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Multiple dimensions of dietary diversity in large mammalian herbivores

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Abstract

1. Theory predicts that trophic specialization (i.e. low dietary diversity) should make consumer populations sensitive to environmental disturbances. Yet diagnosing specialization is complicated both by the difficulty of precisely quantifying diet composition and by definitional ambiguity: what makes a diet 'diverse'?
2. We sought to characterize the relationship between taxonomic dietary diversity (TDD) and phylogenetic dietary diversity (PDD) in a species-rich community of large mammalian herbivores in a semi-arid East African savanna. We hypothesized that TDD and PDD would be positively correlated within and among species, because taxonomically diverse diets are likely to include plants from many lineages.
3. By using DNA metabarcoding to analyse 1,281 faecal samples collected across multiple seasons, we compiled high-resolution diet profiles for 25 sympatric large-herbivore species. For each of these populations, we calculated TDD and PDD with reference to a DNA reference library for local plants.
4. Contrary to our hypothesis, measures of TDD and PDD were either uncorrelated or negatively correlated with each other. Thus, these metrics reflect distinct dimensions of dietary specialization both within and among species. In general, grazers and ruminants exhibited greater TDD, but lower PDD, than did browsers and non-ruminants. We found significant seasonal variation in TDD and/or PDD for all but four species (Grevy's zebra, buffalo, elephant, Grant's gazelle); however, the relationship between TDD and PDD was consistent across seasons for all but one of the 12 best-sampled species (plains zebra).
5. Our results show that taxonomic generalists can be phylogenetic specialists, and vice versa. These two dimensions of dietary diversity suggest contrasting implications for efforts to predict how consumers will respond to climate change and other environmental perturbations. For example, populations with low TDD may be sensitive to phylogenetically 'random' losses of food species, whereas populations with low PDD may be comparatively more sensitive to environmental changes that disadvantage entire plant lineages—and populations with low dietary diversity in both taxonomic and phylogenetic dimensions may be most vulnerable of all.

KEYWORDS

community phylogenetics, food web networks, grazer–browser continuum, megafauna, niche partitioning, specialism–generalism trade-off, ungulate foraging ecology

1 | INTRODUCTION

Dietary niche breadth—the diversity of foods that animals eat (Roughgarden, 1972)—influences the geographic distribution of species (Brown, 1984; Slatyer, Hirst, & Sexton, 2013), the structure of ecological networks (Dunne, Williams, & Martinez, 2002; Layman et al., 2015), and the sensitivities of populations and individuals to environmental change (Bolnick et al., 2011; Boyles & Storm, 2007; Colles, Liow, & Prinzing, 2009). Theories such as the specialization-disturbance hypothesis (Vazquez & Simberloff, 2002) predict that animals with diverse diets (generalists) should be more robust to natural or anthropogenic fluctuations in resource availability than animals with low dietary diversity (specialists), because the broader portfolio of resources used by generalists provides a buffer against the loss of any particular resource (Colwell, Dunn, & Harris, 2012; Pin Koh et al., 2004). However, empirical tests of this prediction have been inconclusive (Colles et al., 2009; Vazquez & Simberloff, 2002), in part because 'specialization' can be measured in various ways that reflect distinct ecological and/or evolutionary processes, and that therefore have different implications for how animals respond to perturbations of their food base (Vazquez & Simberloff, 2002).

The aim of this study was to explore the nature of dietary specialization by comparing the taxonomic and phylogenetic diversity of diets in a community of African large herbivores. A herbivore may have a 'diverse' diet if it eats many plant species (i.e. high taxonomic dietary diversity, TDD), or if it eats many plant lineages (i.e. high phylogenetic dietary diversity, PDD). The relationship between TDD and PDD is unknown because PDD has rarely been quantified. To the extent that TDD and PDD are decoupled, they may have different ecological implications. A herbivore with low TDD (taxonomic specialist) may be vulnerable to disturbances that cause local extinctions of plant species, because the loss of even a single species could deprive the herbivore of most of its diet. A herbivore with low PDD (phylogenetic specialist) may be vulnerable to environmental changes that alter the food base—even if the herbivore has high TDD—if the disturbance disproportionately affects the plant lineage(s) on which the herbivore depends. This is an ecologically realistic scenario, because environmental conditions can filter phylogenetically conserved plant traits (Cavender-Bares, Kozak, Fine, & Kembel, 2009) in ways that radically alter the relative abundances of entire lineages—for example, of grasses and sedges (Poaceae and Cyperaceae, both order Poales) relative to legumes and milkworts (Fabaceae and Polygalaceae, both order Fabales).

To illustrate this possibility, consider a herbivore that eats 60 species of plants from a single plant family versus one that eats 10 species from each of three plant families. Although the former's diet is twice as species-rich and may therefore be less sensitive to random plant extinctions (Colwell et al., 2012), its diet is evolutionarily narrow and may thus be more sensitive to non-random declines that disproportionately affect that one plant lineage. Such sensitivity to phylogenetically biased shifts in resource availability is likely to be relevant to understanding food webs in a changing world. To continue with the hypothetical scenario outlined above, multiple types of natural and anthropogenic perturbations are known to disadvantage grasses and sedges relative to other plant lineages, including bush encroachment (Bond, 2008; Higgins & Scheiter, 2012; Stevens, Erasmus, Archibald, & Bond, 2016), alteration of fire and precipitation regimes (Staver, Archibald, & Levin, 2011), and shifts in human land use (Aleman, Blarquez, & Staver, 2016).

Assemblages of 20 or more sympatric species of large mammalian herbivores (here defined as ≥2 kg) occur in many African savannas (and more widely prior to the end-Pleistocene extinctions). Ecologists often categorize large-herbivore diets based on the proportional representation of major plant types (Bell, 1971; du Toit & Olff, 2014; Gagnon & Chew, 2000; Jarman, 1974). The terms 'grazer' and 'browser' refer to herbivores with diets comprising mostly monocots (especially grasses) or mostly eudicots (forbs and woody plants), respectively (du Toit & Olff, 2014); herbivores that consume substantial amounts of both are 'mixed-feeders' (Cerling, Harris, & Passey, 2003). The evolution of grazing and browsing strategies is associated with behavioural and morphophysiological adaptations to consuming plants with different growth forms, nutritional qualities, and defenses (Gordon & Prins, 2008). Across guilds, smaller species and ruminants differ from larger species and non-ruminants with respect to diet quality: all else equal, the former eat smaller quantities of higher-quality food (du Toit & Olff, 2014; Hofmann, 1989).

Fine-grained metrics of dietary diversity, such as TDD and PDD, have long been difficult to measure and compare within and among large-herbivore populations (Kartzinel et al., 2015), owing to the difficulty of accurately identifying large-herbivore diets to the species-level in field observations (but see, e.g. Kleynhans, Jolles, Bos, & Olff, 2011; Owen-Smith, Le Roux, & Macandza, 2013). The temporal dynamism of large-herbivore diets compounds this challenge. The availability of different plant taxa varies seasonally, and mixed-feeders often consume more grasses during the wet season and switch to browse-based diets during the dry season (Codron et al., 2007). Evaluating dietary specialization therefore entails sampling in multiple seasons to capture the full breadth of a population's diet and to avoid mischaracterizing generalists as specialists based on single-season snapshots. PDD is even harder to quantify than TDD, because it requires not only precise measurement of TDD but also a reliable phylogeny for the resource community. For all of these reasons, it remains unclear how savanna ungulates compare in terms of TDD and PDD, whether these metrics are largely redundant or instead represent potentially distinct axes of dietary specialization, and to what extent these metrics and the relationship between them vary with seasonal changes in forage availability.

Using DNA metabarcoding (Taberlet et al., 2007), we generated diet profiles for 25 large-herbivore species that co-occur in a Kenyan savanna for which a plant DNA reference database and community phylogeny have been assembled (Gill et al., 2019). These 25 herbivore species spanned >3 orders of magnitude in body mass (2–4,000 kg), >50 million years of evolutionary history (five taxonomic orders), the entire grazer–browser spectrum, and distinct gut architectures (ruminant and non-ruminant). We tested four hypotheses. (*i*) TDD and PDD are positively correlated, both among species and among individuals within species, because taxonomically diverse diets are likely to include plants from many lineages. (*ii*) Both TDD and PDD are highest for mixed-feeders and lowest for grazers and browsers (i.e. both metrics exhibit a hump-shaped relationship with proportional grass consumption), because the latter guilds consume only a subset of plant types. (*iii*) Smaller-bodied species and ruminants have lower TDD and PDD, owing to their more-selective feeding strategies, than do larger-bodied species and non-ruminants (Bell, 1971; du Toit & Olff, 2014; Jarman, 1974). (*iv*) The degree of TDD and PDD within populations varies in concert with seasonal changes in forage availability (Codron et al., 2007; McNaughton & Georgiadis, 1986)—either increasing in the wet season due to the greater number of forage taxa available or decreasing in the wet season due to a greater ability to forage selectively on a preferred subset of the abundant food taxa—but the relationship between TDD and PDD relationship remains consistent across seasons.

2 | MATERIALS AND METHODS

2.1 | Data sources

We used faecal DNA metabarcoding to determine the composition of plants in the diets of large herbivores in the Mpala and Ol Jogi Conservancies, two adjacent properties in the semi-arid savannas (mean annual rainfall ~600 mm) of Laikipia County in central Kenya (Goheen et al., 2018). Our dataset is based on a collection of 1,281 faecal samples from 25 large-herbivore species (≥10 samples/species, median = 30, interquartile range = 19–80; Table 1; Table S1; Figure 1). These samples were collected as uniformly as practical from a ~440-km^2 area that is managed for both wildlife and a set of regionally common livestock (cattle, goats, sheep, camels, donkeys) that range across the area according to semi-traditional herding practices. Samples were collected over five periods spanning wet and dry seasons (rainfall over 90 days prior to sampling: June–July, 2013 = 225 mm; October–November, 2014 = 170 mm; February–March, 2015 = 19 mm; April, 2016 = 71 mm; July–August, 2016 = 215 mm).

Our field and laboratory protocols were similar to those described by Kartzinel et al. (2015), and Kartzinel, Hsing, Musili, Brown, and Pringle (2019a); Appendix S1 contains a detailed account of the procedures used in sample collection, processing, sequencing, and quality control. Briefly, we extracted DNA from fresh (at most several-hours old) faecal samples, which we preserved in the field using Zymo Soil/Fecal Mini Kits (Appendix S1). All samples were extracted and processed in small batches (range = 3–23; typically 15), together with extraction blanks and negative controls to monitor for contamination (Appendix S1). Extracted DNA was amplified using broad-spectrum PCR primers for the chloroplast *trn*L-P6 marker: *trn*L(UAA)g and *trn*L(UAA)h (Taberlet et al., 2007). The resulting amplicons were sequenced on an Illumina HiSeq 2500. To identify food plants, we compared plant DNA sequences from faecal samples with reference DNA sequences from vouchered specimens (Gill et al., 2019; Kartzinel et al., 2015). In most cases, we either observed animals defecating or could identify species of origin based on dung size, shape, and consistency. To confirm uncertain identifications for a minority of samples, we used mammalian mitochondrial DNA markers to verify the herbivore species based on comparison to sequences available in GenBank (Kartzinel et al., 2015, 2019; Appendix S1).

The local plant DNA library comprised 1,781 fertile vouchers (representing ~460 species from 66 families, nearly the entire local flora) collected in the study area from 2012 to 2018 (Gill et al., 2019). Specimen identifications were verified or refined by botanists (Dr. Paul Mutuku Musili and colleagues) at the East African Herbarium of the National Museums of Kenya, and with reference to five DNA markers: three standard plant DNA barcodes (*rbc*L, *mat*K, and *psb*A-*trn*H), nuclear ITS, and the *trn*L sequences used as dietary markers (Gill et al., 2019; Kartzinel et al., 2015). Of the full-length reference data evaluated by Gill et al. (2019), *trn*L provided a higher degree of taxonomic resolution than did any other marker. The shorter *trn*L-P6 reference sequences that we used to identify dietary plant sequences obtained from faecal samples also enabled precise taxonomic assignments: 65% to species-level, 27% to genus and 8% to family (Appendix S1). We supplemented this local reference library with *trn*L-P6 sequences from the global European Nucleotide Archive (Appendix S1). To identify plant DNA from faecal samples, we used *Obitools* (Boyer et al., 2016), which employs the taxonomic nomenclature of the National Center for Biotechnology Information (NCBI). Because NCBI taxonomy follows the controversial splitting of African *Acacia* spp. into the genera *Senegalia* and *Vachellia* (Smith & Figueiredo, 2011), these latter names appear in our tables and figures, but we refer to 'acacias' inclusively in the text.

We calculated dietary diversity metrics for each individual faecal sample, and at the population level for each herbivore species. Sample-wise analyses were based on sequence data that were rarefied to normalize sequencing depths across samples based on the minimum number of sequences available for any sample (N = 1,293). Rarefying may not eliminate all statistical artefacts generated by variation in sequence read counts among samples (McMurdie & Holmes, 2014), but it can be an effective strategy for reducing biases when comparisons are based on large sample sizes (here, a median of 30 samples/species) and metrics that differ in their sensitivity to variation in sequencing depth (e.g. richness vs. diversity). To create population-level diet profiles for each herbivore species, we first combined sequence-count data from all samples within species and then randomly drew without replacement the minimum number of sequences available for any species (i.e. 12,930 sequences per species, corresponding to the equivalent of 10 rarefied samples per species). We used these normalized datasets to calculate the proportional contribution of each plant taxon to the diet profile of each sample or species—i.e. sequence relative read abundance (RRA).

We use RRA as the basis for our primary analyses, for several reasons. First, although RRA may not provide a reliable quantitative proxy in all DNA-metabarcoding applications (De Barba et al., 2014; Deagle et al., 2019), its use for herbivore diet analysis with *trn*L-P6 has

TABLE 1 Metrics of dietary diversity for 25 large-herbivore species. Species' body masses (kg) and sample sizes (*N*) are listed in order of decreasing grass RRA. We report three metrics of taxonomic diversity (richness, ^0D; diversity, ^1D; evenness, ^2D) and two metrics of phylogenetic diversity (*ses*MPD, *ses*MNTD). For the latter, bold values differ significantly from 0

Species	Body mass (kg)	*N*	Grass RRA	^0D	^1D	^2D	*ses*MPD	*ses*MNTD
Plains zebra	279	106	0.97	84	12.66	9.06	**−20.38**	**−3.76**
Grevy's zebra	408	91	0.95	101	16.80	12.02	**−23.77**	**−4.20**
Warthog	83	30	0.90	103	18.85	12.90	**−23.41**	**−4.09**
Hartebeest[a]	161	27	0.89	90	16.53	10.12	**−18.37**	**−3.66**
Donkey[b]	165	29	0.84	109	15.15	7.99	**−12.78**	**−2.67**
S. white rhino	2,286	13	0.74	102	17.43	9.85	**−11.13**	**−2.77**
Hippo[c]	1,536	23	0.64	136	23.40	11.56	**−8.74**	**−2.92**
Buffalo[a]	593	92	0.62	142	35.01	22.54	**−13.58**	**−3.60**
Cattle[a,b]	619	163	0.56	130	28.45	18.25	**−8.45**	**−2.31**
Oryx[a]	201	22	0.51	117	26.94	17.71	**−7.02**	**−2.43**
Hare A	2	11	0.28	97	12.70	7.88	−1.23	**−1.86**
Sheep[a,b]	39	48	0.25	140	27.12	13.66	−1.45	−1.20
Elephant	3,825	80	0.23	120	15.57	6.88	**−3.01**	−1.06
Impala[a]	53	129	0.22	130	27.33	13.42	**−3.35**	**−1.54**
E. black rhino	996	18	0.07	97	17.25	7.84	**−2.07**	−0.62
Eland[a]	563	54	0.06	130	25.36	13.87	**−2.71**	0.98
Goat[a,b]	47	19	0.05	113	10.24	4.12	**−3.54**	−0.45
Bushbuck[a]	43	12	0.05	115	18.81	9.11	**−3.88**	−0.70
Gerenuk[a]	39	10	0.05	78	5.86	2.96	**−4.07**	−0.11
Grant's gazelle[a]	55	46	0.04	124	22.63	11.76	**−3.98**	−0.37
Dik-Dik[a]	5	120	0.03	114	19.41	10.14	**−5.58**	−0.63
Camel[b,c]	493	39	0.02	93	5.03	2.55	−0.12	−0.38
Klipspringer[a]	13	13	0.02	98	19.82	11.01	**−4.78**	0.39
Giraffe[a]	965	58	0.01	102	10.46	6.33	**−4.18**	−0.14
Kudu[a]	206	28	0.01	105	9.16	4.70	−0.46	−0.05

Abbreviations: MNTD, mean nearest-taxon distance; MPD, mean phylogenetic distance; RRA, relative read abundance; *ses*, standardized effect size.

[a] Ruminant species.

[b] Domestic species.

[c] Pseudo-ruminant species.

been supported by strong correlations between (a) the RRA of food-plant taxa and the proportional biomass of those taxa consumed by sheep in feeding trials (Willerslev et al., 2014) and (b) the RRA of C_4 grasses and estimates of proportional C_4-plant consumption derived from carbon stable-isotope ratios, including a nearly 1:1 correlation across seven ruminant and non-ruminant species in our study system (Kartzinel et al., 2015). Moreover, RRA is less sensitive than presence–absence-based approaches to the inclusion of low-abundance reads (including potential sequencing errors and contaminants) and does not require the use of arbitrary thresholds for deciding whether rare taxa are present in or absent from a sample (Deagle et al., 2019; Kelly, Olaf Shelton, & Gallego, 2019). Importantly, we do not compare the absolute value of any diversity metric to those reported in other studies, but instead focus exclusively on the relative patterns of diversity obtained based on many samples that were analysed using identical PCR protocols. We also explored the sensitivity of our results to the use of alternative presence–absence-based metrics (see Section 2.5).

We constructed a phylogeny of food plants by using the *trn*L-P6 sequences retrieved from faecal samples to refine a megaphylogeny (Appendix S1). For mammals, we used a time-calibrated megaphylogeny (Figure 1; Fritz, Bininda-Emonds, & Purvis, 2009). We categorized herbivores as either ruminants or non-ruminants, with the non-ruminant category including all species that lack four-chambered stomachs: hares, hyraxes, warthogs, donkeys, zebras, and elephants (all hindgut fermenters), camels (hindgut fermenters that ruminate), and hippos (ruminant-like foregut fermenters that do not ruminate). Body masses (Table 1) were obtained from PanTHERIA (Jones et al., 2009).

2.2 | Plant availability

We surveyed vegetation at the landscape scale to evaluate how the consumption of plant taxa reflected the diversity and relative availability of those taxa (i.e. selectivity/avoidance). To do this, we

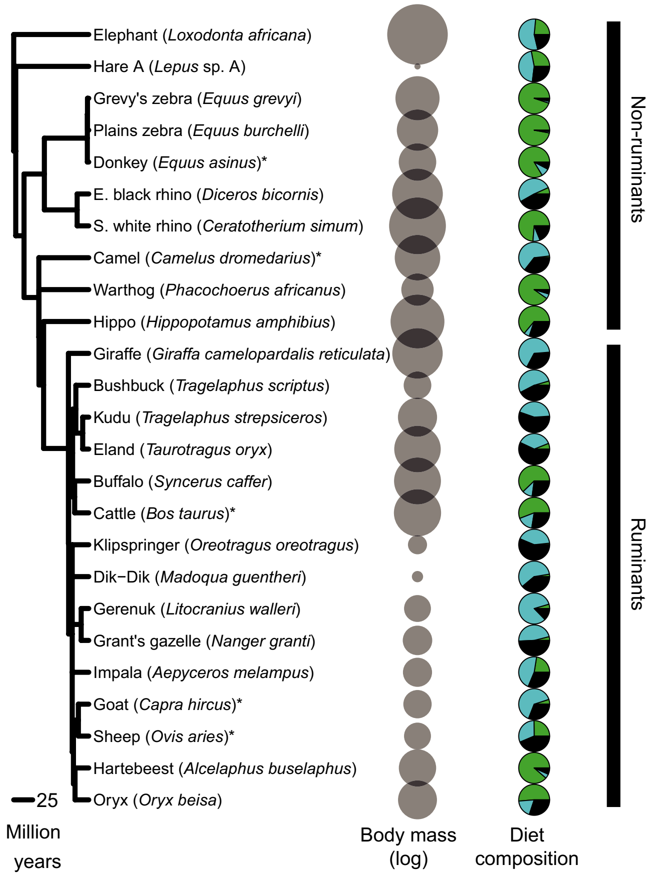

FIGURE 1 Phylogeny of the 25 large mammalian herbivores in our study. Grey circles represent relative body mass on a log scale. Pie charts depict the proportion of diet profiles consisting of grasses (green), legumes (blue), and other plant families (black). Bars on the right indicate gut architecture; asterisks denote domestic species

modified the canopy-intercept method commonly used to characterize understorey plant communities (Augustine, 2003; Frank & McNaughton, 1990) so as to quantify the availability of both understorey and overstorey plants in a common currency. We extended a vertical pole from the ground to the canopy top and counted all contacts between the pole and each plant species up to 6 m (the maximum foraging height of giraffe and far taller than the vast majority of trees in this ecosystem). We obtained data from July to September 2017 (intermediate between the long rains and the dry season) at each of 163 locations at 0.5-km intervals throughout an unpaved road network within the study area; this transect spanned the range of soil types and microhabitats encompassed by our dung collections. At each location, two pole-placement sites were selected by randomly drawing distances (0–100 m) perpendicular to both sides of the road (N = 326 total sites). All plants were identified to species, with the aid of our taxonomically verified reference library, except for a subset of sedges (*Cyperus* spp., 0.6% of observations) that are exceedingly difficult to identify in the field and were therefore lumped at the genus level. We compared the relative abundance of the three broadest plant lineages in the environment (monocots, superrosids, superasterids) to the RRA of those lineages in animal diets. We further evaluated the richness, diversity, and evenness of these broad plant lineages, as well as the top five most abundant plant families recorded in these surveys. We used Hill numbers (Jost, 2006) to compare species richness (^{0}D, the count of species present in a sample), diversity (^{1}D, the exponential of Shannon entropy), and evenness (^{2}D, the inverse of the Simpson index) in the VEGETARIAN package in R (Charney & Record, 2012; R Core Development Team, 2014).

2.3 | Measuring dietary diversity

For each sample and each population-level diet profile, we calculated three TDD and two PDD metrics that collectively encompass multiple definitions of dietary diversity. For TDD, we calculated Jost's (2006) metrics for species richness (^{0}D), diversity (^{1}D), and evenness (^{2}D). For PDD, we selected two common metrics from community phylogenetics: the mean phylogenetic distance (MPD) and mean nearest-taxon distance (MNTD) between all plant taxa in each diet profile (weighted by each taxon's RRA). MPD reflects specialization on plant lineages that diverged deep in the phylogeny, whereas MNTD reflects specialization arising near the tips (Kembel et al., 2010). These measures of PDD facilitate comparisons of diets that contain a high or low degree of phylogenetic diversity relative to the number of plant species present—as opposed to simpler measures of phylogenetic diversity such as total branch length, which has an inherently positive relationship with species richness because each species contributes unique branch length to a phylogeny (Faith, 1992). Standardized effect sizes (*ses*) of the PDD metrics were determined by randomly shuffling plant taxa across the tips of the plant phylogeny (square-root-transformed time spans), with 999 permutations to determine if each observed PDD value differed significantly from the distribution of PDD values obtained from this set of 'null communities' (Kembel et al., 2010). A diet is phylogenetically generalized or specialized if *ses* is >0 or <0, respectively; otherwise it is indistinguishable from random draws of plants in the phylogeny. We focus primarily on taxonomic diversity (^{1}D) and MPD (*ses*MPD) as metrics of TDD and PDD, respectively, but we found qualitatively similar results for all metrics.

2.4 | Hypothesis testing

To test hypothesis *i*, that taxonomic and phylogenetic diversity are positively correlated both within and among herbivore species, we evaluated pairwise Pearson correlations between each TDD and PDD metric in the composite population-level diet profiles. A non-significant or negative correlation between the two metrics indicates that they are non-redundant dimensions of diversity. We used phylogenetic generalized least squares (PGLS; Revell, 2010) to verify that the relatedness of herbivores did not generate phylogenetic structure in the residuals of these correlations (Appendix S1). Within and among species, we used linear models to test for differences between the slope and intercept of each TDD–PDD relationship, with one TDD metric as the predictor variable and one PDD metric as the response variable.

We tested hypotheses about the effects of herbivores' feeding characteristics on species-level TDD and PDD metrics—that mixed-feeders have higher TDD and PDD than grazers or browsers (hypothesis *ii*) and that smaller species and ruminants have lower TDD and PDD than larger species and non-ruminants (hypothesis *iii*)—using a model-selection approach (Burnham & Anderson, 2002). We created candidate sets of models with all possible additive combinations of four predictors: grass RRA, body size (log-transformed), gut architecture (ruminant vs. non-ruminant), and a quadratic version of grass RRA to account for the expected hump-shaped relationship between dietary diversity and proportional grass consumption. Thus, we fit a candidate set of 12 models: an intercept-only null model (M_1); each of the linear predictor variables singly ($M_{2–4}$); all pairwise combinations of linear predictors ($M_{5–7}$); all linear predictors (M_8); grass RRA + grass RRA^2 (M_9); grass RRA + grass RRA^2 + each other predictor singly ($M_{10–11}$); and grass RRA + grass RRA^2 + all other predictors (M_{12}). We used Akaike's information criterion (AICc) to identify the 95% confidence set of models and calculate model-averaged coefficients (Bartoń, 2016). The 95% confidence set never contained the null model. We used the mammal phylogeny and PGLS to verify that no model contained in the 95% confidence sets had phylogenetic structure in its residuals. We omitted 'domestication' from the candidate model set given the small number of domesticated species within groups (three ruminants, two non-ruminants). We instead compared the TDD and PDD of wild versus domesticated species using univariate PGLS. The differences were non-significant for all but one metric (*ses*MPD; see Section 3), suggesting that effects of domestication on TDD and PDD are weak and that our omission of this factor from multivariate models is justified.

Finally, to test our hypothesis *iv*—that seasonality influences TDD and PDD but not the relationship between them—we used (a) ANOVA to test for differences between grass RRA and sampling period, (b) ANOVA to test for differences between each dietary diversity metric and sampling period, and (c) generalized linear models to evaluate the TDD × sampling period effect on PDD. For these analyses, we compared the relationship between TDD and PDD during each of the 2–4 sampling periods (spanning wet and dry seasons) for each of the 12 species that were well sampled across multiple sample periods (i.e. ≥30 samples overall and ≥10 within each sampling period). In the models, we used TDD metrics as the independent variables to predict the PDD metrics. We applied Bonferroni corrections for multiple comparisons; with $\alpha = 0.05$ and 12 comparisons, $p \le 0.004$ is a stringent criterion for a significant difference.

2.5 | Sensitivity analyses

We evaluated the sensitivity of our main results to (a) the minimum sample size used for any species in analysis ($N = 10$) and (b) the use of dietary RRA data as opposed to presence/absence data (Appendix S1). First, we used rarefaction to determine the sensitivity of each diversity metric to sample size; we calculated the mean and variance of each diversity metric in the range of 1–10 samples per species and evaluated whether the rarefaction curve closely approached its asymptote. Second, we compared RRA-based measures of TDD and PDD with those obtained by converting sequence-count data into presence/absence of plant taxa in each population-level diet profile (Deagle et al., 2019; Kartzinel et al., 2015). This conversion eliminates information on food-plant abundance and thus only enables analysis of taxonomic richness (^0D) against versions of the PDD metrics that do not account for relative abundance; it precludes calculation of dietary diversity and evenness by assigning equal value to all taxa present in a sample, regardless of relative abundance. This conversion also requires the use of threshold RRA levels to conclude that a taxon is 'present'. A threshold of 1% RRA is frequently used (Deagle et al., 2019; Pansu et al., 2019; Pringle et al., 2019), and we have also used a more conservative 5% threshold in a previous study in this system (Kartzinel et al., 2015). We therefore evaluated the relationship between taxonomic richness and PDD metrics using both of these thresholds.

3 | RESULTS

3.1 | Overview of dietary diversity

Collectively, the 1,281 samples included 213 unique *trn*L-P6 sequences (henceforth 'taxa') from 54 plant families (Tables S2 and S3). Rarefying to even sequencing depth eliminated two plant taxa with very low RRA, so the individual-level diet profiles used for analysis retained 211 taxa from 53 plant families. The 25 population-level diet profiles collectively contained 206 plant taxa from 51 families (Table S2). The richness of these composite population-level diet profiles ranged from 78 taxa (gerenuk) to 142 taxa (buffalo), with a median of 109 (Table 1).

Across the population-level diet profiles, two plant families accounted for 0.71 RRA across all herbivore species: Poaceae (grasses, 0.36 RRA) and Fabaceae (acacias and other legumes, 0.35 RRA). The top 10 plant taxa in terms of RRA across all herbivore species were exclusively from these two families (Table S2). Across the grazer–browser spectrum, plains and Grevy's zebra diets comprised ≥0.95 grass RRA, whereas 11 browser species had diets with ≤0.07 grass RRA (Figure 1; Table 1). Across the deepest angiosperm nodes in the phylogeny, most RRA was concentrated within the superrosids (88 taxa, collectively 0.50 RRA; Fabaceae = 0.35 RRA; Malvaceae = 0.05 RRA) and monocots (39 taxa, collectively 0.37 RRA; Poaceae = 0.36 RRA), with the remainder being superasterids (79 taxa, collectively 0.13 RRA; Figure 2; Figure S1).

Twenty-one of the 25 herbivore species specialized on one or more long-divergent plant lineages (*ses*MPD), and 12 specialized on sets of closely related plant taxa (*ses*MNTD; Table 1). All 10 species with diets comprising >50% grass RRA exhibited significant specialization in both of these PDD metrics, as did impala, a mixed-feeder with 22% grass RRA (Table 1). Ten species—all with <25% grass RRA—specialized on long-divergent clades (significant *ses*MPD) but did not specialize on closely related taxa within these clades (non-significant *ses*MNTD; Table 1). Only one species (a hare) exhibited significant *ses*MNTD but non-significant *ses*MPD, indicating specialization on sets of closely related species that were distributed across the plant phylogeny (Table 1). Three species (sheep, camel, and kudu) did not exhibit significant specialization in either PDD metric (i.e. their diets were essentially phylogenetically random). Notably, however, no species' diet was phylogenetically overdispersed: 48 of the 50 population-level PDD metrics were negative, and neither of the positive values was significant (Table 1).

3.2 | Plant availability

Our vegetation survey recorded 108 plant species from 28 families. The relative availability of monocots (0.62; mostly Poaceae, 0.59) was much greater than that of superrosids (0.29; mostly Fabaceae, 0.18) and superasterids (0.10; predominantly Acanthaceae, 0.03) combined. Despite these strong differences in relative availability, there was similar species richness, diversity, and evenness across these plant lineages (Figure S2A). The vast majority of monocots in this system were from the grass family (Poaceae), whereas the superrosids and superasterids were more broadly distributed across plant families (9 and 15 respectively). Because monocot species were so concentrated within the grass family, there was 2- to 3-fold greater richness, diversity, and evenness of Poaceae than of the next most abundant plant family (Fabaceae; Figure S2B). Consumption of these plant lineages differed considerably across herbivore species' diet profiles, ranging from the selective utilization (RRA » availability) to the selective avoidance (RRA « availability) of each clade (RRA ranges: monocots 0.01–0.98; superrosids 0.02–0.87; superasterids 0–0.34; Table S2). Herbivore species' diet profiles thus did not simply reflect plant availability or diversity in the environment.

3.3 | Hypothesis testing

Contrary to our hypothesis *i*, herbivore species with the highest TDD did not necessarily have the highest PDD. The three TDD metrics (richness, diversity, evenness) were all positively correlated with each other at the population level, as were the two PDD metrics (Figure 3; Table S4). However, all correlations between TDD and PDD metrics were either non-significant or negative (Figure 3). Thus, TDD and PDD represent distinct dimensions of dietary diversity.

The relationship between TDD and PDD within species exhibited similar patterns. In general, MPD (*ses*MPD) was uncorrelated or negatively correlated with taxonomic diversity (^1D) within species, although the slopes and intercepts of these relationships varied considerably among species (Figure 4a; Table S5). Whereas some species showed a strong negative relationship between TDD and PDD (notably the strictest grazers, hartebeest, warthog, and zebras) and others showed little change in PDD depending on TDD (most of the browsers and mixed-feeders), no species exhibited the strong positive relationship that we had hypothesized (Figure 4a). The intraspecific relationships between the other TDD and PDD metrics were similar in exhibiting substantial species-specific heterogeneity in slope and intercept, with a preponderance of negative or neutral

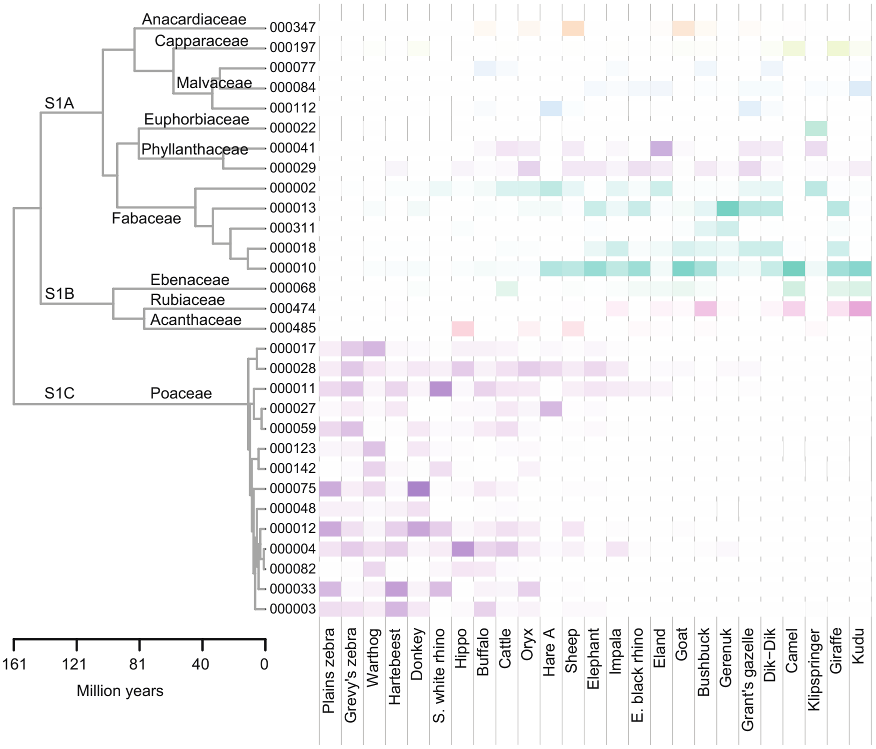

FIGURE 2 Phylogeny of the 30 plant taxa with highest total RRA summed across the diet profiles of all species. Colours represent different plant families; darker shading indicates greater RRA. Plant taxa can be identified (to the finest taxonomic level possible) by matching tip labels to sequence names in Table S2. The three deepest plant lineages correspond to the superrosid (S1A), superasterid (S1B), and monocot clades (S1C), which are shown in full detail in Figure S1A–C respectively. RRA, relative read abundance

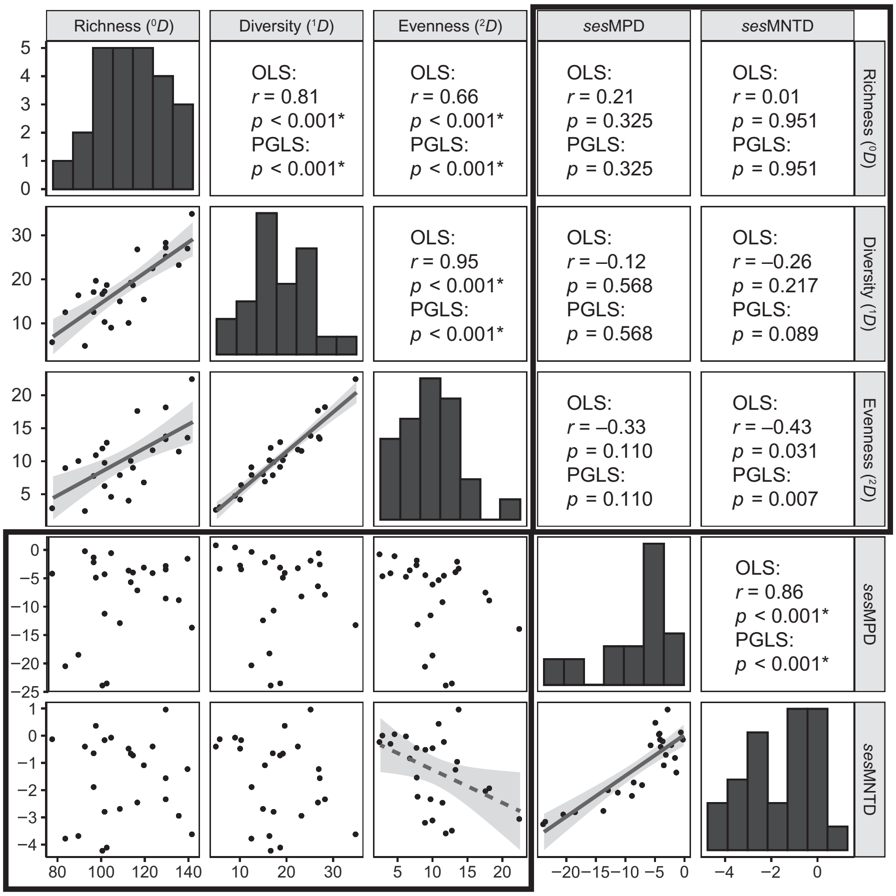

FIGURE 3 Correlations between the three taxonomic dietary diversity (top left) and two phylogenetic dietary diversity (bottom right) metrics, revealing non-significant or negative correlations between taxonomic and phylogenetic dimensions of dietary diversity (dark bounding boxes). Histograms (diagonal) show the distribution of each metric across all species' dietary profiles. Correlations between each metric are plotted (below diagonal), and trend lines fit by OLS regression are drawn (±*SE*) when the correlations approached statistical significance using either OLS or PGLS (above diagonal; Table S4). Asterisks next to *p* values indicate significant relationships after Bonferroni correction for multiple comparisons: with 10 comparisons, $\alpha = 0.05$ requires $p \leq 0.005$ to conclude the result is significant (solid trend lines); $\alpha = 0.1$ requires $p \leq 0.01$ (dashed trend lines). In each plot, $N = 25$ large-herbivore species. MNTD, mean nearest-taxon distance; MPD, mean phylogenetic distance; OLS, ordinary least squares; PGLS, phylogenetic generalized least square; *ses*, standardized effect size

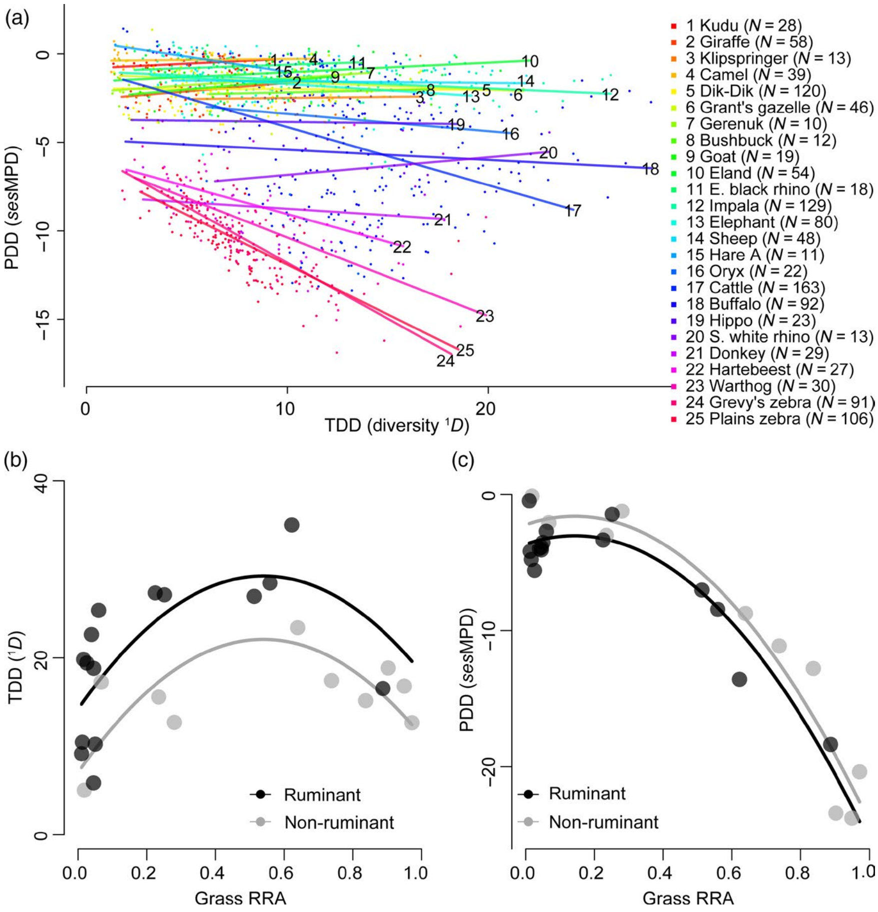

FIGURE 4 Relationships between TDD and PDD within and among herbivore species. (a) The relationship between TDD and PDD within all 25 herbivore species, showing generally null or negative correlations within species, along with substantial heterogeneity among species (see Figure S3 for analogous graphs between all other pairs of TDD and PDD metrics; see Table S5 for statistical results of the linear models). The number at the right side of each regression line matches the species in the legend, which are ordered in order of increasing grass RRA values reported in Table 1 (grazers at the bottom); sample sizes for each species are in parentheses. (b) TDD and (c) PDD are plotted against grass RRA for the 25 large-herbivore species. Lines represent the model-averaged 95% confidence set of OLS models based on AICc (Table 2), which were plotted using the median body mass of herbivore species in this study (see Figure S4; Table S6 for the complete set of plots and model results for all TDD and PDD metrics). AIC, Akaike's information criterion; MPD, mean phylogenetic distance; OLS, ordinary least squares; PDD, phylogenetic dietary diversity; RRA, relative read abundance; *ses*, standardized effect size; TDD, taxonomic dietary diversity

intraspecific correlations. Strong positive relationships were observed in only a small minority of species for certain pairs of metrics (e.g. for kudu, camel, and giraffe in comparisons involving *ses*MNTD; Figure S3; Table S5).

Across species, all TDD and PDD metrics were strongly associated with proportional grass consumption (Table 2; Table S6). Grass RRA, grass RRA^2, gut architecture, and body mass all occurred in the 95% confidence set of models for all diversity metrics, although body mass was never included in the best-fitting models and was not a statistically significant predictor of any metric based on model-averaged coefficients (Table 2). Grass RRA was included in all models in the 95% confidence sets for all diversity metrics, and most of these models also included grass RRA^2, indicating nonlinearity (Table 2; Table S6). Consistent with our hypothesis *ii*, all TDD metrics peaked at intermediate levels of grass RRA (that is, among mixed-feeders; Figure 4b; Figure S4). The decline in TDD from mixed-feeders to grazers (the descending arms of the hump-shaped curves in Figure S4) grew progressively weaker for TDD metrics that reduce emphasis on rare taxa (from richness to diversity to evenness), indicating that grazers had higher dietary diversity and evenness on average than did browsers. In contrast to TDD, both PDD metrics decreased sharply with increasing grass RRA (concave-down for *ses*MPD, linear for *ses*MNTD), indicating that the diets of browsers were considerably more phylogenetically diverse than those of grazers (Figure 4c; Figure S4). These differences in TDD and PDD with respect to the grass content of diets reinforce the finding (Figure 3) that TDD and PDD are non-redundant dimensions of dietary diversity.

Contrary to hypothesis *iii*, body mass did not predict dietary diversity, and gut architecture influenced TDD and PDD in different ways (Table 2). For a given position along the grazer–browser spectrum, ruminant species had greater TDD (Figure 4; Figure S4), reflected in positive model-averaged coefficients for gut architecture in the models of dietary diversity and evenness (Table 2). In contrast, non-ruminants had slightly but significantly greater *ses*MPD than did ruminants, and gut architecture had no effect on *ses*MNTD (Table 2; Figure 4; Figure S4). Livestock had significantly greater *ses*MPD on average than did wild species, but no other

TABLE 2 Models relating herbivore characteristics to dietary diversity. The best-fitting models shown for each metric were those in the 95% confidence set based on Akaike's information criterion (AICc). Predictors included proportional grass consumption (RRA), grass RRA^2, gut architecture (GA, positive values indicate greater dietary diversity in ruminants), and log-transformed body mass (BM). ΔAICc is the difference in AICc value between each model and the best in the set. Akaike's weights (w_i) reflect the likelihood that the *i*th-ranked model is the best in the set and sum to ≤0.95 for the 95% confidence set of models shown for each metric. Model-averaged coefficients (±*SE*) and statistical significance ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$) are shown for each predictor (see Table S6 for the complete candidate sets of models tested for each dietary diversity metric)

				Coefficients ± *SE*			
Model	**AICc**	**ΔAICc**	w_i	**RRA**	**RRA^2**	**GA**	**BM**
Richness (^0D)				125.39 ± 33.08***	−138.45 ± 35.75***	6.12 ± 7.18	0.26 ± 0.87
~RRA + RRA^2	209.5	0.0	0.381				
~RRA + RRA^2 + GA	209.6	0.1	0.366				
~RRA + RRA^2 + BM + GA	211.7	2.2	0.129				
Diversity (^1D)				55.88 ± 12.85***	−51.77 ± 13.86***	7.17 ± 2.49**	0.03 ± 0.27
~RRA + RRA^2 + GA	163.1	0.0	0.774				
~RRA + RRA^2 + BM + GA	166.4	3.4	0.143				
Evenness (^2D)				33.30 ± 7.77***	−27.50 ± 8.37**	4.99 ± 1.50**	0.02 ± 0.16
~RRA + RRA^2 + GA	137.9	0.0	0.804				
~RRA + RRA^2 + BM + GA	141.3	3.4	0.145				
*ses*MPD				8.75 ± 4.93	−30.59 ± 5.33***	−1.96 ± 0.94*	0.06 ± 0.24
~RRA + RRA^2 + GA	114.2	0.0	0.578				
~RRA + RRA^2	115.9	1.7	0.249				
~RRA + RRA^2 + BM + GA	117.6	3.4	0.104				
*ses*MNTD				−4.80 ± 1.14***	0.79 ± 1.21	0.02 ± 0.04	0.00 ± 0.08
~RRA	39.5	0.0	0.318				
~RRA + RRA^2	40.0	0.6	0.239				
~RRA + BM	41.1	1.7	0.140				
~RRA + RRA^2 + BM	41.4	1.9	0.123				
~RRA + GA	42.3	2.9	0.076				
~RRA + RRA^2 + GA	43.2	3.7	0.050				

Abbreviations: MNTD, mean nearest-taxon distance; MPD, mean phylogenetic distance; RRA, relative read abundance; *ses*, standardized effect size.

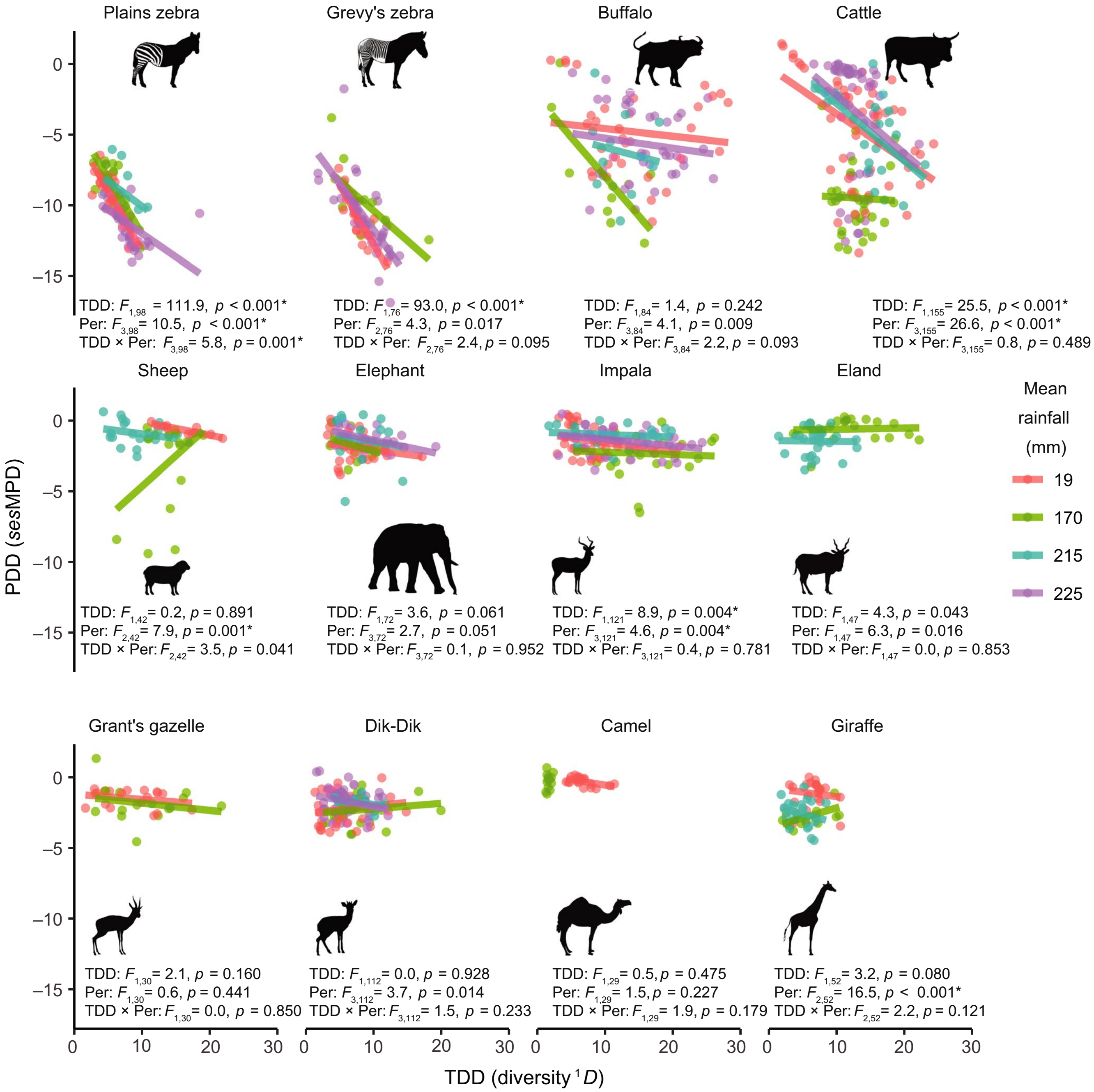

FIGURE 5 Relationship between PDD and TDD across sample periods for 12 herbivore species. For each species, we show the relationship between TDD and PDD across 2–4 sampling periods based on linear models including TDD, sampling period (Per), and the TDD × sampling period interaction. Line and point colours indicate sampling period, with the mean rainfall over the 90 days prior to each collection interval shown in the legend (range, 19–225 mm). Asterisks next to p values indicate statistically significant effects after Bonferroni correction (with $\alpha = 0.05$ and 12 models, $p \leq 0.004$ indicates a significant difference). Analogous comparisons of the other TDD and PDD metrics are shown in Figure S7. MPD, mean phylogenetic distance; PDD, phylogenetic dietary diversity; *ses*, standardized effect size; TDD, taxonomic dietary diversity

dietary diversity metric differed between wild and domesticated species (Figure S5).

The data were broadly consistent with our hypothesis *iv*—that dietary diversity varies seasonally, but the relationship between TDD and PDD does not. Grass consumption generally peaked during periods with intermediate rainfall and differed significantly between sampling periods for seven species, which spanned the grazer–browser spectrum (Figure S6). At least one metric of both TDD and PDD differed between sampling periods for 6 of the 12 species analysed (including grazers, browsers, and mixed-feeders), and at least one PDD metric differed between sampling periods for an additional two species (cattle and dik-dik; Figure S6). The relationship between

TDD and PDD was generally consistent across seasons (per hypothesis *iv*) and was generally either negative or neutral (consistent with our central conclusion that TDD and PDD are distinct dimensions of dietary diversity). In linear models of the relationship between taxonomic diversity (^1D) and MPD (*ses*MPD) by sample period, four species exhibited significantly different PDD across periods and five species exhibited significant negative relationships between TDD and PDD across seasons (with non-significant relationships for the remainder; Figure 5). Only one species (plains zebra) exhibited a difference in the relationship between TDD and PDD across seasons, as measured by a significant TDD × season interaction—but this difference was quantitative, not qualitative, reflecting differing degrees of negative slope (Figure 5). Pairwise comparisons between the other TDD and PDD metrics showed qualitatively similar patterns; among the few exceptions were a handful of positive correlations between TDD and *ses*MNTD for browsers such as eland, camel, and giraffe (Figure S7). Each of the significant seasonal differences was established using Bonferroni correction for multiple comparisons.

3.4 | Sensitivity analyses

Rarefaction curves revealed that all TDD and PDD metrics for all species approached asymptotes with 10 samples (Figure S8), as did the total number of food-plant taxa and the cumulative phylogenetic diversity (branch length) represented in the diet profiles of all herbivore species combined (Figure S9). Our core conclusion that TDD and PDD are distinct dimensions of dietary diversity was also obtained when we used diet profiles based on presence/absence data in lieu of RRA. Using two common thresholds for determining that a food taxon is 'present' in a diet (RRA ≥1% or ≥5%), the correlations between taxonomic richness and PDD were either non-significant or significantly negative (Figure S10), similar to the results based on RRA (Figure 3).

4 | DISCUSSION

4.1 | Multiple dimensions of dietary diversity in large herbivores

Contrary to our initial expectation, herbivores that ate many plant species did not necessarily eat many plant lineages—in other words, taxonomic generalists can be phylogenetic specialists, and vice versa. An explanation for this counterintuitive finding is rooted in the grazer–browser continuum that typifies large-herbivore assemblages (Cerling et al., 2003; Codron et al., 2007; Jarman, 1974; Kartzinel et al., 2015). Although grazers and mixed-feeders consumed a greater diversity of plant taxa on average than did browsers, the high diversity of taxa available within the grass family (Poaceae) comprises a phylogenetically much narrower plant lineage than the suite of forb, shrub, and tree taxa from the 53 other families that we detected in herbivore diets. Accordingly, species that consumed >20% grass had substantially reduced PDD (Figures 2 and 4). In this ecosystem, the species richness of grasses (83 of 460 taxa in our reference collection) is as almost as great as the second and third-most speciose families combined (44 Fabaceae, 40 Asteraceae; Gill et al., 2019), and the available diversity of grasses was much greater than that of the next four most abundant plant families (Figure S2). Grasses also lack pronounced defenses and occur in the understorey where they are accessible to herbivores of all sizes. All of these factors help to explain how grazers and mixed-feeders can have high TDD despite having low PDD. Conversely, despite the ample richness and availability of non-grasses in this ecosystem (Figure S2), browsers may often concentrate on the smaller number of species from different lineages with defenses that they can tolerate, or that are sufficiently abundant to sustain animals of a given size (du Toit & Olff, 2014), which could lead to phylogenetically diversified but taxonomically limited diets.

Our finding that TDD and PDD are non-redundant axes of dietary specialization in this assemblage can be intuitively visualized by ranking each species according to its average degree of taxonomic and phylogenetic specialism relative to other species in the community (Figure 6). This heuristic graph illustrates the existence of specialist–generalist continua in two dimensions. The upper-left quadrant of this space contains browsers such as camel and kudu, which were phylogenetically generalized but taxonomically specialized relative to other co-occurring species. In the lower-right quadrant are species such as buffalo, hippo, and cattle, which had taxonomically generalized diets that were nonetheless relatively specialized phylogenetically. Eland stand out as being relatively generalized in both dimensions (upper right), whereas plains zebra and hartebeest were relatively specialized in both dimensions (lower left). Other species in the community occupied various positions within this two-dimensional continuum.

4.2 | How general is the decoupling of TDD and PDD?

The observation that TDD and PDD can be decoupled within and among species allows us to conclude that a positive TDD–PDD correlation should not be assumed a priori for large mammalian herbivores. Our results inevitably reflect patterns of plant availability within the study area, but the considerable diversity of plant species and lineages in this system (Figure S2; Gill et al., 2019) and the general consistency of our results through time (Figure 5; Figure S7) give no reason to believe that the decoupling of TDD and PDD is an artefact of system- or season-specific peculiarities in forage availability. Such an artifact could arise if, for example, there were many fewer available eudicot species than monocot species, leading to deterministically lower TDD in browsers than in grazers. Yet although the available diversity of grass species was indeed higher than that of other plant families (Figure S2), browsers (eland, Grant's gazelle) had some of the highest observed

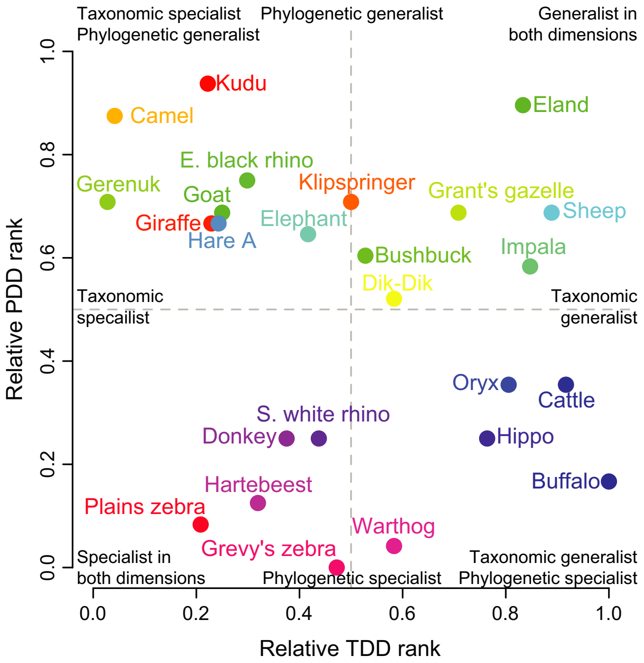

FIGURE 6 Heuristic illustration of dietary specialism and generalism in two dimensions. To generate this figure, we first ranked the 25 large-herbivore species according to each of the three TDD metrics and two PDD metrics (Table 1); we then averaged the TDD and PDD ranks across metrics for each species to obtain its relative degree of taxonomic and phylogenetic specialization within the community. For graphical convenience, these average rank-order values were normalized on a scale from 0 (most specialized) to 1 (most generalized). Quadrants are demarcated at 0.5 along each axis to aid visualization. This graph illustrates how, in comparison to the rest of the community, herbivore species could be relative generalists in both dimensions (e.g. eland), relative specialists in both dimensions (e.g. plains zebra), phylogenetically specialized taxonomic generalists (e.g. buffalo), taxonomically specialized phylogenetic generalists (e.g. camel), or intermediate in one or both dimensions. Thus, simple assumptions about the relevance of specialization for evaluating ecological 'vulnerability' may be misleading, because a specialist in one dimension may be a generalist in others. Species' colours match those in Figure 4a. PDD, phylogenetic dietary diversity; TDD, taxonomic dietary diversity

TDD values while others (camel, gerenuk) had some of the lowest. Because PDD has not previously been evaluated for large-herbivore assemblages, comparative research in other savanna systems will be necessary to evaluate the generality of our results and their sensitivity to factors such as plant community composition and productivity.

Spatiotemporal variation in plant availability or productivity is likely to alter the levels of TDD and PDD within and among species. Because grasses constitute the vast majority of monocot species richness and biomass in this system and contribute heavily to the decoupling of TDD and PDD, seasonal and geographic variation in the timing and extent of herbivory on grasses should have a strong influence on patterns of dietary diversity in African herbivore assemblages. Studies in other areas have found that grass consumption peaks in the wet season (Codron et al., 2007) and sometimes closely tracks fine-grained temporal variation in rainfall (Cerling, Wittemyer, Ehleringer, Remien, & Douglas-Hamilton, 2009). In a subtle contrast, grass consumption in our study peaked at intermediate rainfall levels (Figure S6), suggesting that the timing and extent of herbivory on grasses may differ within and among assemblages (Codron et al., 2007). Moreover, whereas our data indicated that the relationship between TDD and PDD was generally qualitatively consistent across seasons, differences in grass consumption may explain some (but not all) of the variation in this relationship observed within species (Figure 4; Figure S3) and across seasons using different metrics (Figure 5; Figure S7).

Even though browsers generally consumed a greater phylogenetic diversity of plants than did grazers and mixed-feeders, no diet was phylogenetically overdispersed (i.e. distributed evenly across the phylogeny). Phylogenetic dispersion might arise if herbivores avoid overdosing on particular plant-defense compounds (Freeland & Janzen, 1974), which are often lineage-specific (Pichersky & Lewinsohn, 2011), by consuming an even representation of foods from different lineages (Clauss et al., 2003). Our results showed that herbivore diets were concentrated within two major plant lineages (monocots and superrosids), but not a third (superasterids). This result could reflect herbivores avoiding traits common to superasterids, the relatively low local availability of superasterids (10% of vegetation; Figure S2), or a preference × availability interaction if browsers select and suppress superasterids to the point that these plants become locally rare (Bryant et al., 1991). Relationships between plant availability and herbivore diets illuminate how plant functional traits and numerical responses to herbivory could modulate the diet composition of herbivores in both taxonomic and phylogenetic dimensions.

Although body size exerts a major influence on large-herbivore foraging ecology (du Toit & Olff, 2014), we found little influence of body size on dietary diversity. Our hypothesis that selective feeding by smaller herbivores on higher-quality foods would translate into low dietary diversity may have been unsupported because herbivores can select for nutritionally different parts of the same plant species (Hofmann, 1989; Jarman, 1974). We did however find greater *ses*-MPD in domesticated species than in wild ones. This could reflect characteristics selected by humans to facilitate livestock hardiness to spatiotemporal variability in food availability, and/or local husbandry practices whereby foraging routines are determined by herders to reduce competition and predation risk (Kartzinel et al., 2019a). We also observed positive TDD–*ses*MNTD relationships for some of the strictest browsers (kudu, camel, giraffe), but not others (dik-dik, bushbuck). The former group includes relatively large, wide-ranging, gregarious species, whereas the latter group includes smaller, more solitary, and territorial species. These contrasts suggest that the TDD–PDD relationship could differ between species that occupy similar locations on the grazer–browser spectrum owing to differential reliance on foods with high available biomass (expected for larger species) versus patchily distributed foods of high nutritional quality (expected for smaller species; Bell, 1971; Jarman, 1974)).

5 | CONCLUSIONS

Because collecting precise data on complex ecological networks has historically been rate-limiting, molecular approaches to quantifying species interactions create new opportunities to develop and test predictions about dietary diversity and specialization. The discrepancies between TDD and PDD exemplify how different conceptualizations of diversity can complicate theoretical predictions that are based on dietary breadth. If specialization indeed confers vulnerability to environmental perturbations (Colwell et al., 2012), then one might speculate that species in the lower-left quadrant of Figure 6—the strict grazers with relatively narrow TDD and PDD—will be most sensitive to such perturbations. Yet our results suggest that sensitivity will also depend on which plant types are affected, and whether these effects are phylogenetically biased or random. For example, if environmental changes randomly eliminate the food species that specialists require, then our TDD results suggest that a subset of grazers and browsers with similarly narrow diets will be most susceptible (far left side of Figure 6). If, however, environmental changes non-randomly suppress plant lineages (e.g. monocots, as a result of woody encroachment or fire suppression), then our PDD results suggest a different expectation—namely that grazers and mixed-feeders should be most sensitive (bottom side of Figure 6). Relative trophic specialization, therefore, may not be a straightforward predictor of relative sensitivity (Vazquez & Simberloff, 2002).

Ambiguity in the usage and interpretation of the term 'diversity' in ecology can complicate efforts to confront theory with data (Tuomisto, 2011). Our results suggest that accounting for multiple dimensions of dietary diversity may be necessary to accurately predict how changes in resource availability impact consumers. Taxonomic richness remains by far the most frequent currency of biodiversity: even within a single trophic level, <25% of studies account for >1 dimension of diversity (Naeem et al., 2015). However, DNA-based analyses of animal diets and trait-based analyses of plant communities should increasingly make it possible to characterize the relationships among TDD and PDD, and how these properties influence population-level responses to environmental variability.

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AUTHORS' CONTRIBUTIONS

T.R.K. and R.M.P. conceived and wrote the paper; T.R.K. performed the analyses.

DATA AVAILABILITY STATEMENT

DNA metabarcode data obtained from Dryad Digital Repository: https://doi.org/10.5061/dryad.c119gm5 (Kartzinel, Hsing, Musili, Brown, & Pringle, 2019b). Utilized data and phylogeny: Appendix S1 and Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh70vv (Kartzinel & Pringle, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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