

1 **Generality of cryptic dietary niche differentiation in diverse large-herbivore** 2 **assemblages**

3
4 Johan Pansu^{1,2,*}, Matthew C. Hutchinson¹, T. Michael Anderson³, Mariska te Beest^{4,5}, Colleen M. Begg⁶, Keith
5 S. Begg⁶, Aurelie Bonin^{7,8}, Lackson Chama⁹, Simon Chamaille-Jammes^{10,11}, Eric Coissac⁷, Joris P.G.M.
6 Cromsigt^{4,5,12}, Margaret Y. Demmel¹, Jason E. Donaldson^{3,13}, Jennifer A. Guyton¹, Christina Hansen¹,
7 Christopher I. Imakando⁹, Azwad Iqbal¹, Davis F. Kalima¹⁴, Graham I.H. Kerley⁵, Samson Kurukura¹⁵,
8 Marietjie Landman⁵, Ryan A. Long¹⁶, Isaack Norbert Munuo¹⁷, Ciara M. Nutter¹, Catherine L. Parr^{18,19,20},
9 Arjun B. Potter¹, Stanford Siachoono⁹, Pierre Taberlet^{7,21}, Eusebio Waiti⁶, Tyler R. Kartzinel^{22,23}, Robert M.
10 Pringle^{1,*}

11
12 ¹ Dept. of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, USA

13 ² ISEM, Univ. Montpellier, CNRS, IRD, Montpellier, France

14 ³ Dept. of Biology, Wake Forest University, Winston-Salem, NC, USA

15 ⁴ Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands

16 ⁵ Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa

17 ⁶ Niassa Carnivore Project, Niassa National Reserve, Mozambique

18 ⁷ Université Grenoble Alpes, CNRS, LECA, Grenoble, F-38000, France

19 ⁸ Argaly, Bâtiment Cleanspace, 354 Voie Magellan, Alpespace, F-73800 Sainte Hélène du Lac, France

20 ⁹ School of Natural Resources, Dept. of Zoology & Aquatic Sciences, Copperbelt University, Kitwe, Zambia

21 ¹⁰ CEFÉ, Univ. Montpellier, CNRS, EPHE, IRD, Montpellier, France

22 ¹¹ Mammal Research Institute, Dept. of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

23 ¹² Dept. of Wildlife, Fish & Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

24 ¹³ Odum School of Ecology, University of Georgia, Athens, GA, USA

25 ¹⁴ Dept. of National Parks and Wildlife, Lilongwe, Malawi

26 ¹⁵ Mpala Research Centre, Nanyuki, Kenya

27 ¹⁶ Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, USA

28 ¹⁷ Serengeti Wildlife Research Institute, Seronera, Tanzania

29 ¹⁸ School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom

30 ¹⁹ Dept. of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

31 ²⁰ School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

32 ²¹ UiT – The Arctic University of Norway, Tromsø Museum, Tromsø, Norway

33 ²² Dept. of Ecology, Evolution, and Organismal Biology, Brown University, Providence, RI, USA

34 ²³ Institute at Brown for Environment and Society, Brown University, Providence, RI, USA

35 * To whom correspondence may be addressed. Email: johan.pansu@gmail.com or rpringle@princeton.edu

36
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40 TRK conducted DNA metabarcoding analyses for all sites except Addo, and JP, MCH, TRK processed
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42 data for Addo. JP, RMP analyzed data and wrote the manuscript. All authors made revisions and approved
43 the manuscript.

44 **Competing Interest Statement:** PT holds patents related to the g/h primers and the use of the P6 loop of
45 the chloroplast *trnL* (UAA) intron for plant identification using degraded template DNA. These patents
46 pertain to commercial applications and have no impact on the use of this locus and primers by academic
47 researchers.

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49 **Keywords:** community assembly | dietary niche partitioning | ecological network analysis | ungulate
50 foraging behavior | modern coexistence theory

51 **ABSTRACT**

52 Ecological niche differences are necessary for stable species coexistence but are often difficult to
53 discern. Models of dietary niche differentiation in large mammalian herbivores invoke the quality,
54 quantity, and spatiotemporal distribution of plant tissues and growth-forms but are agnostic towards
55 food-plant species identity. Empirical support for these models is variable, suggesting that additional
56 mechanisms of resource partitioning may be important in sustaining large-herbivore diversity in
57 African savannas. We used DNA metabarcoding to conduct a taxonomically explicit analysis of
58 large-herbivore diets across southeastern Africa, analyzing ~4,000 fecal samples of 30 species from
59 10 sites in 7 countries over 6 years. We detected 893 food-plant taxa from 124 families, but just two
60 families—grasses and legumes—accounted for the majority of herbivore diets. Nonetheless,
61 herbivore species almost invariably partitioned food-plant taxa; diet composition differed
62 significantly in 97% of pairwise comparisons between sympatric species, and dissimilarity was
63 pronounced even between the strictest grazers (grass eaters), strictest browsers (non-grass eaters),
64 and closest relatives at each site. Niche differentiation was weakest in an ecosystem recovering from
65 catastrophic defaunation, indicating that food-plant partitioning is driven by species interactions, and
66 stronger at low rainfall, as expected if interspecific competition is a predominant driver. Diets
67 differed more between browsers than grazers, which predictably shaped community organization:
68 grazer-dominated trophic networks had higher nestedness and lower modularity. That dietary
69 differentiation is structured along taxonomic lines complements prior work on how herbivores
70 partition plant parts and patches and suggests that common mechanisms govern herbivore
71 coexistence and community assembly in savannas.

72 **SIGNIFICANCE STATEMENT**

73 The diversity of ungulates in African savannas has inspired generations of biologists to investigate
74 how similar species coexist, which requires that each be limited by different factors. Resource
75 partitioning is key to understanding this diversity, but prevailing theories of competition and
76 coexistence disregard the identity of food-plant species. Using high-resolution data on thousands of
77 large-herbivore diets from 10 savanna ecosystems, we identify several apparent generalities.
78 Sympatric herbivore species eat different plants in differing proportions, and variation in the
79 strength of these differences is consistent with the hypothesis that interspecific competition and
80 species' traits interact to shape diet composition and food-web topology. We conclude that
81 partitioning of food-plant species, while difficult to detect, contributes to the niche differences that
82 stabilize coexistence.

83 INTRODUCTION

84 Understanding the maintenance of species diversity is one of ecology's first and foremost challenges
85 (1–5). Once framed as a paradox (6), coexistence is no longer a theoretical mystery. Work over the
86 last 50 years has illuminated many paths to stable coexistence, all of which require stabilizing niche
87 differences to outweigh the fitness differences that promote competitive exclusion (7–9). Today, the
88 primary challenges are empirical, and gaps in our understanding of niche differentiation are among
89 the main obstacles to applying modern coexistence theory to the real world (9, pp. 154–156). This is
90 ironic, as niches have always been central to theories of biodiversity. Yet, niche differences are often
91 difficult to discern: “Ecologists have long been puzzled by the fact that there are so many similar
92 species in nature” (10, p. 6230). A recurring theme in the literature, however, is that seemingly
93 similar co-occurring species turn out, upon closer scrutiny, to differ in fundamental ways (11–14). If
94 such cryptic niche differences are common, then they have profound ramifications for
95 understanding competition, coexistence, ecological networks, and biodiversity at large (15).

96

97 Constraints on coexistence should be acute for big, wide-ranging consumers that occur at low
98 densities and require large quantities of substitutable resources (4, 7). In these respects, the diverse
99 ungulate assemblages in African savannas have long drawn attention (2, 16–18). Identifying the
100 factors that structure these assemblages is especially important given their precarious conservation
101 status and key functional roles in ecosystems (19, 20). Food is often limiting for ungulate
102 populations (21–23) and food partitioning by sympatric species is thus considered crucial for
103 coexistence (24). Prior research has focused mainly on two broad axes of dietary differentiation. One
104 is consumption of monocots vs. eudicots, a spectrum along which species are often categorized into
105 guilds typified by morphological adaptations to different diets: grazers eat grasses, browsers eat non-
106 grasses, mixed-feeders eat both (25–31). The other is essentially a quantity-quality tradeoff that can
107 manifest in several related ways—differential selection of plant parts and/or patches that differ in
108 biomass, nutritive value, and/or height—and also depends on herbivore morphology. Large-bodied
109 and non-ruminant species eat larger quantities of lower-quality food than small and ruminant species
110 (32–35); tall species have exclusive access to abundant canopy foliage but are less competitive for
111 sparser low-lying food (35–37).

112

113 Theoretically, either of these axes might suffice to allow many species to coexist in spatiotemporally
114 heterogeneous landscapes. Consumer-resource models have explored this possibility by

115 incorporating body-size-based tradeoffs in forage quantity, quality, and height (38–41). Empirically,
116 however, it is unclear that these tradeoffs alone are sufficiently strong and consistent to sustain
117 coexistence. There is often an inverse correlation between body size and diet quality, but it is noisy
118 and inconsistent (42–45). Support for size-based partitioning of forage height and patch size is
119 likewise variable (46–48). Last, although the grazer-browser spectrum is a robust generality (35),
120 species cluster bimodally along it (18), suggesting high niche overlap within grazer and browser
121 guilds. One recent study (18) theorized that competition promotes stabilizing dietary differences
122 between clusters, while equalizing effects of competitive similarity enable coexistence within them
123 (10). However, such clumpy patterns along a niche axis may reflect cryptic niche differences, rather
124 than ecological equivalence, within clusters (49).

125
126 Strikingly, although plant taxa vary in their accessibility and palatability to ungulates (50),
127 frameworks for understanding ungulate community assembly do not explicitly consider food-plant
128 identity (51). Unlike the literature on insect herbivores, where the role of plant taxonomic and
129 functional diversity has long been recognized (52–54), models of food partitioning by large
130 herbivores tend to be at most two-dimensional and to minimally require just one or two resources:
131 one from which herbivores select different parts at different places/times/heights, or two that create
132 a continuum of proportional use. By contrast, African savannas contain hundreds of plant species
133 that differ markedly in physical and chemical traits (51). In Kenya, 460 plant species from 66 families
134 occur in a 200-km² conservancy (55), which is smaller than an elephant’s home range (56). Serengeti
135 contains 200 species of grasses alone (57). If herbivores have taxonomically diverse diets and differ
136 in which taxa they eat, then dietary niche space may be many-dimensional, with scope for
137 segregation along axes defined by plant traits (51). In this case, divergent use of plant species would
138 be a basis for niche differences within grazing and browsing guilds, additional to differences in
139 selectivity for parts or patches of any given species.

140
141 Evaluating this possibility requires taxonomically precise diet data, which are scarce (15). The few
142 site-specific studies that have gathered high-resolution diet data for multiple sympatric species have
143 used varying methods, which hinders comparative analysis. Fecal DNA metabarcoding of the
144 chloroplast *trnL*-P6 marker (58) enables community-level diet profiles with large sample sizes and
145 high taxonomic resolution, and the relative read abundance (RRA) of plant sequences conveys
146 information about the proportional representation of food-plant taxa (59–61) (see **Methods**). Two

147 previous studies used this method for single-site/single-season analyses of 7 species in Kenya (61)
148 and 14 species in Mozambique (62), with contrasting results: the pattern of food-plant partitioning
149 was much starker in Kenya. But this discrepancy is difficult to interpret because the Mozambican
150 site, Gorongosa National Park, is actively recovering from extreme human disturbance (63–65). It
151 thus remains unclear whether there are any generalities in diet composition, food-plant partitioning,
152 or trophic-network structure among savanna herbivores. To plug this gap, we used DNA
153 metabarcoding to assess the diets of individuals and populations of 30 species in 10 savannas, 4 of
154 which we sampled in multiple seasons and years.

155

156 We explored this unique dataset for general patterns in herbivore diet composition and diversity. We
157 hypothesize that competition and differences in herbivore and plant functional traits give rise to
158 food partitioning at the level of plant species, which stabilizes coexistence and structures trophic
159 networks. This hypothesis implies support for four specific, testable predictions. (i) Large-herbivore
160 assemblages eat many taxa and each population eats only a subset, although the identity of that
161 subset may vary in space and time (for grazers, browsers, and mixed-feeders alike). (ii) Dietary
162 dissimilarity is always greater between than within sympatric species: interspecific differences in diet
163 composition manifest not just across the grazer-browser spectrum or among distant relatives, but
164 also between ecologically similar pairs of grazers, browsers, and congeners. (iii) The strength of
165 food-plant partitioning depends on the competitive environment, being strongest at low rainfall
166 when food is most limited (24) and weakest in non-equilibrial systems where interspecific
167 competition is weak. Gorongosa offers a natural experiment to test the latter proposition: there,
168 herbivore populations declined by >90% during the Mozambican Civil War but were increasing
169 when we sampled, and 3 dominant species accounted for 79% of all individuals (64). (iv) The
170 strength of food-plant partitioning also depends on species' traits, increasing with size discrepancy
171 between herbivore species (because size affects which plants animals can access and subsist on (51))
172 and being weaker between grazers than between browsers (because monocots are phylogenetically
173 and functionally less diverse than eudicots and thus offer less scope to partition taxa with distinct
174 traits (31, 51)); accordingly, grazer-dominated assemblages exhibit higher niche overlap and less
175 compartmentalized trophic networks (lower modularity, higher nestedness).

176

177 **RESULTS**

178 We sampled herbivore assemblages at 10 sites in southeastern Africa from 2013–2018 (**Fig. 1**).
179 These sites span diverse savanna physiognomies, latitudes (0.40° to –33.68°), rainfall regimes (400–
180 1200 mm yr⁻¹), elevations (100–2300 m), and disturbance histories (*SI Appendix, Table S1*). We
181 analyzed 3,928 fecal samples of 30 species, most of which were sampled in multiple sites and in
182 multiple seasons/years (“bouts”) in at least one site (24 total bouts; **Table 1**). These 30 species
183 represent 7 families, span orders of magnitude in mass (5–5,000 kg) and height (50–500 cm), and
184 include ruminants and nonruminants. We tried to sample at least the half-dozen most common
185 species at each site but did not succeed in all bouts; coverage ranged from 3–13 species per bout
186 (median 7, IQR 6–11). Except where noted, we restricted analyses to populations represented by
187 ≥10 samples per bout ($n = 167$). We sampled relatively small areas (median 106 km², IQR 49–366)
188 and ensured that samples were interspersed to minimize effects of spatial heterogeneity and
189 temporal variability in plant availability (*SI Appendix, Fig. S1*). We thus assume that all sampled
190 species had access to the same plant taxa at least in principle, even if they exhibit fine-scale spatial
191 segregation in practice. DNA extraction and sequencing followed established protocols (61, 62) and
192 were similar for all sites except Addo (**Methods** and *SI Appendix, Text S1*), which we excluded
193 from comparative analyses of dietary diversity and network structure.

194

195 **Taxonomic dimensionality of large-herbivore diets (prediction 1)**

196 Across all 10 sites, we detected 893 food-plant taxa from 124 families. Excluding Addo and rarefying
197 to a common depth of 10 samples, the median population’s diet comprised 31 taxa (IQR 25–37),
198 which is ~30% of the taxa consumed by the median assemblage (100, IQR 93–120, for bouts with
199 ≥5 species; *SI Appendix, Fig. S2*). Population-level dietary richness and diversity peaked at
200 intermediate grass RRA, indicating greatest niche breadth in mixed-feeders (*SI Appendix, Fig. S3*).
201 These hump-shaped curves were shallow, however, reflecting the narrow range of diet breadth
202 across sites; we found little additional effect of body mass, digestive morphology, or rainfall on
203 population-level dietary richness or diversity (*SI Appendix, Text S2, Tables S2 & S3*).

204

205 Most diets were dominated by two plant families, Poaceae (grasses) and Fabaceae (legumes) (**Fig. 2**).
206 The proportional contribution (mean RRA) of these families to each species’ average diet across
207 sites and bouts ranged 17–99% (median 61%). For 70% of species (21 of 30), grasses and legumes
208 together made up >50% of the average diet. The mean RRA of grasses in population-level diets
209 reveals a full grazer-browser spectrum (**Fig. 2A**) and the overall distribution of populations along

210 this spectrum (*SI Appendix, Fig. S4*) resembles that reported elsewhere (18). However, many
211 species' positions on this spectrum contrasted with their standard categorizations. Roan, Thomson's
212 gazelle, waterbuck, oribi, buffalo, and oryx are typically considered grazers (27–30), but grasses were
213 a minority of their diets in our data (26–49%). Some archetypal grazers exhibited extreme plasticity
214 in grass consumption—notably buffalo, reedbuck, hartebeest, and warthog, with mean grass RRA
215 ranging 5–84%, 48–74%, 46–96%, and 41–99%, respectively (**Fig. 2A**). Grass RRA of populations
216 and assemblages trended positively with rainfall in the preceding 90 d (*SI Appendix, Fig. S5*), but
217 these correlations were weak, nonlinear, and driven by low values of rainfall (0 mm) and grass RRA
218 in two sites, Niassa and Kafue.

219
220 Most populations ate substantial proportions of legumes (typically >10%, sometimes >50%) and
221 even strict grazers supplemented their diets with legumes. Among species sampled at multiple sites,
222 only spiral-horned antelopes (*Tragelaphus* spp.)—bushbuck, nyala, kudu, eland—always ate diets
223 dominated (>50% RRA) by 'other' plant families. Several widely sampled species exhibited broad
224 intraspecific variability in dominant food family—notably elephant, impala, and buffalo, with mean
225 RRA of 'other' families ranging 6–85%, 15–80%, and 15–82%, respectively (**Fig. 2C,D**). The
226 predominant 'other' families varied across sites and included Malvaceae, Acanthaceae, Rosaceae,
227 Combretaceae, Myrtaceae, Phyllanthaceae, Rhamnaceae, Euphorbiaceae, Asteraceae, and
228 Anacardiaceae (*SI Datasets 1–24*).

229

230 **Generality of food-plant partitioning in space and time (prediction *ii*)**

231 Across all sites and bouts, herbivore species' diets were compositionally distinct from those of most,
232 if not all, other sampled species. At the assemblage level, the generality and repeatability of plant-
233 taxon partitioning is clear from non-metric multidimensional scaling (NMDS) ordinations of dietary
234 dissimilarity between individual fecal samples: with few exceptions, species formed discrete clusters
235 of points, reflecting differences in the identity and RRA of food plants (**Fig. 3; SI Appendix, Fig.**
236 **S6**). To further probe these patterns while minimizing the effect of differing species' numbers and
237 identities, we analyzed subsets of ecologically similar species. First, we analyzed just 4 species from
238 each of the 8 best-sampled sites—the two with the highest grass RRA (grazers) and the two with the
239 lowest grass RRA (browsers) (**Fig. 4; SI Appendix, Fig. S7**). The starkest examples of within-guild
240 differentiation involved browsers (e.g., **Fig. 4A-C,E**), but even grazers often segregated almost
241 completely (e.g., **Fig. 4B-E**). Sympatric close relatives—species in the same genus, tribe, or

242 subfamily—likewise clustered separately (*SI Appendix, Fig. S8*). This pattern held for plains and
243 Grevy’s zebras (*Equus* spp.) in Laikipia; for Thomson’s and Grant’s gazelles (Antilopini) in Serengeti;
244 for warthog and bushpig (Suinae) in Addo; for waterbuck and puku (*Kobus* spp.) in Kafue; and for
245 spiral-horned antelopes (*Tragelaphus* spp.) in Laikipia, Nyika, Gorongosa, and Addo. Among the 3
246 species of Alcelaphini in Serengeti, wildebeest segregated from hartebeest and topi, but the latter
247 two species overlapped more extensively (*SI Appendix, Fig. S8B*).

248

249 Consistent with these ordinations, dietary dissimilarity was greater between than within species at all
250 sites (*SI Appendix, Fig. S9*). In 17 of 24 bouts, each species’ diet differed significantly from *every*
251 other sympatric species in pairwise permutational MANOVA (perMANOVA) with Holm-
252 Bonferroni adjustment for multiple comparisons (*SI Appendix, Fig. S10A*). Overall, 700 of 723
253 (97%) pairwise comparisons of dietary dissimilarity between sympatric species were significant (adj. p
254 < 0.05 ; **Table S4**); these included 89 pairs where we relaxed sample size to $n < 10$ for one or both
255 species (**Methods**), but the result was the same without those pairs (619 of 634 significant, 98%; *SI*
256 *Appendix, Text S2*).

257

258 **Ecological context and the strength of food-plant partitioning (prediction *iii*)**

259 While almost all pairwise differences were statistically significant, their strength varied (as indexed by
260 the perMANOVA r^2 , the variance in dietary dissimilarity attributable to species identity; *SI*
261 *Appendix, Fig. S10B*). To explain this variation, we analyzed the r^2 values using AIC_c-based
262 selection of 16 linear mixed-effects models with random intercepts for site (*SI Appendix, Text S2*);
263 fixed effects included rainfall and the difference between each pair of species in body mass, digestive
264 system, and grass RRA. The top model (Akaike weight = 0.56, marginal $r^2 = 0.28$, conditional $r^2 =$
265 0.54) included grass RRA, body mass, and rainfall; the negative coefficient of rainfall indicates that
266 dietary differences diminish as food availability increases, consistent with our prediction (*SI*
267 *Appendix, Table S5, Fig. S11A*).

268

269 Among sites, plant partitioning was weakest in Gorongosa, where the dominant herbivore species
270 (waterbuck, reedbuck, warthog) ate individually variable and broadly overlapping diets (**Fig. 3F**; *SI*
271 *Appendix, Fig. S6C*). Gorongosa accounted for 13 of the 23 non-significant pairwise contrasts
272 (and 11 of 15 with $n \geq 10$ for both species); waterbuck, reedbuck, and warthog accounted for 11 of
273 these. The remaining 10 non-significant contrasts included 1 from Laikipia, 7 from Serengeti, and 2

274 from Hwange, and 6 of these were among the 89 with limited power owing to inclusion of species
275 with $n < 10$ samples (*SI Appendix, Table S4*). While the vast majority of pairwise contrasts in
276 Gorongosa were still statistically significant (85 of 98, 87%), the r^2 values were lower than at other
277 sites (mean \pm SE = 0.15 ± 0.03 , vs. 0.32 ± 0.02 across other sites/bouts; *SI Appendix, Fig. S9 &*
278 **S10B**).

279

280 **Species' traits and trophic-network structure (prediction iv)**

281 As noted above, body-mass differential was a strong (positive) predictor of pairwise niche
282 differences, occurring in all empirically supported models (*SI Appendix, Table S5, Fig. S11B*).
283 Digestive system, by contrast, had little effect after accounting for the other predictors; dietary
284 differences were strongest between pairs of nonruminants and weakest between pairs of ruminants
285 (*SI Appendix, Table S5*).

286

287 As predicted, the structure of herbivore-plant networks depended on the relative prevalence of
288 grazing and browsing in the community. Across sites and bouts, mean pairwise niche overlap
289 between species increased linearly with the mean grass RRA of all sampled species ($r^2 = 0.76$; **Fig.**
290 **5A**), in keeping with the greater compositional similarity of grazer diets (**Figs. 3, 4**). Further,
291 network modularity decreased ($r^2 = 0.76$; **Fig. 5B**), and nestedness increased ($r^2 = 0.62$; **Fig. 5C**), as
292 linear functions of grass RRA.

293

294 **DISCUSSION**

295 **Taxonomic dimensionality of large-herbivore diets**

296 The data supported our first prediction: if herbivore species partition plant taxa, then each should
297 eat only a fraction of the foods used by the assemblage at any given time. This fraction, roughly
298 30%, is an upper bound given that assemblage-level diet breadth should depend on the number of
299 species sampled but population-level breadth should not. While assemblage-level dietary richness
300 varied, the range of population-level richness was surprisingly consistent across sites and bouts.
301 Variation within this range was best predicted by grass RRA and poorly predicted by body size,
302 digestive morphology, and rainfall. These results generalize recent findings from Kenya (66) but
303 contrast with intuition that large and nonruminant species should have more varied diets because
304 they range farther and eat more (43) (*SI Appendix, Text S2*). Despite the consistency in
305 population-level diet breadth, intraspecific variation in food-plant identity was pronounced: the 30

306 species in our study collectively ate roughly $\frac{1}{4}$ of extant plant families. These patterns are consistent
307 with our hypothesis that competition constrains the realized population-level diets of species whose
308 fundamental niches are much broader (67–69). Savanna ungulates appear to act as facultative
309 generalists (*sensu* 68), able to eat a wide range of available plant diversity but foraging
310 disproportionately on a small subset of these in any given place/time (69).

311
312 The bimodal distribution of grazers and browsers in our study matches that in a recent synthesis
313 (18). However, eudicot consumption was prevalent in our data; at the species level, there were few
314 strict grazers. 9 species always had <20% grass RRA, but just 3 always had >80%. Several ostensible
315 grazers (27, 30) mainly browsed (>70% eudicots; Grant’s gazelle, roan) or spanned nearly the entire
316 spectrum (Thomson’s gazelle, buffalo). The grazer/browser/mixed-feeder trichotomy is a useful
317 heuristic, but this intraspecific variability shows that categories are misleading if treated as fixed
318 species-level traits. Continuous measures of grass consumption convey information about context-
319 dependent dietary flexibility, which may be an important behavioral mechanism for sustaining
320 population persistence and coexistence by enabling animals to rapidly adjust diets in response to
321 fluctuating environmental conditions and competitive regimes (70–72). Rainfall explained only a
322 modest amount of the variance in grass RRA, again suggesting a role for biotic interactions in
323 delineating realized diets.

324
325 We found that legumes are the 2nd major constituent of diets behind grasses, accounting for $\geq 10\%$
326 of RRA in 95 of 167 population–bout combinations. Grasses and legumes were the 1st- and 2nd-
327 ranked families in 8 of 10 sites and accounted for the majority of diet in most species. Savanna
328 herbivore diets can thus be described in triaxial space as the proportion of grasses, legumes, and all
329 other families (cf. 73). The prevalence of legumes reflects the composition of woody communities in
330 African savannas (74), where acacia (*Senegalia*, *Vachellia*), miombo (*Julbernardia*, *Brachystegia*), mopane
331 (*Colophospermum*), and other leguminous trees are abundant. However, it also reflects consumption of
332 forbs, which are often ignored despite accounting for most of the plant diversity in grassy biomes
333 (75, 76). Nitrogen-fixing forbs are protein-rich compared to C₄ grasses and thus nutritionally
334 valuable for both grazers and browsers (60). For example, *Indigofera* spp. were eaten by all 17 species
335 in Laikipia and were among the top foods overall there and in Serengeti (*SI Datasets 1–10*). The
336 extensive use of forbs by savanna grazers highlights the functional importance of this often-
337 overlooked growth form (60, 75, 76).

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Generality of food-plant partitioning in space and time

In support of our second prediction, we detected interspecific differences in diet composition at the assemblage level, between pairs of grazers and browsers, among close relatives, and indeed in 97% of all 723 pairwise comparisons. This typically resulted in discrete clusters of samples in ordinations, but even when such clusters overlapped, intraspecific variation helped to separate species' average diets.

Our results complement the longstanding emphasis on how large herbivores partition food based on quantity and quality. The factors that shape herbivores' selection of bites and patches—nutrient-rich vs. fibrous tissue, tall vs. low foliage, concentrated vs. dispersed biomass—differ among plant species as well as within them (51). Thus, any morphophysiological trade-offs that promote spatiotemporal differentiation in the use of plant parts should also promote differential use of plant taxa (and vice versa). We illustrate the compatibility of these mechanisms with reference to two classic models of food partitioning, browsing stratification and grazing succession (35). Giraffe, kudu, and dik-dik in Laikipia all ate the shrub *Senegalia brevispica* (20%, 35%, and 27% RRA in March 2015) and surely partitioned its foliage by feeding at different heights (browsing stratification (35)). But these herbivores also ate different species: the tree *Enclea divinorum* was >20% RRA for giraffe and kudu but just 1% for dik-dik; the tree *Senegalia mellifera* was >20% RRA for giraffe and dik-dik but just 1% for kudu; and the small shrubs *Melbania ovata* and *Plicosepalus sagittifolius* were 9% RRA for dik-dik but 0% for giraffe and kudu (**SI Datasets 1-4**). Similarly, zebra, wildebeest, and Thomson's gazelle in Serengeti all ate the grass *Digitaria macroblephara* (18%, 25%, and 5% RRA in May–June 2018), as per the grazing-succession model (35). Yet, the low-lying annual forbs *Euphorbia inaequilatera* and *Monsonia angustifolia* dominated gazelle diets (61% RRA) but were just 9% RRA for wildebeest and 0% for zebra; the grasses *Themeda triandra* and *Sporobolus fimbriatus* together were 15% RRA for zebra but just 4% for wildebeest; and a half-dozen forb species (*Indigofera*, *Euphorbia*, *Pentanisia*, *Monsonia*, *Phyllanthus* spp.) were 29% RRA for wildebeest but just 4% for zebra (**SI Datasets 5-10**). Species at similar positions on the grazer-browser spectrum (18) thus have multiple non-redundant paths to dietary differentiation, perhaps explaining why interspecific differences in sward-height and patch-size selection are not always clear-cut (46, 47).

369 The consistency of plant partitioning probably reflects interspecific competition in both modern (22,
370 35, 36) and evolutionary time (24, 37, 77), although diet data alone cannot prove it (78). Competition
371 should pressure herbivores to eat plants that they have a relative advantage in harvesting and
372 processing, which should simultaneously promote food partitioning and select for morphological
373 and behavioral trait differentiation (24, 79). Differences among herbivore species in size, mouth
374 width, dentition, prehensile organs, digestive system, sensory perception, gut microbiota, etc. (31, 37,
375 47, 80, 81) should map onto differences among plant species in height, leaf size, fiber, spines, toxins,
376 etc. (31, 50, 51, 68), resulting in both differential use of plant taxa in a patch and differential
377 selection of patches with distinct vegetation. Strong competition should accentuate these
378 associations; weak competition should relax them (24). Yet, other interactions may contribute to
379 plant partitioning, and these are not mutually exclusive. Grazing succession is hypothesized to arise
380 from facilitation ((32) but see (35)), in which case the forb-rich diets of Thomson's gazelles may be
381 enabled by zebra and wildebeest clearing tall grass and increasing ground-level light availability.
382 Predation risk can promote spatial segregation and hence diet differentiation by confining prey to
383 different safe spaces (e.g., open areas for 'runners' (82) vs. thickets for 'hidiers' (83)). However,
384 facilitation and risk can also increase spatial and dietary overlap—as when large grazers create lawns
385 that attract smaller grazers (35, 42, 84) or when predators force prey into refuges with limited food
386 options (85, 86)—suggesting that these interactions alone are unlikely to explain the ubiquity of
387 food-plant partitioning in our data.

388

389 **Ecological context and the strength of food-plant partitioning**

390 The support for our third prediction bolsters the inference that competition enforces diet
391 differences. The strength of pairwise differentiation was inversely related to rainfall, as expected
392 given that food is most limited during dry periods (34). This pattern is common across taxa and has
393 been interpreted in terms of foraging theory as a product of interspecific competition operating on
394 multiple timescales (24, 79): strong selection in times of food scarcity favors traits that enable species
395 to use certain foods more efficiently than their competitors; in lean times, competition forces each
396 species to forage mainly on those foods; in times of plenty, species converge on foods that are most
397 profitable, even if these are not the foods for which each species is most competitive.

398

399 The weak partitioning in Gorongosa is consistent with release from interspecific competition but
400 also illustrates how multiple biotic interactions can interact with spatial heterogeneity and habitat

401 selection to influence realized diets. Gorongosa's post-war recovery is marked by explosive
402 population growth of waterbuck (57,000 individuals in 2018, 20-fold higher than pre-war) and to a
403 lesser extent warthog and reedbuck (11,000 each), while buffalo, hippo, zebra, and wildebeest
404 numbers remained $\leq 1,000$ (1–16% of pre-war) (64). The 3 superabundant species have increasingly
405 saturated space. In 2018, the logistically growing waterbuck population reached 81 individuals
406 ($\sim 16,000$ kg) km^{-2} in its preferred floodplain habitat, depleting its preferred food plants; in response,
407 individuals expanded into nearby woodland where they ate different plant species (87). In this way,
408 intraspecific competition and density-dependent habitat selection in the absence of an intact
409 competitor guild led to high individual variation and diffuse dietary overlap with species such as
410 oribi and wildebeest. At the same time, bushbuck (1,800 individuals in 2018) expanded in the
411 opposite direction, from woodland into floodplain, owing not to density dependence but to
412 relaxation of predation risk (83); this, too, led to high inter-individual variation and diffuse
413 interspecific overlap with species such as impala and oribi.

414

415 **Species' traits and trophic-network structure**

416 Consistent with our fourth prediction, plant partitioning was stronger between species of different
417 size. The role of size in differentiating savanna herbivore diets is classically understood in terms of a
418 tradeoff in the quantity vs. quality of bites and patches (33–35); our results suggest that this tradeoff
419 extends to differences in dietary species composition. Partitioning was also stronger between
420 browsers than grazers, which regulated network topology: the mean grass RRA of species at a site
421 was highly correlated with niche overlap, network nestedness, and modularity. This suggests the
422 prediction that resource partitioning and food-web structure should differ between open, grassy
423 savannas and densely wooded ones. One caveat is that although well-sampled assemblages *did* differ
424 in mean grass RRA (highest in open, grassy Serengeti), the grass consumption of a partially sampled
425 assemblage also depends on which species are sampled. Mean grass RRA in Serengeti ranged from
426 51% in July–October 2018 (7 species with ≥ 10 samples) to 93% in August–October 2017 (4 species
427 with ≥ 10 samples), and the latter bout had the highest niche overlap and nestedness and lowest
428 modularity (**Fig. 5**). Insufficient sampling can bias network metrics (88) but our results show that
429 this bias is predictable depending on the grass consumption of sampled species. We note, however,
430 that the strength of plant partitioning did not strongly covary with the absolute *number* of species
431 sampled (**SI Appendix, Text S2**), suggesting that our core results are qualitatively robust to the
432 incomplete sampling of assemblages.

433

434 **Conclusions**

435 Our study reveals several general patterns. Chiefly, we show that sympatric species consistently
436 partition plant taxa, which suggests unrecognized dimensions of the dietary niche and the need for a
437 more taxonomically explicit conceptualization of stabilizing niche differences. The ubiquity of this
438 pattern shows that it is not peculiar to specific communities or contexts, and its variable strength
439 suggests an underlying influence of interspecific competition (even if other factors also contribute).
440 The outlier to this pattern, in an otherwise intact savanna recovering from severe defaunation, shows
441 that niche differences are relaxed by major perturbations to community structure—further evidence
442 that the general pattern is enforced by biotic interactions. Large herbivores can and do eat many
443 plant taxa (fundamental niches are broad and overlapping) but locally each population eats a
444 compositionally distinct subset (realized niches are narrower and differentiated) except when
445 released from the biotic interactions that prevail in stable assemblages. These differences are ‘cryptic’
446 because dietary species composition has long been difficult to measure (15). DNA metabarcoding
447 thus has a key role to play in clarifying the taxonomic dimensions of resource partitioning and
448 bridging stubborn theory-data gaps in the study of species coexistence and ecological networks (61,
449 89–91).

450

451 We refer to differences in dietary species composition as stabilizing because that is their only
452 plausible effect on coexistence: whatever their cause, their *effect* can only be to relax interspecific
453 competition and intensify intraspecific competition relative to the scenario in which all herbivore
454 species eat the same plant taxa. The near-universality of these differences further suggests that they
455 are not just incidental but integral in the regulation of diversity, consistent with theory predicting
456 that the number of coexisting animal species is constrained by the number of resource species (4)
457 and with evidence that ungulate and plant diversification are evolutionarily coupled in Africa (92).
458 While our results thus identify a general facet of niche differentiation that is not captured in
459 prevailing models of community assembly (34, 35), they do not obviate other stabilizing
460 mechanisms: herbivores may simultaneously segregate in space, eat different plant species, select
461 different parts of those species, and be differentially limited by different predators (34, 35).
462 Analyzing diets in light of the functional traits and spatial distributions of plants and herbivores (51)
463 will help to bridge these outlooks by identifying how body size and other attributes predict
464 consumption of particular plant taxa, how many plant-trait axes suffice to discriminate species’ diets,

465 and the extent to which dietary differences arise from spatial segregation vs. food preference. A
466 unified theoretical framework integrating these mechanisms and their hierarchical structure (if any)
467 would enable a more nuanced understanding of coexistence and the likely responses of large-
468 herbivore communities to global change.

469
470 Importantly, however, no study has yet established that any of these stabilizing mechanisms is either
471 necessary or sufficient for causing intraspecific limitation to exceed interspecific limitation, much
472 less their relative importance in combination. We note one opportunity for a more direct empirical
473 assault on this problem. Species translocations for conservation and rewilding are increasingly
474 common and offer quasi-experimental insights into processes that are otherwise intractable in large
475 mammals (93–95). Successful invasion of a stable community without collapse of any resident
476 population is evidence for coexistence (85, 96), and accompanying displacement of resident species
477 along one or more niche axes is evidence that those axes are important for enabling coexistence.
478 Failed invasions are similarly illuminating in light of the degree of niche overlap between introduced
479 species and residents (85). This approach to inference has been fruitful in other animal systems (85,
480 97, 98) and can be extended to reintroduced large-herbivore populations. Several of the populations
481 sampled in this study—white rhinoceros in Laikipia, elephant and giraffe in Hluhluwe-iMfolozi,
482 black rhinoceros in Addo—are the product of reintroductions within the last 60 years, but to our
483 knowledge these events have not been systematically probed for insights into coexistence
484 mechanisms. To this end, demographic time series, coupled with the expanding arsenal of powerful
485 tools for quantifying diet composition and space use (87), may yield major advances in linking niche
486 relationships to coexistence outcomes.

487

488 **METHODS**

489 We collected fresh fecal samples during road surveys in 24 sampling bouts. Our main unit of analysis
490 is the ‘population-bout’, the diet of a species at a particular place and time. We restricted most
491 analyses in the main text to populations with ≥ 10 fecal samples per sampling bout. We relaxed this
492 threshold only where explicitly noted to include more sites and species, mainly for supplementary
493 visual analysis (*SI Appendix, Figs. S6–S8*) but also in models of pairwise dissimilarity (*SI*
494 *Appendix, Figs. S9–S11 and Table S5*). In the latter case, we verified that results were equivalent
495 using the $n \geq 10$ threshold and were not confounded by the number of species sampled per site (*SI*
496 *Appendix, Text S2*).

497
498 At each site except Addo, samples were pre-processed to stabilize DNA and then frozen until
499 transport to a dedicated facility at Princeton University, where we extracted total DNA from fecal
500 samples using commercial kits (61, 62, 81). At Addo, extracellular DNA was extracted in the field
501 (99) and transferred to Université Grenoble Alpes. For all samples, the P6 loop of the *trnL*(UAA)
502 intron (58) was amplified by PCR, purified, and sequenced on an Illumina HiSeq, but protocols and
503 data processing differed for Addo vs. other sites (***SI Appendix, Text S1***). We curated sequence data
504 using *OBITools* (100). We performed taxonomic assignment using both local reference databases
505 (from Laikipia, Serengeti, and Gorongosa) and a global reference database from the European
506 Molecular Biology Laboratory (Addo sequences were assigned only to a local database). Unique
507 sequences retained after filtering and accounting for $\geq 1\%$ RRA per sample were considered
508 molecular operational taxonomic units (mOTUs, ‘taxa’). We generated one sample \times mOTU matrix
509 per sampling bout to calculate the RRA of each mOTU per sample. Details of laboratory protocols
510 and data filtering are in ***SI Appendix, Text S1***. We used RRA data for analyses, because (a) grass
511 RRA in studies of large-herbivore diets using *trnL*-P6 is highly correlated with estimates of % grass
512 consumption based on stable-isotope analysis and feeding trials (59–61), suggesting that RRA is a
513 broadly reliable indicator of proportional consumption; and (b) RRA-based inferences about
514 resource partitioning are generally qualitatively equivalent to those based on presence-absence in
515 diverse animal groups, including large herbivores (61, 62, 85, 91). We first calculated mean (± 1 SE)
516 RRA of each plant family in the diet of each population in each bout (**Fig. 2A-C**). For species-level
517 statistics (**Table 1, Fig. 2D**), we calculated the ranges and means of grass and legume RRA across all
518 population-bouts per species.

519
520 For 7 of the 10 sites—excluding Addo due to methodological differences (***SI Appendix, Text S1***)
521 and Hwange and Kruger due to low sample sizes—we calculated dietary species richness and
522 diversity for each population in each bout. To control for differences in sampling intensity, we
523 iteratively rarefied the number of reads per sample to 2,000 (using *vegan*), randomly resampled 10
524 samples per species, and averaged 100 iterations. Dietary richness was calculated as the total number
525 of mOTUs. Dietary diversity was calculated as the Shannon index (a common metric of niche width
526 (62) that reflects both richness and evenness) using *RInSp* (101). To explore predictors of
527 population-level dietary richness and diversity, we used AIC_c-based model selection to evaluate
528 support for 16 candidate mixed-effects models with fixed effects of body mass, digestive type, local

529 rainfall, and grass RRA (details and rationale in **SI Appendix, Text S2**). To assess relationships
530 between rainfall and the mean grass RRA of species and assemblages, we extracted daily rainfall
531 from CHIRPS (102) as a raster file with gridded 0.25° resolution, using *heavyRain* (103); for each
532 bout, we calculated the centroid of sample-collection locations and used that point to calculate total
533 rainfall during the 90 d before the onset of sampling.

534

535 To analyze dietary niche differences, we calculated the Bray-Curtis compositional dissimilarity index
536 between each pair of samples in each bout and contrasted inter- vs. intra-specific dissimilarity at
537 each site. We visualized these patterns using NMDS for each site and bout, as well as for subsets of
538 species in each of the 8 best-sampled sites (excluding Hwange and Kruger) to contrast (a) the
539 species with the 2 highest and 2 lowest mean grass RRA values and (b) closely related sympatric
540 species. We used perMANOVA in *vegan* (104) to test for significant differences in diet composition
541 among all species in each of the assemblages visualized using NMDS. We further conducted
542 pairwise perMANOVA to test for dietary differences between each pair of sympatric species in each
543 bout (total $n = 723$), using the Holm method to control the family-wise error rate for comparisons
544 within bouts (false-discovery rate and Bonferroni corrections gave similar results). We used the
545 perMANOVA r^2 to index the strength of pairwise dietary differences and again used AIC_c to rank 16
546 candidate mixed-effects models fitted to the r^2 values (details and rationale in **SI Appendix, Text S2**
547 **and Table S5**).

548

549 We used assemblage-level proportional grass consumption (the mean grass RRA across all
550 populations per bout) as a quantitative index of the degree to which assemblages were dominated by
551 grazers or browsers. To evaluate assemblage-level niche overlap, we calculated Pianka's index (105)
552 for each pair of species based on their population-level average diets and then calculated the mean \pm
553 1 SE across all pairs using *EcoSimR* (106). We calculated weighted bipartite modularity of each
554 network using the DIRTLPAwb+ algorithm (107), selecting the maximum value from 10 iterations
555 of the algorithm. We calculated nestedness as weighted NODF (108) in *bipartite* (109).

556

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572

573 DATA ACCESSIBILITY

574 Raw and filtered sequencing data and R code are deposited in Dryad Digital Repository (*doi pending*).

575

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800

801 **FIGURE CAPTIONS**

802 **Fig. 1. We collected large-herbivore fecal samples for diet analysis from 10 sites in 7**
803 **countries.** Numbers in parentheses beneath each site name indicate, respectively, the total number
804 of species and bouts (i.e., distinct seasons and/or years) sampled at each site. Three-letter country
805 codes are those used by the International Olympic Committee. Background shading shows mean
806 annual precipitation (MAP) from 2013–2018, extracted from the CHIRPS database (102). Sites,
807 sampling years, and 95% minimum convex polygons of sampled areas (range, km²) from north to
808 south are: Laikipia, Kenya (2013–2016, 68–151 km²); Serengeti National Park, Tanzania (2017–2018,
809 267–835 km²); Nyika National Park, Malawi (2017, 352 km²); Niassa National Reserve, Mozambique
810 (2017, 149 km²); Kafue National Park, Zambia (2017, 61 km²); Gorongosa National Park,
811 Mozambique (2016–2017, 49–350 km²); Hwange National Park, Zimbabwe (2016, ~570 km²);
812 Kruger National Park, South Africa (2017, 9–20 km²); Hluhluwe-iMfolozi Park, South Africa (2017,
813 370 km²); Addo Elephant National Park, South Africa (2013–2014, 22–49 km²). Maps of sample-
814 collection locations and detailed information on site characteristics are in ***SI Appendix, Fig S1 and***
815 **Table S1.**

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818 **Fig. 2. Proportional representation of plant families in African savanna large-herbivore diets.**
819 Mean (± 1 SE) RRA of **(A)** grasses (Poaceae), **(B)** legumes (Fabaceae), and **(C)** all other plant
820 families ($n = 124$) in the diet of each herbivore population in each sampling bout ($n \geq 10$ fecal
821 samples per point). Colors denote site. For populations sampled repeatedly at the same site, we
822 show data from each bout (season/year) separately. Black crosses (+) are species-level means across
823 all sites and bouts. **(D)** Mean RRA of grasses (x -axis) and legumes (y -axis) for each species (indicated
824 by colors and two-letter identifiers within the central points). Small points are values for each site
825 and bout; large points are species-level averages across all sites and bouts. Solid diagonal line
826 corresponds to 100% of diet; dashed line corresponds to 50% of diet.

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829 **Fig. 3. Community-level dietary dissimilarity of large herbivores in 10 savanna ecosystems.**
830 NMDS ordinations visualize dietary dissimilarity (Bray-Curtis metric) within and among species.
831 Points correspond to individual fecal samples; points farther apart are more dissimilar. Ellipses show
832 1 SD. Stress value and perMANOVA testing for significant dissimilarity among all species are
833 shown in each panel. For repeatedly sampled sites, we chose one illustrative period from among
834 those with the largest number of species and samples; data from all sampling bouts at these sites are
835 shown together in ***SI Appendix, Fig. S6***. Panels are ordered from northernmost (top left) to
836 southernmost (bottom right) site. **(A)** Laikipia, Kenya, July 2016 ($n = 149$ samples, 10 species; wet
837 season, 90-d rainfall 156 mm). **(B)** Serengeti, Tanzania, February-April 2018 ($n = 129$ samples, 8
838 species; wet season, 90-d rainfall 205 mm). **(C)** Nyika, Malawi, August 2017 ($n = 137$ samples, 6
839 species; dry season, 90-d rainfall 71 mm). **(D)** Niassa, Mozambique, August-September 2017 ($n =$
840 134 samples, 6 species; dry season, 90-d rainfall 0.2 mm). **(E)** Kafue, Zambia, August 2017 ($n = 153$
841 samples, 7 species; dry season, 90-d rainfall 0 mm). **(F)** Gorongosa, Mozambique, June-August 2016

842 ($n = 262$ samples, 13 species; early dry season, 90-d rainfall 233 mm). **(G)** Hwange, Zimbabwe,
843 August-September 2016 ($n = 36$ samples, 5 species; dry season, 90-d rainfall 0 mm). **(H)** Kruger,
844 South Africa, May 2017 ($n = 59$ samples, 3 species; early dry season, 90-d rainfall 106 mm). **(I)**
845 Hluhluwe-iMfolozi, South Africa, November 2017 ($n = 105$ samples, 7 species; wet season, 90-d
846 rainfall 135 mm). **(J)** Addo, South Africa, February 2014 ($n = 273$ samples, 11 species; summer, 90-d
847 rainfall 108 mm). Here, we relaxed the sample-size threshold used elsewhere ($n \geq 10$ per species)
848 only for 4 populations in Hwange (G).

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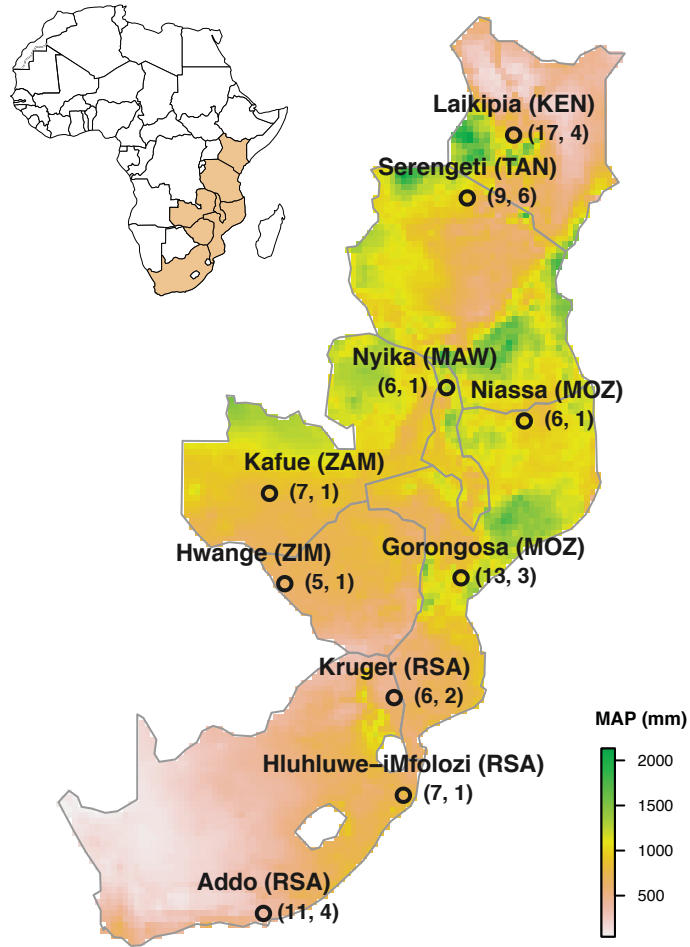
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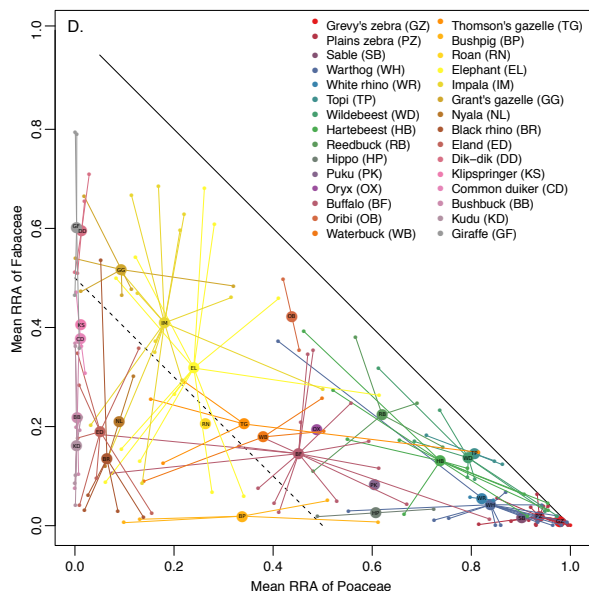
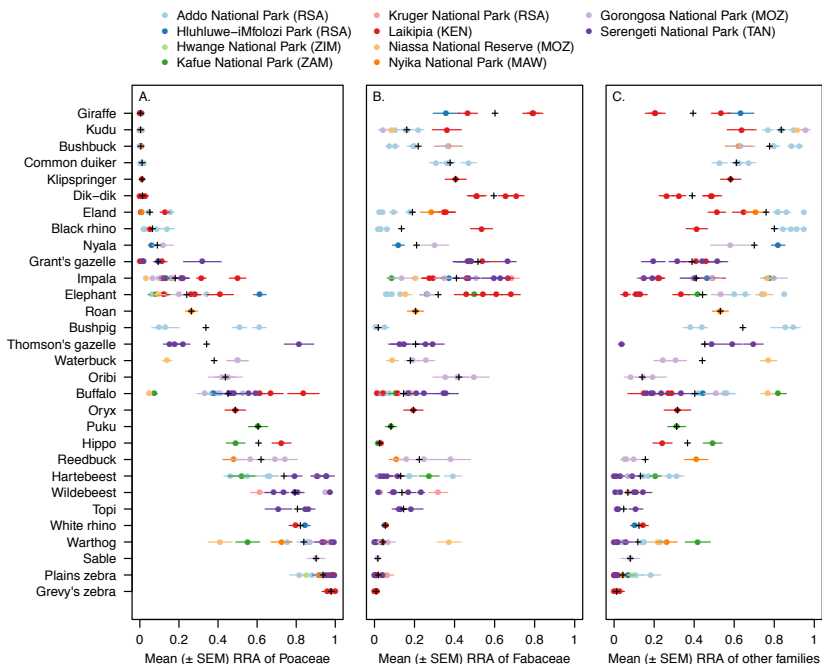
851 **Fig. 4. Resource partitioning within and between guilds along the grazer-browser spectrum.**
852 NMDS ordinations of Bray-Curtis dietary dissimilarity for the two strictest browsers (lowest grass
853 RRA; triangles) and two strictest grazers (highest grass RRA; diamonds, circles) at the 8 best-
854 sampled sites in 6 countries. Points correspond to individual fecal samples; points farther apart are
855 more dissimilar. Stress value and permutational analysis of variance testing for significant
856 dissimilarity among species are in each panel. For repeatedly sampled sites, we used the same
857 sampling bout as in **Fig. 3**; corresponding plots from all sampling bouts at these sites are shown
858 together in **SI Appendix, Fig. S7**. Analogous results for sets of closely related sympatric species are
859 in **SI Appendix, Fig. S8**.

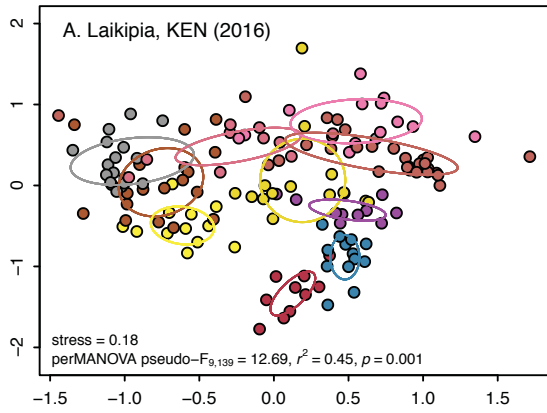
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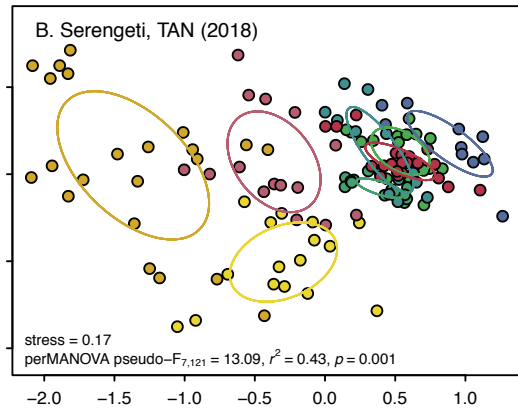
862 **Fig. 5. Assemblage-level proportional grass consumption regulates trophic-network**
863 **structure.** **(A)** Mean Pianka niche-overlap index ($r^2 = 0.76$, $F_{1,15} = 46.89$, $p < 0.001$), **(B)** bipartite
864 network modularity ($r^2 = 0.76$, $F_{1,15} = 47.56$, $p < 0.001$), and **(C)** bipartite network nestedness ($r^2 =$
865 0.62 , $F_{1,15} = 24.77$, $p < 0.001$) as functions of assemblage-level mean grass RRA across all bouts at 7
866 well sampled sites. Error bars are ± 1 SE; shading shows 95% CIs. We included all bouts at
867 repeatedly sampled sites owing to substantial within-site variability in the species sampled and their
868 mean grass RRA (see **Fig. 2**; **SI Appendix, Fig. S5**); in general, the across-site trends are also
869 qualitatively evident within sites.



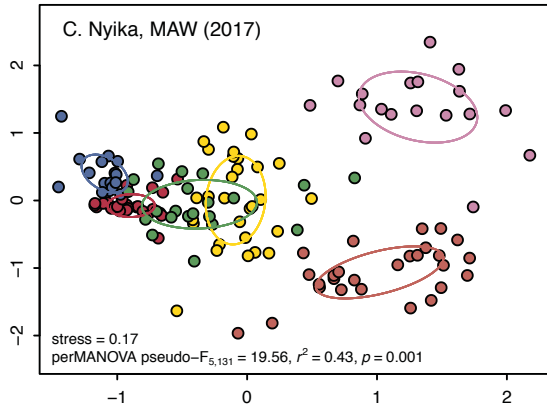




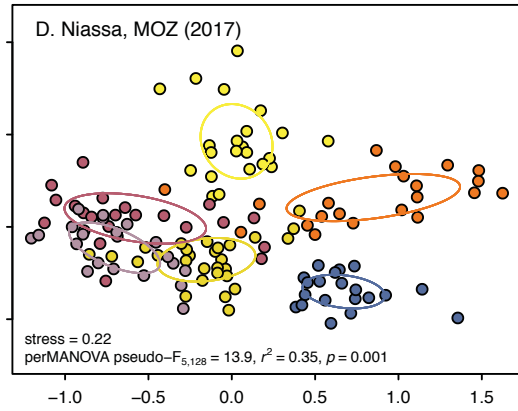
- Black rhino
- Dik-dik
- Eland
- Elephant
- Giraffe
- Impala
- Klipspringer
- Oryx
- Plain's zebra
- White rhino



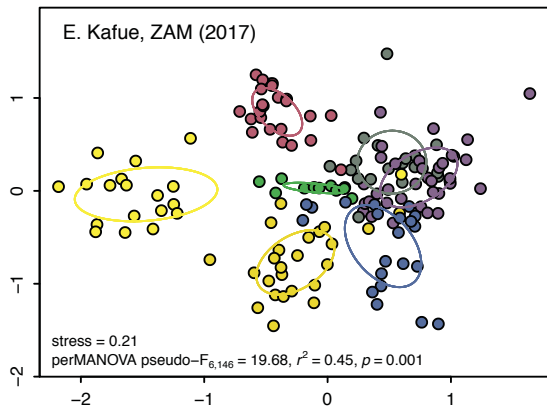
- Buffalo
- Grant's Gazelle
- Hartebeest
- Impala
- Plain's zebra
- Topi
- Warthog
- Wildebeest



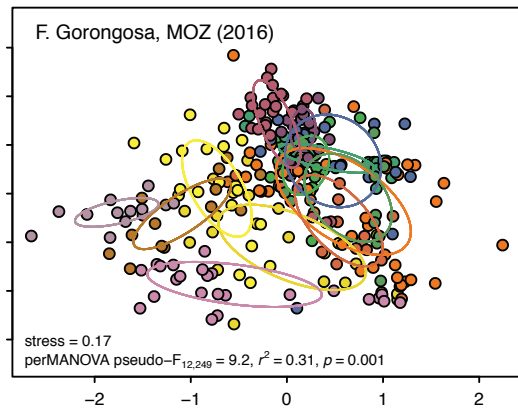
- Bushbuck
- Eland
- Plain's zebra
- Reedbuck
- Roan antelope
- Warthog



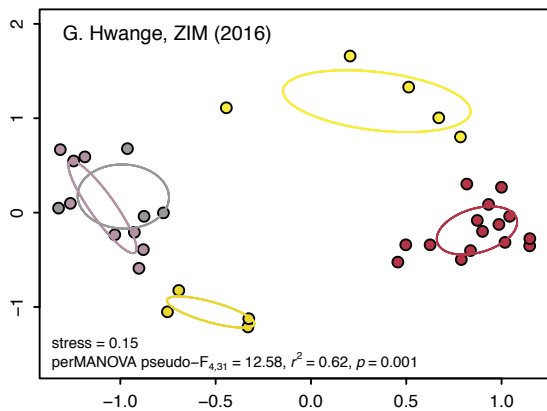
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- Elephant
- Impala
- Kudu
- Warthog
- Waterbuck



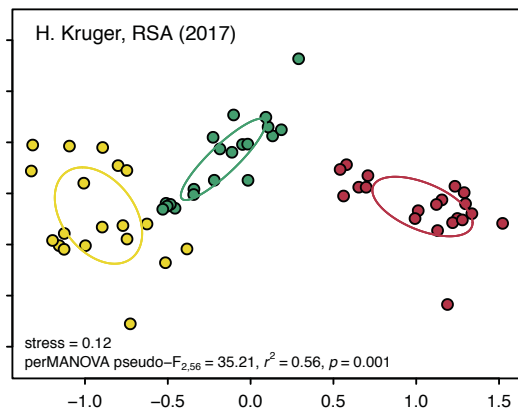
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- Elephant
- Hartebeest
- Hippo
- Impala
- Puku
- Warthog



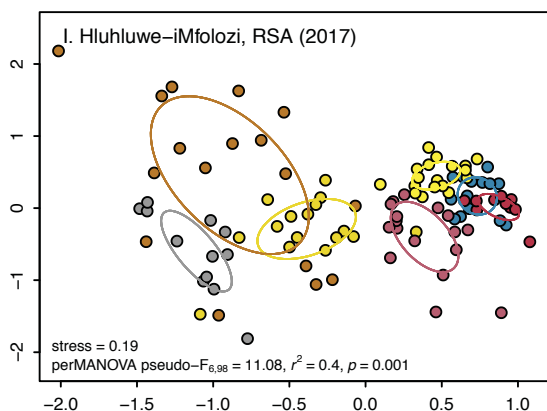
- Buffalo
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- Impala
- Kudu
- Nyala
- Oribi
- Reedbuck
- Sable
- Warthog
- Waterbuck
- Wildebeest



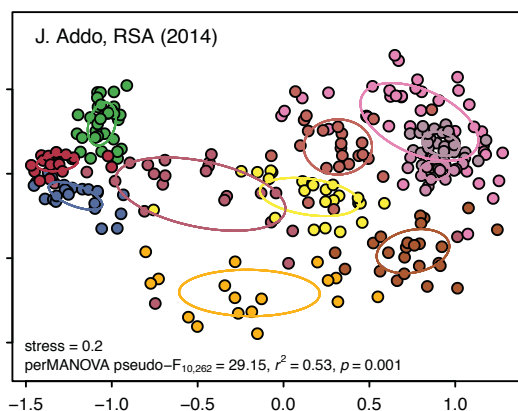
- Elephant
- Giraffe
- Impala
- Kudu
- Plain's zebra



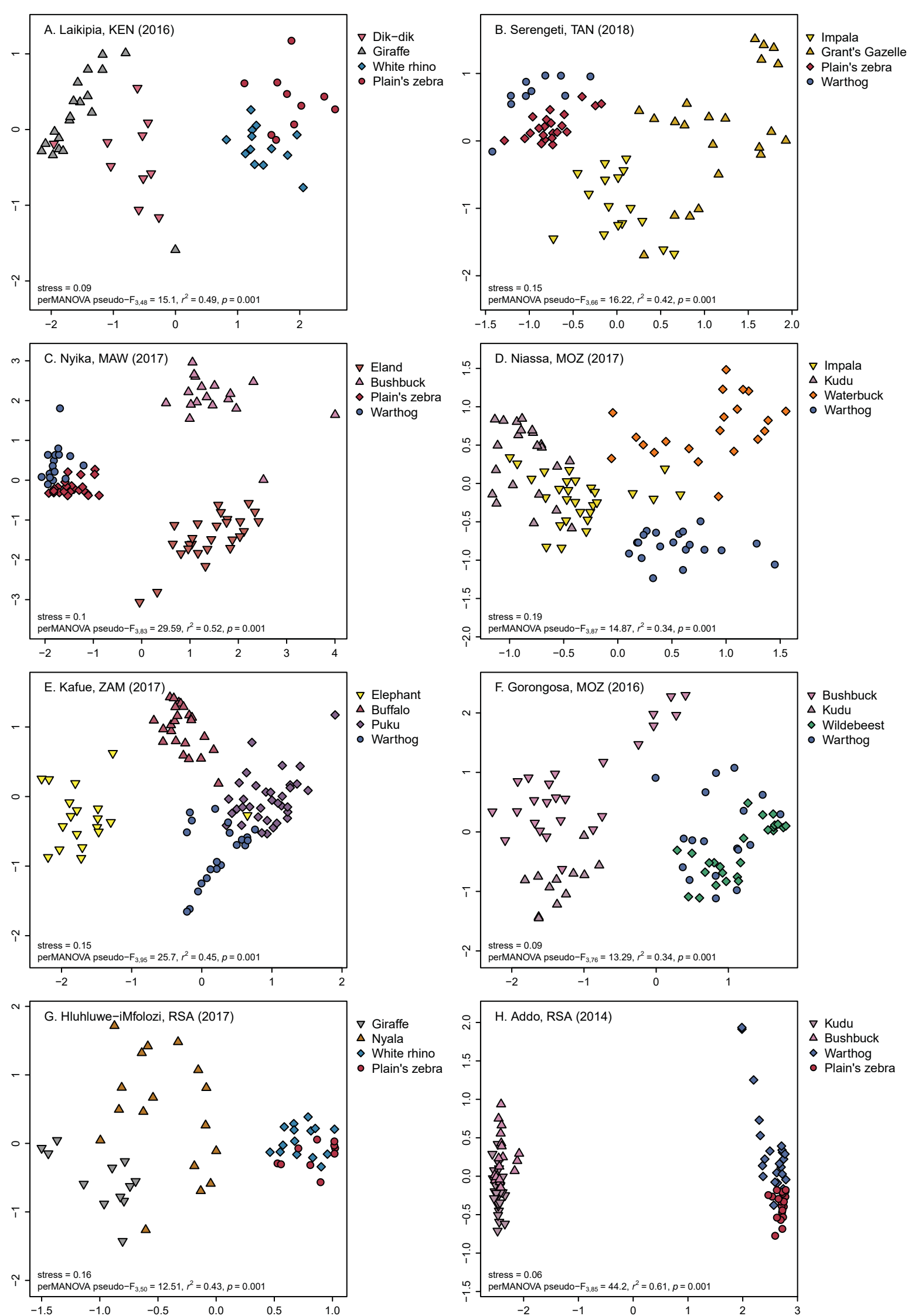
- Impala
- Plain's zebra
- Wildebeest

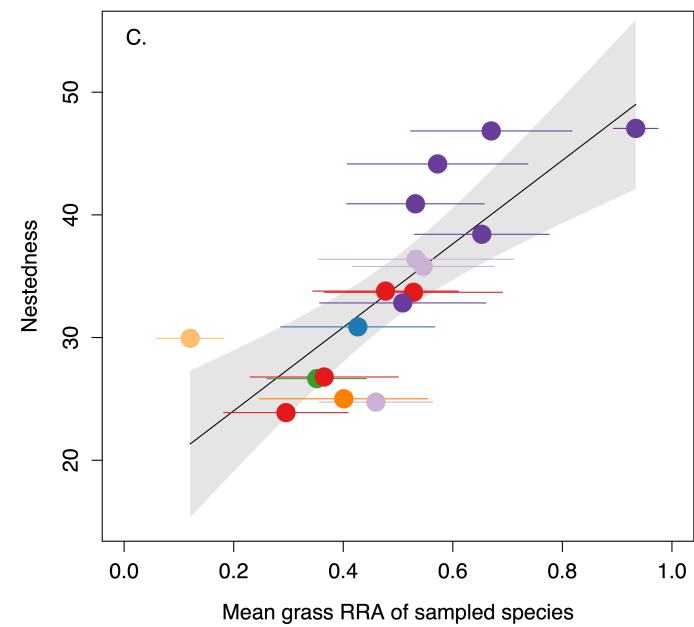
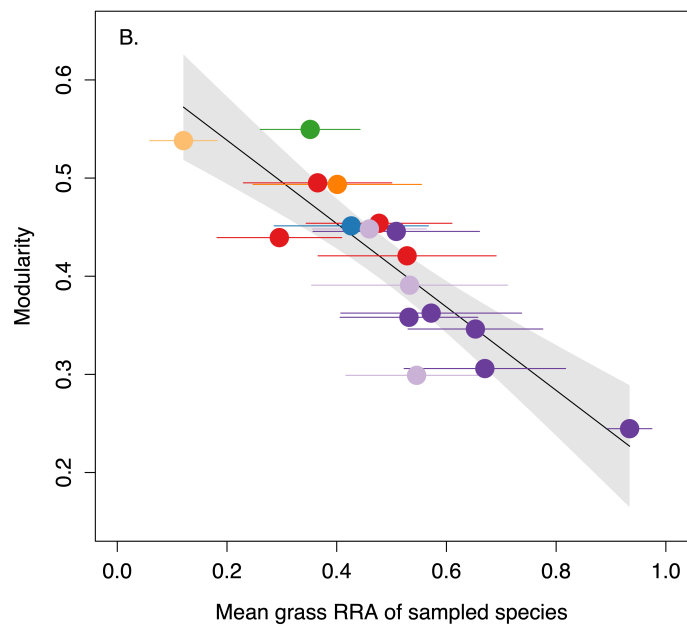
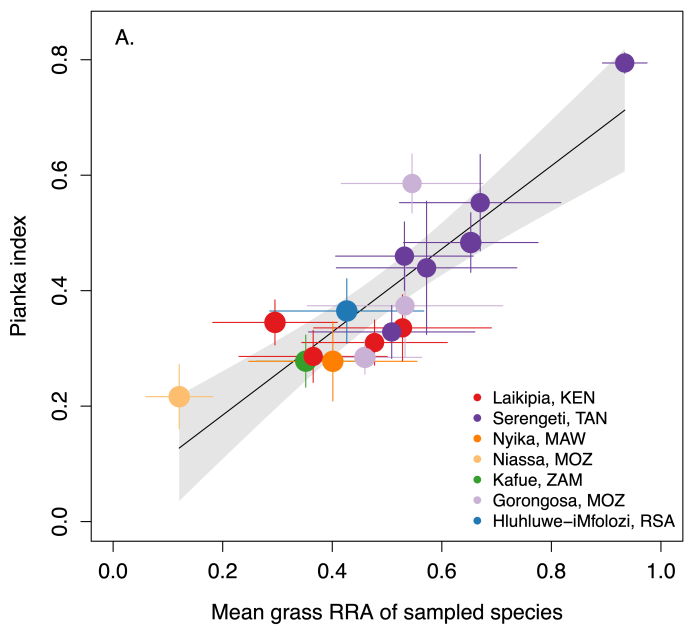


- Buffalo
- Elephant
- Giraffe
- Impala
- Nyala
- Plain's zebra
- White rhino



- Black rhino
- Buffalo
- Bushbuck
- Bushpig
- Common duiker
- Eland
- Elephant
- Hartebeest
- Kudu
- Plain's zebra
- Warthog





1 **Table 1. Herbivore species and their characteristics.** Summary data here are based on 3,547
2 fecal samples from 30 large-herbivore species represented by ≥ 10 samples per bout (of 3,928 total
3 samples analyzed). Species are listed in order of increasing body mass (from panTHERIA (110)).
4 Several sites were sampled repeatedly; we show the number of sites sampled, number of sampling
5 bouts, and sample size for each species. For each species in each bout, we calculated the population-
6 level mean RRA of grasses and legumes (rounded to integer percent values), along with population-
7 level dietary richness and diversity; these data are shown as ranges spanning all sites and sampling
8 bouts for each species (site- and bout-specific tables are in *SI Datasets 1–24*). Dietary richness and
9 Shannon diversity (here based on the complete set of samples collected in each bout, elsewhere
10 rarefied to $n = 10$ for comparative analysis) were not calculated for Addo because methodological
11 differences precluded comparable estimates with other sites (**Methods**); thus, two species sampled
12 only in Addo (common duiker and bushpig) lack values for these metrics. Site characteristics are in
13 *SI Appendix, Table S1*.

Common name	Latin name	Body mass in kg	Sites sampled (total bouts)	n samples	Mean % grass RRA	Mean % legume RRA	Dietary richness	Dietary diversity
Dik-dik	<i>Madoqua cf. guentheri</i>	5	1 (4)	119	0 – 3	51 – 71	34 – 52	2.05 – 2.69
Klipspringer	<i>Oreotragus oreotragus</i>	14	1 (1)	13	1	41	49	2.82
Common duiker	<i>Sylvicapra grimmia</i>	16	1 (4)	140	0 – 2	31 – 47		
Oribi	<i>Ourebia ourebi</i>	17	1 (3)	56	42 – 45	35 – 50	34 – 44	2.29 – 2.88
Thomson’s gazelle	<i>Endorcas thomsonii</i>	23	1 (4)	79	15 – 81	13 – 29	24 – 49	2.05 – 2.93
Cape bushbuck	<i>Tragelaphus sylvaticus</i>	43	3 (6)	142	0 – 1	7 – 37	34 – 51	2.38 – 2.69
Impala	<i>Aepyceros melampus</i>	53	7 (14)	320	3 – 50	9 – 69	29 – 81	2.01 – 3.20
Grant’s gazelle	<i>Nanger granti</i>	56	2 (6)	110	0 – 32	46 – 66	31 – 60	2.27 – 2.82
Southern reedbuck	<i>Redunca arundinum</i>	58	2 (4)	71	48 – 74	11 – 38	19 – 54	2.31 – 2.72
Bushpig	<i>Potamochoerus larvatus</i>	69	1 (4)	78	10 – 61	1 – 5		
Puku	<i>Kobus vardonii</i>	72	1 (1)	35	60	8	58	2.52
Common warthog	<i>Phacochoerus africanus</i>	83	7 (14)	266	41 – 99	0 – 37	19 – 42	2.00 – 2.64
Nyala	<i>Tragelaphus angasi</i>	88	2 (2)	30	6 – 12	12 – 30	44 – 52	2.76 – 3.06
Topi	<i>Damaliscus lunatus</i>	127	1 (3)	55	71 – 86	12 – 18	27 – 42	2.50 – 2.8
Hartebeest	<i>Alcelaphus buselaphus</i>	161	4 (10)	200	46 – 96	2 – 39	25 – 48	2.18 – 2.78
Blue wildebeest	<i>Connochaetes taurinus</i>	199	3 (7)	151	61 – 97	2 – 32	25 – 48	1.62 – 2.65
East African oryx	<i>Oryx beisa</i>	201	1 (1)	10	49	19	30	2.65
Waterbuck	<i>Kobus ellipsiprymnus</i>	204	2 (3)	96	14 – 50	9 – 26	42 – 70	2.65 – 3.31
Greater kudu	<i>Tragelaphus strepsiceros</i>	206	4 (7)	163	0 – 1	4 – 36	26 – 46	1.76 – 2.52
Sable	<i>Hippotragus niger</i>	236	1 (1)	17	90	2	34	2.08
Roan	<i>Hippotragus equinus</i>	264	1 (1)	29	26	21	42	2.81
Plains zebra	<i>Equus quagga</i>	279	7 (16)	338	82 – 100	0 – 6	19 – 40	1.58 – 2.54
Grevy’s zebra	<i>Equus grevyi</i>	408	1 (3)	68	96 – 100	0 – 1	17 – 38	2.26 – 2.57
Common eland	<i>Tragelaphus oryx</i>	563	3 (7)	161	1 – 16	3 – 36	36 – 67	2.23 – 2.83
Cape buffalo	<i>Syncerus caffer</i>	593	7 (16)	313	5 – 84	1 – 36	22 – 76	1.42 – 3.35
Giraffe	<i>Giraffa camelopardalis</i>	964	2 (4)	64	0 – 1	36 – 79	18 – 26	1.74 – 2.62
Black rhinoceros	<i>Diceros bicornis</i>	996	2 (5)	111	2 – 14	2 – 53	51 – 51	2.65 – 2.65
Hippopotamus	<i>Hippopotamus amphibius</i>	1536	2 (2)	31	49 – 72	2 – 3	39 – 77	2.64 – 2.69
White rhinoceros	<i>Ceratotherium simum</i>	2286	2 (2)	28	80 – 84	5 – 6	37 – 42	2.19 – 2.62
Savanna elephant	<i>Loxodonta africana</i>	3825	6 (12)	253	6 – 61	6 – 73	24 – 76	1.90 – 3.18