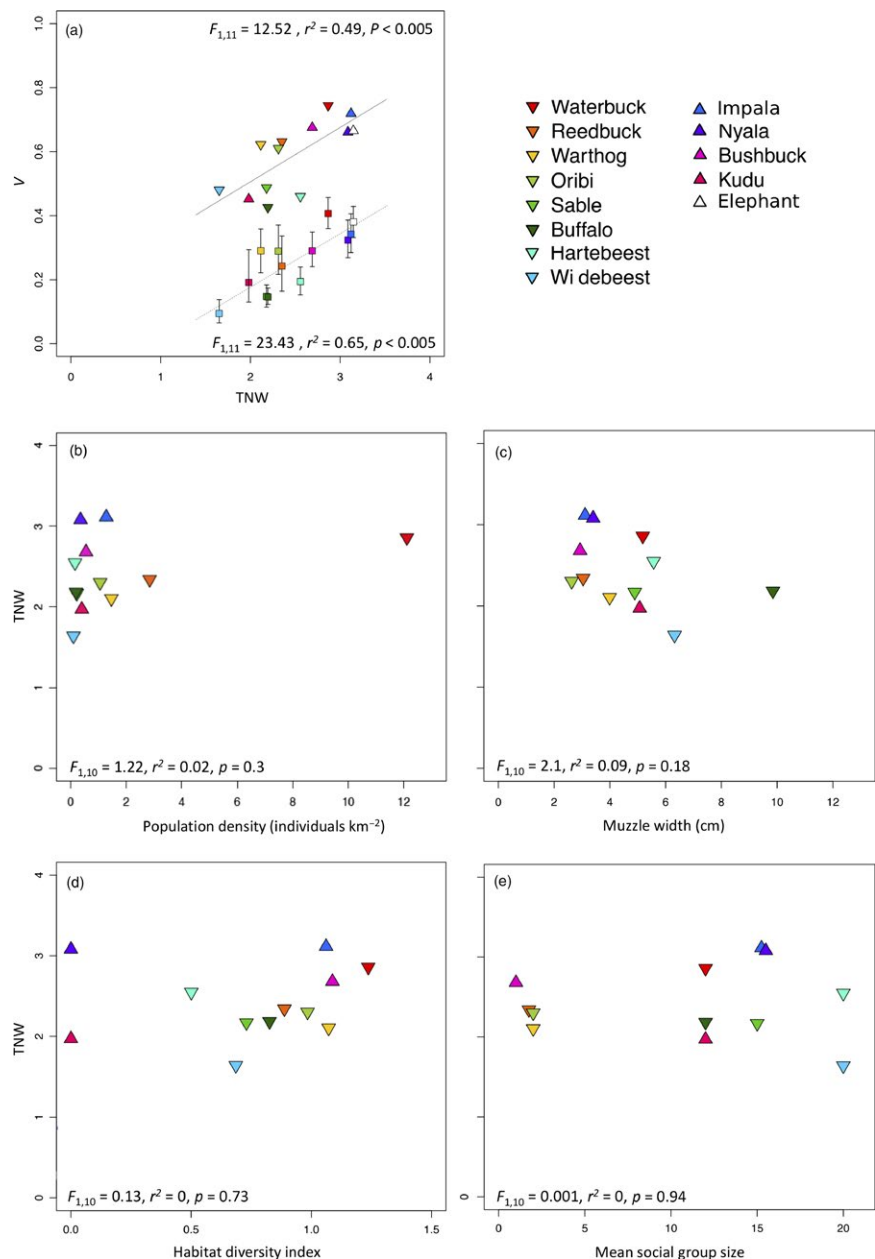
## 4 | DISCUSSION

We assembled a thorough 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. 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). As our study represents one of the few detailed analyses of consumer–resource interactions in a

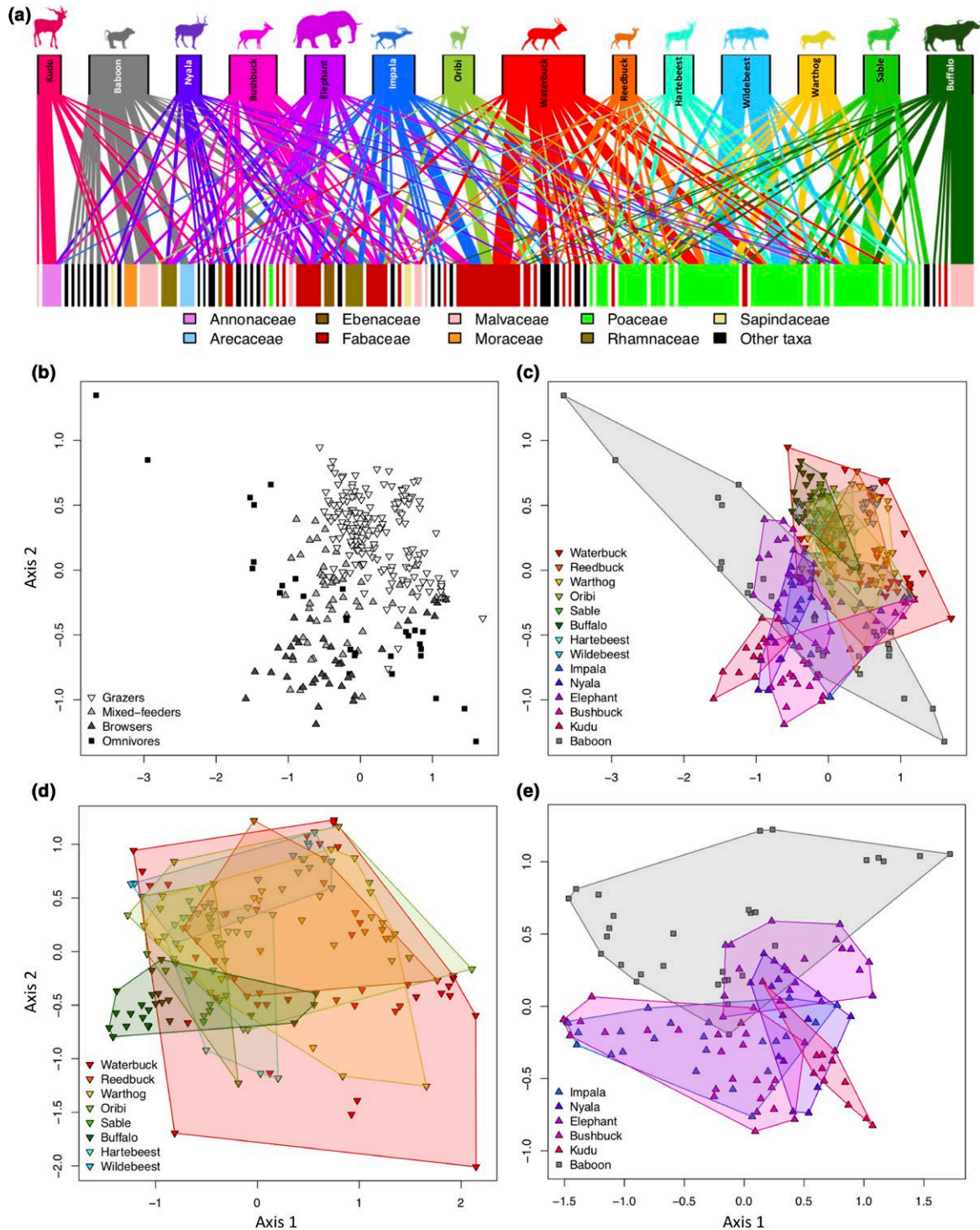
community that is recovering from near-extirpation, we are able to identify patterns that diverge from those observed in more intact systems and suggest approaches to test their generality and mechanistic basis. Below, we discuss our results in the context of each hypothesis in turn and outline a series of next steps for future research.

### 4.1 | 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



**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 (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 colours correspond to herbivore species. Elephants are included in panel a only (thus  $n = 13$ ); in panels b–e,  $n = 12$  ungulate species, as in Figure 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, coloured by plant family). Widths of upper boxes reflect the number of samples analysed 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 coloured by species to show community-wide interspecific 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 faecal sample; minimum convex polygons are shown for each species. Analogous results based on the presence-absence of plant mOTUs are shown in Supporting Information Appendix S8



to exploit resources that are less utilized by conspecifics (Araújo et al., 2011; Svanbäck & Bolnick, 2005, 2007). 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 (Jones & Post, 2016; Svanbäck & Bolnick, 2005, 2007)—for example, by expanding into novel habitats that support different resource assemblages (Møbak, Mysterud, Loe, Holand, & Austrheim, 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 postwar exponential growth in waterbuck numbers, however, the proportion of individuals occupying wooded areas has steadily increased (Stalmans & Peel, 2016). More generally, Supporting Information 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 (Figure 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 (Supporting Information Appendix S1) that were lumped 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 (Arsenault & Owen-Smith, 2008; Gordon & Illius, 1988; Janis & Ehrhardt, 1988; Jarman, 1974). 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 exhibit greater among-individual variation. Given the importance of bite size in forage selection by ungulates (Arsenault & Owen-Smith, 2008; Gordon & Illius, 1988), 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 intra-specific variation in this trait and others (see Bolnick et al., 2011; Clutton-Brock, Iason, & Guinness, 1987; du Toit, 2005), 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 et al., 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  $V$ .

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

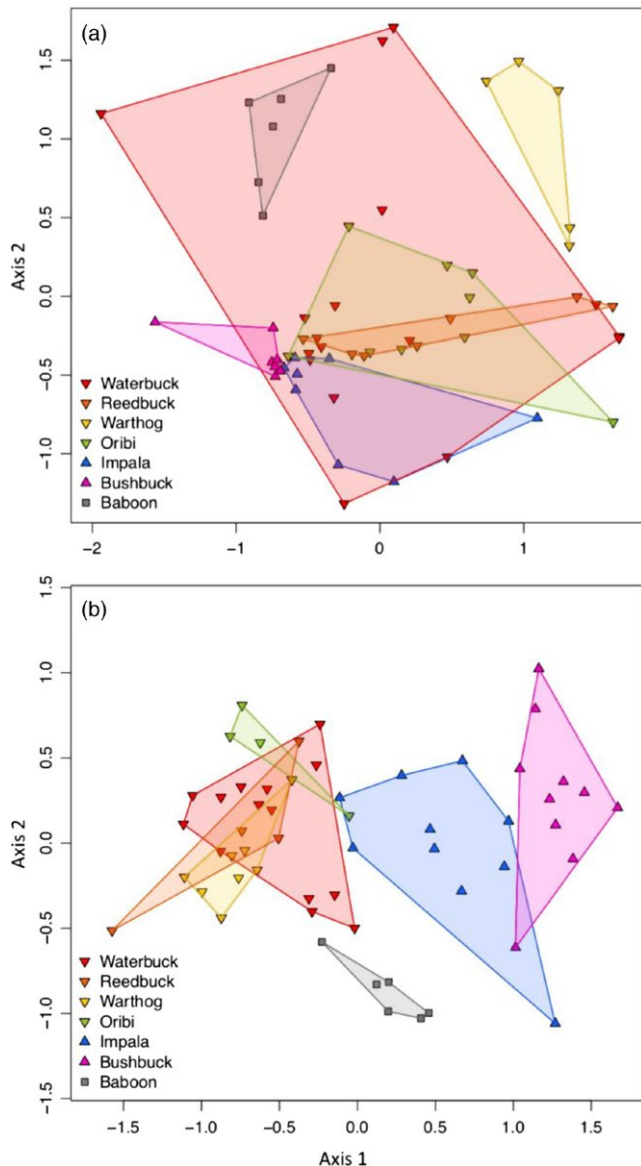
The slope of the positive correlation between  $V$  and TNW did not differ from that of a null model in which individual diets were drawn randomly from the population-level diet (Figure 2a). Thus, we cannot exclude the possibility that the observed correlation was a sampling artefact nor conclude that dietary generalists exhibit greater individual variation than specialists. Support for this latter 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, Emande, Ching-Maria, and Sebastien (2017), in studies of Brazilian frogs and marine fish, respectively, found as we did that observed positive  $V \sim \text{TNW}$  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 (Araújo et al., 2009; Van Valen, 1965). In postwar Gorongosa, the largest-bodied LMH species remain at fractions of their prior abundances and three large carnivores present in 1972 have yet to recover, which may have 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



**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 1,000 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 right 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 Supporting Information Appendix S9

	Grazer								Non-grazer					
	Waterbuck	Reedbuck	Warthog	Oribi	Sable	Buffalo	Hartebeest	Wildebeest	Impala	Nyala	Elephant	Bushbuck	Kudu	Baboon
Waterbuck <sup>(1)</sup>		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 <sup>(2)</sup>	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 <sup>(3)</sup>	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 <sup>(5)</sup>	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 <sup>(9)</sup>	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 <sup>(10)</sup>	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 <sup>(12)</sup>	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 <sup>(13)</sup>	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 <sup>(4)</sup>	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 <sup>(8)</sup>	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 <sup>(11)</sup>	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 <sup>(6)</sup>	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 <sup>(7)</sup>	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 <sup>(na)</sup>	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 4** Niche partitioning as a function of habitat type. Non-metric dimensional scaling (NMS) ordinations of Bray-Curtis dissimilarities for faecal 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 colours correspond to species. Analogous results based on the presence-absence data are presented in Supporting Information Appendix S10

by the population (Araújo et al., 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

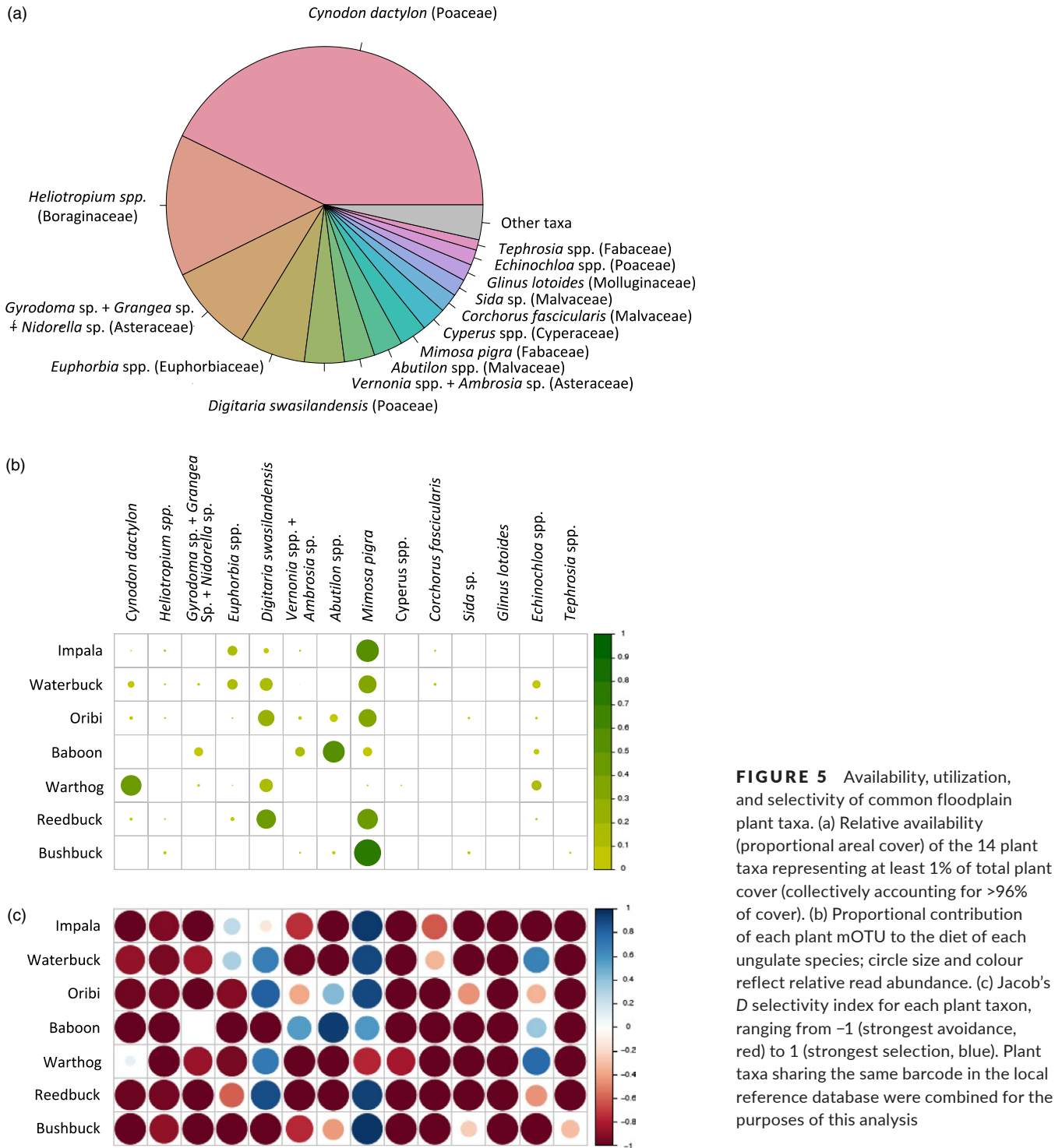
between patches through time, their overall niche breadths will be broader and likely more overlapping—and  $V$  will be lower—than can be inferred from a temporally static series of faecal samples. Stable-isotope approaches, which integrate diet over longer time periods, will be less susceptible to 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 faecal 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 (Figure 2b,c, Supporting Information 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; Supporting Information Appendix S5). The lack of concordance in the predictors of  $V$  and TNW can arise because TNW 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 (Supporting Information 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.

#### 4.3 | 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, Figure 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 2 years preceding our study (Supporting Information Appendix S2a), and they had among the highest habitat-use diversity scores (Figure 1c, Supporting Information 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.

These results are consistent with the interpretation that intra-specific 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 et al., 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 forage becomes severely depleted during the dry season (Supporting Information Appendix S11). The aforementioned postwar expansion of waterbuck out of the floodplain and into

savanna (Stalmans & Peel, 2016) may be a response to resource limitation in the floodplain. The depletion of Gorongosa's predator guild likely promotes 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 behaviour; 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 defences 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 (Arsenault & Owen-Smith, 2011; Hansen, Mugambi, & Bauni, 1985; Kleynhans et al., 2011; Lamprey, 1963; Macandza et al., 2012; Owen-Smith & Cooper, 1987; Owen-Smith et al., 2013; Prins et al., 2006). Other studies, however, have emphasized high within-guild similarity in forage species utilized (de longh et al., 2011; O'Shaughnessy et al., 2014; Sinclair, 1985). Because different investigators have quantified diets in different ways, direct quantitative comparisons across studies may not 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 analysed 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 relatively stable and having an intact large-carnivore assemblage.

We hypothesize that interspecific dietary niche overlap is anomalously high in postwar Gorongosa for two interrelated 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 multisite 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 (Angier, 2018; Pringle, 2017), which should enable a test of whether the return of top carnivores shrinks the dietary niches of mid-sized ungulate species.

#### 4.4 | 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. Thus, our results are consistent with the hypothesis that structural habitat heterogeneity promotes separation in the taxonomic composition of LMH diets (see also du Toit, 2003; du Toit & Olff, 2014; Jarman, 1974). 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.

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

We found mixed support for our prediction that the 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 vs. 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 (Figure 5b) and strongly avoided relative to its availability (Figure 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 (Dougall & Glover, 1964; Grzimek & Grzimek, 1960; Lamprey, 1963; Sinclair, 1977; Stewart & Stewart, 1970); Tinley (1977) found it to be the most frequently grazed plant overall in prewar 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. It is also possible that *Cynodon* is more heavily consumed during wetter periods than studied here.

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 defences might explain why forbs such as *Heliotropium* were consumed only rarely, despite their abundance. Ultimately, a mechanistic understanding of LMH forage selection will require analysing diet-composition data in light of multiple plant functional traits (Cingolani et al., 2005; Codron, Lee-Thorp, Sponheimer, & Codron, 2007; 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 long-standing difficulty of identifying the full range of plant taxa eaten. We believe that community-level, trait-based analyses of LMH diets will yield fresh insights about the factors governing forage selection, in addition to reinforcing principles already gleaned from the study of intraspecific trait variation.

## 5 | CONCLUSIONS

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 trophic rewilding 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 re-established. 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 the 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 behaviour, diet composition, and niche structure of their large-herbivore prey.

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## AUTHORS' CONTRIBUTIONS

J.P., T.R.K., and R.M.P. conceived and designed the study; J.P., A.B.P., J.L.A., and R.M.P. collected faecal samples; J.A.G. and B.W. collected and identified plant specimens for the local reference database; J.H.D. created the tree-cover map and contributed to spatial analysis; J.P. and A.B.P. conducted DNA analyses; J.P. performed bioinformatic analyses and analysed the data; J.P. and R.M.P. 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 et al., 2018). Local reference database sequences have also been deposited in BOLD (process ID's: PNG001-18 to PNG575-18).

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## SUPPORTING INFORMATION

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