Bayesian prediction of multivariate ecology from phenotypic data yields novel insights into the diets of extant and extinct taxa

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Abstract

Morphology often relates to ecology in a well-defined manner, enabling prediction of ecological roles for taxa that lack direct observations, such a fossils. Diet is a particularly important component of a species' ecology. However, in order to predict diet it must first be codified, and establishing metrics that effectively summarize dietary variability without excessive information loss remains challenging. We employed a dietary item relative importance coding scheme to derive multivariate dietary classifications for a sample of extant carnivoran mammals, and then used Bayesian multilevel modeling to assess whether these scores could be predicted from a set of dental metrics, with body size as a covariate. There is no "one size fits all" model for predicting dietary item importance; different topographical features best predict different foods at different body sizes, and model-averaged estimates perform especially well. We show how models derived from living taxa can be used to provide novel insights into the dietary diversity of extinct carnivoran species. Our approach need not be limited to diet as an ecological trait of interest, to these phenotypic traits, or to carnivorans. Rather, this framework serves as a general approach to predicting multivariate ecology from phenotypic traits.

Introduction

Species interactions, the structure of communities, and the persistence of lineages through time are all mediated, in part or in whole, by the ecological niches that each species occupies and the degree of overlap between them (Hayward and Slotow, 2009; Hutchinson, 1957, 1959; Peralta et al., 2020; Pigot et al., 2020; Vannette and Fukami, 2014). It is therefore of paramount importance that ecologists and evolutionary biologists are able to effectively and accurately characterize the axes of ecological variation that organize these patterns. Diet is a foundational source of ecological diversity; communities of closely related species are often structured along axes of dietary variation (Hertel, 1994; Kiltie, 1988; Pigot et al., 2020) and dietary ecology fosters phenotypic variance as organisms evolve physiological, morphological, and behavioral adaptations to efficiently acquire and process different food resources (Arnold, 1983; Carroll et al., 2004; Holzman et al., 2012; Santana and Dumont, 2009; Vincent et al., 2009). On short time scales, competition for dietary resources can lead to character displacement and divergence in the morphology of ecologically and phylogenetically similar taxa (Grant and Grant, 2006; Pfennig and Pfennig, 2010; Van Valkenburgh and Wayne, 1994), while on macroevolutionary time-scales dietary ecology may promote differential patterns of speciation and extinction as dynamics between competing lineages and resource availability changes over time (Burin et al., 2016; Farrell, 1998; Lobato et al., 2014; Poore et al., 2017; Price et al., 2012; Wiens et al., 2015).

Given the importance of diet in eco-evolutionary pattern and process, the relationship between diet and phenotype is now manifest in many animal systems. For example, the morphology of insect mouthparts (Krenn, 2019), snake fangs (Cleuren et al., 2021), bird beaks (Olsen, 2017; Pigot et al., 2020), mammalian crania and jaws (Janis and Erhardt, 1988; Morales-García et al., 2021; Spencer, 1995), and vertebrate (especially mammalian) teeth (Christensen and Melstrom, 2021; Melstrom, 2017; Pollock et al., 2021) are all predictive of diet. This performance-mediated relationship between morphology and ecology is particularly useful in analyses that include taxa for which ecological data are not directly available, such as data-deficient extant species, and

especially fossils, which can be critical for robust inference of macroevolutionary parameters (Finarelli and Flynn, 2006; Slater et al., 2012). However, effectively integrating taxa of unknown ecological function into evolutionary studies requires not only that we can construct predictive models to estimate ecology from their morphological characters, but also that we can effectively and accurately quantify the range of ecological roles that species may play in the first place.

Problems quickly arise when determining precisely how to categorize diet based on the range of food types that are used and the frequency with which any particular type is consumed. Diet is frequently reduced to one of a small number of discrete categories, often based on trophic level ('herbivore', 'carnivore' and 'omnivore'; Christensen and Melstrom, 2021; Price and Hopkins, 2015; Price et al., 2012). Other studies have expanded this range to include more refined categories, such as 'browser', 'grazer', 'mixed feeder' (Toljagić et al., 2018) and 'hyper-' 'meso-', 'hypocarnivore' (Slater, 2015; Van Valkenburgh, 1988), or even more finely subdivided categories based on variation in foraging behavior and micro-habitat use (Pigot et al., 2020, 2016; Verde Arregoitia and D'Elía, 2021). However all of these schemes still require that taxa be pigeon-holed into a single specialist group. This categorization of diet is unsatisfactorily simplistic for several reasons. Finely divided categories are often created for a particular taxonomic subset, precluding application of the same coding scheme across higher level macroevolutionary studies. For example, a 'hypercarnivorous' weasel, rat, and mole may depredate very different animals (e.g. mice, beetles, and worms), leaving few options but to create a large number of categories (e.g. "vertebrate hypercarnivore", "soft invertebrate hypercarnivore", etc). Furthermore, species frequently consume different proportions of foods, often opportunistically, or have diets that cross category boundaries. For example, many squirrel species, such as the Antelope Ground Squirrel, will occasionally eat vertebrates despite seeds making up an overwhelming portion of their diet (Bradley, 1968). Categorizing a squirrel as "granivore" necessarily ignores the less common, but still nutritionally important, vertebrate food types that are sometimes consumed, while "omnivore" may be too broad a dietary classification in this case. Pineda-Munoz and Alroy (2014) suggested that diet be classified based on both the primary and secondary food types consumed,

with the term "generalist" reserved for taxa in which no individual food type comprises the majority of the diet. Although this method is an improvement on previous approaches, it still fails to capture the full breadth of variation in diet by ignoring the use of foods of tertiary or lower importance. Grundler and Rabosky (2021) overcame this issue by treating diet as multivariate rather than categorical, and inferred the presence and location of dietary niche shifts over snake phylogeny by using a database of proportional occurrences of food items in the diet of 882 species (Grundler, 2020). However, although some level of unobserved data can be accommodated by this approach, it cannot readily be extended to datasets with large numbers of data-deficient taxa such as those based on fossils.

Ideally, animal diet would be codified in a way that preserves its inherently multidimensional structure, while also being amenable to prediction from morphology of poorly studied or extinct taxa, and, ultimately, to large-scale macroevolutionary and macroecological analysis. Rojas et al. (2011) and Kissling et al. (2014) apparently independently developed a coding scheme that, rather than assigning taxa to a single discrete diet category, ranks the relative importance of different food types in a species' diet based on the use of key words in synoptic reviews and primary ecological studies. The result is that diet is represented not as a single code in a classification scheme but, rather, as a vector of ordinal variables. Rojas et al. (2011) and Kissling et al. (2014) ultimately used their codings to classify taxa to standard specialist categories, while Rojas et al. (2018) used them to develop a univariate continuous variable spanning herbivory to carnivory (see also López-Aguirre et al., 2022). However, the original importance codings present a holistic, mulitvariate description of diet that may yield previously overlooked insights into the form-function relationship between phenotype and ecology and the structure of dietary niches. For example, a species may experience selective pressure for traits that are associated with efficient acquisition and processing of seasonally or infrequently consumed food items ("fall-back foods" Marshall et al., 2009), as these nutritional sources may increase an individual's fitness when preferred food items are unavailable. Although item importance ranking has several advantages over traditional classification schemes, it is yet to be widely adopted in ecomorphological studies

(but see Machado, 2020).

Here, we investigate whether ordinal ranking of food type importance can be predicted from ecomorphological traits using a well-established system with rigorously defined functional variation: the molar dentition of the mammalian order Carnivora. We seek to understand how different functional aspects of the carnivoran dentition, such as sharpness, complexity, and surface area, correlate with the relative importance of different food items. Carnivora is an ideal group for such a study. The order is taxonomically and ecologically diverse, comprising over 300 living species (Burgin et al., 2018) that occupy a wide range of dietary niches. Extant carnivorans have been well studied, with a wealth of information available regarding their phylogenetic relationships (Eizirik et al., 2010; Nyakatura and Bininda-Emonds, 2012; Slater and Friscia, 2019), dietary diversity (Ewer, 1998), and ecomorphological variation (Friscia et al., 2007; Sacco and Van Valkenburgh, 2004; Van Valkenburgh, 1988; Van Valkenburgh and Koepfli, 1993). Additionally, carnivorans possess a rich fossil record, making the clade amenable to predictive models of performance. We used extensive literature review to evaluate the relative importance of 13 different food items for 92 species of carnivoran using the approach of Rojas et al. (2011) and Kissling et al. (2014). We then fit a series of Bayesian multi-level regression models with linear and topographic dental metrics as predictors and the relative importance of diet items as ordinal responses. Finally, we used the best-fitting models for each food item to predict the importance of the 13 food types for a sample of data-deficient extant carnivorans, as well as several species of extinct carnivoran spanning the Eocene ($\sim$ 50 myr) to the latest Pleistocene ($\sim$ 13 kyr).

Materials and Methods

Data Collection

Morphological data collection

We compiled data for four ecomorphological metrics that collectively describe area, relief, complexity, and sharpness of the lower molar tooth row from 101 species of extant carnivorans. Species-mean values for Relative Lower Grinding Area (RLGA: Van Valkenburgh, 1988), a measure of the size of the lower molar tooth row dedicated to grinding as opposed to slicing, were obtained from Slater and Friscia (2019) and Friscia et al. (2007). We generated novel topographic metrics from 3D surface scans of carnivoran lower first (m1) and second (m2) molars (see Supplementary Methods for scanning details). Molar scans and measurements were obtained from specimens housed in the mammal collections of the Field Museum of Natural History, Chicago. Relief index (RFI: Boyer, 2008) is the ratio of the 3D surface area of a tooth to its 2D planar area and is a measure of topographic relief. Orientation Patch Count rotated (OPCr: Evans et al., 2007; Wilson et al., 2012) measures the complexity of the tooth by counting the number of "tools", defined as contiguous patches sharing common orientation, present on the surface. Because the orientation of each point is sensitive to the alignment of the tooth model to the global coordinate system, counts are calculated over several small rotations of the model and averaged (Wilson et al., 2012). Finally, the Dirichlet Normal Energy (DNE) measures the average curvature of a surface by calculating its "bending energy" (Bunn et al., 2011) and captures overall tooth sharpness. We used a robustly implemented algorithm for DNE (ariaDNE: Shan et al., 2019) that is less sensitive to artifacts due to 3D modeling, such as smoothing, than early DNE algorithms, and which is implemented via `MATLAB` scripts provided by Shan et al. (2019). RFI and OPCr were calculated using the `molar` package (Pampush et al., 2016) for R (R Core Team, 2022). For carnivoran species without an m2, we assigned a value of zero for all dental topographic measurements. All surface scans are available on the MorphoSource digital repository (to be made

available on acceptance).

We visualized patterns of covariation in the topographic data by performing a principal components analysis on the covariance matrix of standardized dental data using the `prcomp` function in the `stats` package for R (R Core Team, 2022). To evaluate the hypothesis that carnivoran dental shape variation is better explained by phylogeny than by diet (Hopkins et al., 2021), we calculated K_{mult} (Adams, 2014; Blomberg et al., 2003) using the `phylosignal` function in the `geomorph` library (Adams et al., 2021; Baken et al., 2021).

Dietary Data Collection

We sourced dietary information for each carnivoran species in our dataset through review of species accounts and primary ecological studies. We followed Machado's (2020) coding scheme, modified from Kissling et al. (2014), to rank the relative importance of 13 food types: large mammal, small mammal, bird, herptile, fish, egg, carrion, hard-bodied invertebrate, soft-bodied invertebrate, seed, root, fruit and plant. We defined large mammals as species with a mean mass greater the five kilograms. Hard and soft-bodied invertebrates were designated as separate food types because sclerotinized and unsclerotinized cuticle have different material properties that require different mechanical solutions to fracture (Freeman, 1979; Strait and Vincent, 1998). We coded larvae as soft-bodied, irrespective of the properties of the adult cuticle. In contrast with Kissling et al. (2014), we avoided broad or superficial sources (e.g., Nowak and Walker, 1999) to code dietary ranks and attempted to validate primary sources where review papers were used.

Following Kissling et al. (2014) and Machado (2020), but with some minor modifications, food types were assigned to ranks based on the use of keywords and phrases in synoptic reviews or primary analyses of diet in the focal species (Table 1). A single instance of a species consuming a food type was sufficient to assign it rank 2. Seasonally and regionally important foods were generally considered important in the context of the species' diet. We note that this approach considers the full range of individual specialization found within a species to be characteristic of its realized niche, which may be too permissive an assumption in some instances (Bolnick et al.,

2003; DeSantis et al., 2022). In cases where insufficient data were available to assign ranks to food items, such as when a source only listed a set of foods that are eaten or that have been recovered from stomach contents without using keywords to describe the frequency of each, we coded the taxon as unknown.

Table 1: Dietary Importance Ranking Scheme

Rank	Dietary Importance	Keywords and Phrases
1	Never Consumed	”never consumed”, No mention of the dietary item being consumed in any of the sources consulted.
2	Low Importance	“occasionally”, “sometimes”, “small amounts”, “supplemented by”, “a few”, “rarely”, “opportunistically”
3	Moderate Importance	“but also includes”, “may include”, “feeds partly”, “also feeds”,“includes”
4	Primary Importance	“consists mainly”, “feeds mostly”, “concentrates”, “major portion”, “prefers”, “especially significant”, “most frequently consumed”, “almost exclusively”, “also important”

NOTE.- Our keywords are modified from Kissling et al. (2014) and Machado (2020) .

To visualize general trends in dietary item importance, we performed a principal components analysis on the polychoric correlation matrix of importance scores, computed using the `polychor` function in the `polycor` library (Fox, 2021). Polychoric correlations differ from Pearson’s correlations in that they do not assume that the input variables themselves are continuously distributed but that they are discrete outcomes of a liability threshold process on a normally distributed latent variable. As such, they are appropriate for ordinating discrete ordered states, such as Likert scores (Holgado-Tello et al., 2010). We then used the `Mclust` library (Scrucca et al., 2016) to determine the optimal number of clusters in the resulting principal component scores based on a finite

Gaussian mixture model, with a maximum of 20 clusters permitted and model selection based on the Bayesian Information Criterion (BIC). We compared the resulting classification to discrete dietary groupings taken from Animal Diversity Web (`https://animaldiversity.org/`, accessed on February 8, 2022), an increasingly popular source of dietary information in the primary literature (e.g. Lomolino et al., 2012; Morales-García et al., 2021), by computing the adjusted Rand Index using the `adjustedRandIndex` function in the `mclust` library. The Rand Index compares classification schemes based on matches, with its adjusted version accounting for the number of matches that are expected to occur due to chance (Hubert and Arabie, 1985). An adjusted Rand Index of 0 is expected for two completely random classification schemes, while a value of 1 indicates perfect agreement between the two.

Bayesian multi-level modeling

Dietary rankings are neither continuous predictors nor discrete categories but, instead, are categories with a natural order. Therefore, to test the hypothesis that food type importance can be predicted from dental topography in carnivorans, we used ordinal regression with diet ranking represented as a cumulative distribution (Bürkner and Vuorre, 2019). Like polychoric PCA, cumulative ordinal regression models assume the response variable is drawn from a continuous distribution split by $\mathtt{K}$ thresholds that separate $\mathtt{K}+1$ groups; for 4 dietary rankings, 1-4, the model will estimate 3 thresholds within the total distribution of rankings (Bürkner and Vuorre, 2019). The distances between thresholds in a cumulative distribution need not be equal. We used dietary item importance rankings as our responses and the dental topographic metrics for m1 and m2 as our predictors. Because body mass can mediate the type of food that a species is capable of attaining and processing with a given occlusal topography (e.g., Carbone et al., 1999, 2007; Radloff and Du Toit, 2004), we included the natural log of body mass, taken from Jones et al. (2009), as an interaction term for both the m1 and m2 predictors. Species traits may co-vary due to evolutionary history, so we used a phylogenetic correlation matrix generated from the time-scaled molecular phylogeny of Slater and Friscia (2019) as a group-level predictor

(de Villemereuil and Nakagawa, 2014; de Villemereuil et al., 2012; Lynch, 1991). This phylogenetic multi-level modeling approach jointly estimates and incorporates the phylogenetic signal into the model, which then determines the degree of covariance between species (Fulwood et al., 2021; McElreath, 2020).

Our models took the general form

$$ordinal(\text{Diet Rank}) \sim \ \beta_1 \text{mass}\,(\beta_2 \text{m1} + \beta_3 \text{m2}) + R_p,$$

where β_1 represents the effect of body mass on diet category, β_2 and β_3 represent the effect of m1 and m2 topography on diet category, and R_p represents the phylogenetic correlation matrix. The interaction terms $\beta_1 * \beta_2$ and $\beta_1 * \beta_3$ represent the interactions between mass and m1 topography, and mass and m2 topography, respectively.

For each dietary item, we fit five ordinal regression models: one for each of the three dental topographic measures, one for RLGA, and one model that included all 4 of the dental metrics. Models were fit using the `R` package `brms` (Bürkner, 2017), an interface for the Bayesian probabilistic programming language `Stan` (Gelman et al., 2015). Working in a full Bayesian framework allows us to fit these complex ordinal models within a multi-level structure, to provide an intuitive measure of uncertainty in the results (i.e. probability), and to use regularizing priors to minimize overfitting risk. Prior to fitting the models, we standardized all linear predictors to z-scores as is recommended practice when working with predictors on different scales (McElreath, 2020). We used a $\mathcal{N}(0, 1)$ prior on each predictor variable and a custom Dirichlet prior on the estimated threshold values, setting the mean at 0. We used prior predictive simulation to determine that these priors effectively capture effect size probabilities for each scaled predictor while discouraging unrealistic values (Figure S1). Each model was run for four chains, with 2000 iterations of warm-up and 2000 iterations of sampling. Chain convergence was verified with the Gelman-Rubin $\hat{R}$ statistic (Gelman and Rubin, 1992). For each food type we used the leave-one-out (LOO) cross validation approach (Vehtari et al., 2017) to compare the predictive power of each of the 4 models, then estimated the model weights using stacking (Yao et al., 2018).

We used posterior predictive checking via the `pp_check` command in `brms` to confirm that the models indeed generated reasonable estimates of the original dietary importance data (Figure S2). For each food item, we averaged over the model predictions using the LOO stacking weights. Data processing and post hoc analyses heavily relied on the `tidyverse` (Wickham et al., 2019) and `tidybayes` (Kay, 2021) packages. Full model scripts are available in DataDryad (`www.tobepopulatedpriortosubmission.com`)

Predicting food item importance in data-deficient extant and fossil carnivorans

A desirable outcome of any predictive model is the estimation of response variables for observations of unknown state. We first used our fitted models to predict the importance of each food item to the overall diet for the 11 data-deficient extant taxa in our data set. As in our approach above, we predicted the importance of each food type for each data-deficient taxon using the full set of models and computed model-averaged estimates using the LOO stacking scores. We view the resulting predictions as a sanity check, as they can be compared to the limited available information for each species to assess whether they are in general agreement.

To further explore the predictive abilities of our models, we generated model-averaged estimates of food type importance for 8 fossil carnivorans (Table 2). Molar scans and measurements were obtained from specimens housed in the fossil mammal collections of the Field Museum of Natural History, Chicago, while species mean body mass estimates were taken from the literature (Table 2). The selected fossil taxa span a phylogenetic, body size, and putative ecological breadth that should challenge our models to varying degrees. For example, the sabertoothed felid, *Smilodon fatalis*, and nimravids, *Dinctis* and *Hoplophoneus*, might be expected to exhibit dietary similarities to large extant felids due to their high degree of morphological similarity. Likewise, the borophagine canid *Tomarctus* and paleomustelid *Promartes lepidus* are morphologically comparable to crown group representatives of their respective families and so may be expected to exhibit similar dietary profiles. In contrast, the cave bear *Ursus spelaeus* is closely related to the living brown and polar bears but, on the basis of its craniodental morphology and tooth wear

patterns, has been inferred to be a tough plant specialist, generalized omnivore, or seasonal bone cracker (Jones and DeSantis, 2016; Peigné et al., 2009; Pérez-Ramos et al., 2020; Pinto-Llona, 2013; van Heteren et al., 2014), while the daphoenine amphicyonid *Daphoenus* and the stem carnivoran *"Miacis" latidens* have no close extant relatives. Including these taxa in our sample presents an opportunity to gain novel insights into their paleoecology.

Table 2: Fossil Taxa Sampled in this Study.

Species	Family (subfamily)	Body Mass (kg)	Dietary Ecology
Daphoenus sp.	Amphicyonidae†	14.56	omnivore
Dinictis sp.	Nimravidae†	22.9	hypercarnivore
Hoplophoneus primaevus	Nimravidae†	18.2	hypercarnivore
Miacis latidens	stem carnivoran	1.97	faunivore?
Promartes lepidus	Mustelidae	2.49	omnivore
Smilodon fatalis	Felidae (Machairodontinae†)	220	hypercarnivore
Tomarctus	Canidae (Borophaginae†)	16	hypercarnivore
Ursus spelaeus	Ursidae	362.5	herbivore, omnivore

NOTE.- For each fossil taxon, we provide the Family and subfamily to which it is currently classified, the literature derived body mass estimate (in Kg) and approximate estimate(s) of its dietary ecology. Body mass estimates are as follows: *Daphoenus* estimated from m1 length using the general equation Van Valkenburgh; *Dinictis* and *Hoplophoneus* midpoint of range from Andersson (2004); *Miacis latidens* estimated from m1 length using the general equation from Van Valkenburgh; *Promartes lepidus* estimated from m1 length using mustelid equation from Van Valkenburgh; *Smilodon fatalis* average value from Christiansen and Harris (2005); *Tomarctus* average value across species from Van Valkenburgh et al. (2003); *Ursus spelaeus* average value from Christiansen (1999).

Predictions from these models do not come in the form of a single number, but as a vector of probabilities, where the *ith* value is the probability that the dietary item has importance of rank *i* or lower to the diet of that taxon. These vectors of probabilities are not readily comparable to dietary data from extant data-rich species. To overcome this barrier, we computed weighted-

average importance scores for each food item for each taxon as

$$\text{Weighted Importance Score} = \sum_{i=1}^{n} Pr_i \text{Rank}_i, \tag{1}$$

where Pr_i is the probability of the ith of the n ranks. We projected the full set of weighted-average importance scores for each species into the principal components space of importance scores for extant species and identified their nearest neighbors, which we interpret to be the closest analogues to these taxa. A slight bias in importance predictions for some rare food items (see below), means that predictions cannot be compared directly to original codings and so we used a principal components analysis of weighted-average predicted importance scores for extant data-rich species for comparative purposes.

Results

Morphological Data

Principal components analysis of the dental topographic data yields patterns that conform to functional expectations (Figure 1A). PC1 explains 64% of the variance in dental topographic data and separates taxa with large relative grinding areas, complex molars, and tall cusps (positive scores) from those with small grinding areas, relatively simple teeth, and first molars with high relief (negative scores). Qualitatively, this axis appears to separate more omnivorous taxa (e.g. bears, positive scores) from more carnivorous taxa (e.g. felids, hyaenids, *Cryptoprocta*, negative scores). PC2, which explains 18% of the variance in tooth shape data separates taxa with complex molars (negative scores), from those with sharp molars and high relief (positive scores). This axis seems to be associated with degree of insectivory with small insectivorous taxa (herpestids and euplerids, positive scores) separating from taxa with less reliance on insects (negative scores). Broken stick analysis suggests that only the first PC is significant. There is a moderate degree of phylogenetic signal in carnivoran molar morphology that is significantly different from random expectation (K_{mult}=0.58, P=0.001, Effect Size=13.11).

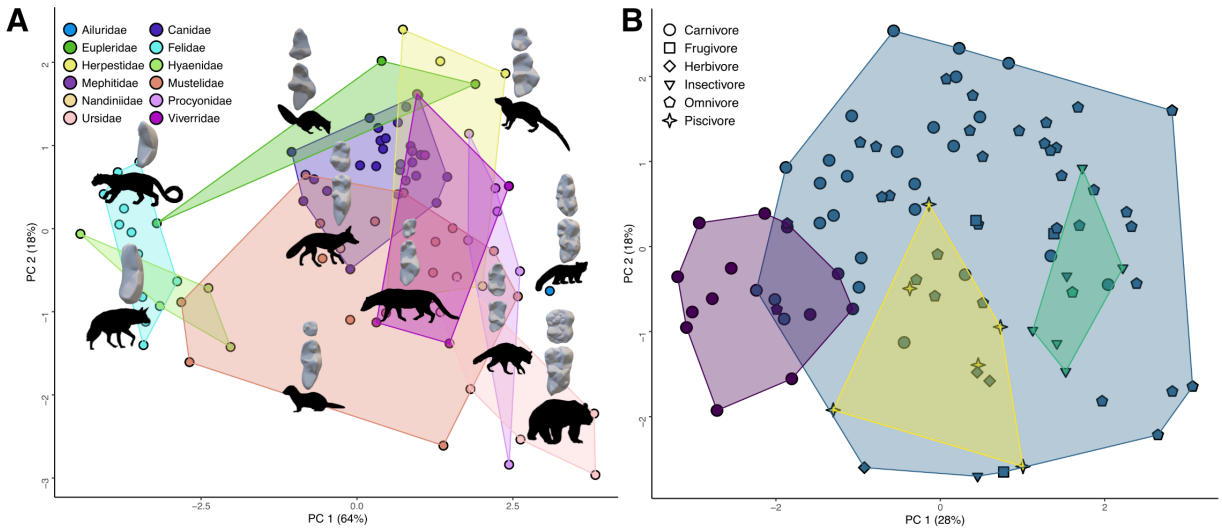

Figure 1: Phylogeny accounts for only a portion of dietary morphology, while categorization falls short of capturing the importance of dietary items. **1A:** Dental morphology contains some phylogenetic signal (K_{mult} = 0.58) as carnivoral families are loosely organized im morphospace. Families with narrow, sharp m1 molars and no m2 molars cluster in the negative values of PC1, while families with large, complex molars have positive PC1 values. **1B:** A cluster analysis of polychoric PCA scores generated from dietary importance data captures some discrete diet categorizations, but misses most. The best supported cluster analyses uses 4 groupings to describe dietary importance. Many species defined as piscivorous and insectivorous, rare categories in Carnivora, form their own clusters (yellow and green), while a portion of carnivorous species form a cluster (purple). However, most species, regardless of category, fall in the largest cluster (blue).

Dietary Data

Of the 101 species for which we collected morphological measurements, 11 lacked sufficiently detailed descriptions of their dietary habits to score important rankings for each food items. These data-deficient taxa were therefore used to evaluate predictions (see below). Figure 1B shows the dietary space defined by the first two polychoric PCs of importance scores from the remaining taxa, with plotting symbols corresponding to discrete dietary groupings taken from Animal Diversity Web. The first PC, which accounts for 27.73% of the variance in the data, separates taxa for which large and, to a lesser degree, small mammals are an important component of the diet (negative scores) from those in which hard and soft invertebrates and fruits (positive scores) are important. The second PC, which accounts for 18.07% of the variance, separates taxa that place high importance on small vertebrates (small mammals, birds, herptiles), as well as eggs and

carrion (negative scores) from those that consume more plants (positive scores).

Multivariate diet data do not appear to conform to existing dietary classification. Mixture-model clustering analyses using the full set of 13 PCs identified a 4 cluster scheme as optimal, based on BIC. Visualizing these clusters in the space defined by the first 2 PCs of the dietary importance data reveals a weak correspondence with the Animal Diversity Web scheme, particularly in the carnivore, omnivore, herbivore, and frugivore classes (convex hulls in Figure 1B), a result that is confirmed quantitatively by an adjusted Rand Index of 0.17. The clustering analysis does effectively collate the 6 piscivorous species into a cluster, most evident on PC5, and places 5 of the 8 insectivorous species into a cluster. A cluster analysis performed using only the significant PCs (determined from eigenvalues > 1.0; n=5) selects a two-cluster scheme, lumping the yellow, green, and blue groups into a single cluster (Figure 1B).

Ordinal Models of Food Types

Chains from all Bayesian ordinal models demonstrated appropriate convergence ($\hat{R} < 1.002$). Detailed model outputs and visualizations are in Figure S3 and Table S1. Calculations of model weights using LOO scores and model stacking showed that different dental topographic metrics best predict the dietary importance of different food types (Table 3). However, these relationship are often mediated by body size and sometimes in very different ways. To visualize these effects, we plotted the posterior probability of belonging to each dietary importance rank for values of the optimal trait, broken down into low (-1.5 *sd*), mean, and high (+1.5 *sd*) body mass groupings for select dietary items (Figure 2). RLGA strongly decreases with increased consumption of Birds (Figure 2A), Large Mammals (Figure 2D), and Small Mammals (Figure 2E), but increases with increased consumption of fish. However, due to the strong interaction between mass and RLGA, a diet containing a large proportion of birds is best predicted in small-bodied carnivores (Figure 2A), a diet rich in small mammals is best predicted in small and medium sized carnivores (Figure 2E), and a diet rich in large mammals is best predicted in large carnivores (Figure 2D), while a high importance of fish is best predicted for large bodied taxa with large grinding areas.

Table 3: Model Support (AIC weight) for Ordinal Regressions of Dietary Item Importance Ranks (rows) on Dental Traits (columns).

Diet	ariaDNE	OPCr	RFI	RLGA	All Predictors
Bird	0	0	0.07	**0.59**	0.34
Carrion	0	**0.57**	0	0.43	0
Egg	0.18	0	**0.82**	0	0
Fish	0	0.27	0	**0.73**	0
Fruit	0	**0.62**	0.28	0.10	0
Hard Invert	0.28	0	0	0.17	**0.55**
Herptile	**0.75**	0.15	0.01	0.09	0.01
Large Mammal	0	0	0	**0.65**	0.35
Plant	**0.61**	0.39	0	0	0
Root	0	0	0	**1**	0
Seed	**0.82**	0	0	0.19	0
Small Mammal	0.21	0	0	**0.79**	0
Soft Invert	**0.90**	0.10	0	0	0

NOTE.- The model (predictor) with highest weight is bolded for each dietary item. Note that body mass is included as a covariate for each model but that its effect is variable across models.

We also found that the significance of first and second molar morphology varied across food types. OPCr of the m2, but not m1, is positively associated with the importance of fruit in small carnivorans but, due to the interaction with mass, high m2 OPCr values are negatively associated with fruit consumption in larger carnivorans (Figure 2B). Similarly, high aDNE values for the first lower molar are associated with a high importance of soft invertebrates in small-bodied carnivorans, while low aDNE values are predictive of high importance of soft invertebrates in large-bodied taxa (Figure 2F). Other models are more complex still. Based LOO weights, a model that includes all tooth metrics, mass, and their interactions is the best predictor of hard

invertebrate importance (Table 3). Small-bodied carnivores consume more hard invertebrates than larger species, especially in species with high m1 aDNE values. However, an increased lower grinding area is strongly associated with increased hard invertebrate consumption across all body sizes. Across the range of carnivoran body mass, a high aDNE value on m2, but not m1, increases the probability of plants in the diet.

Rarer food types present a range of challenges to our predictive models. Obligate herptile consumption is uncommon in carnivorans, but the best fitting model incorporating aDNE and body mass (Table 3) finds a moderate probability that reptiles and amphibians are very important to the diet of small-bodied taxa, regardless of the sharpness of m1 and m2. However, the effect of aDNE on herptile consumption changes as mass increases, resulting in a high probability of herptile consumption in large-bodied carnivorans with high m1 and low m2 aDNE (Figure 2C). Similarly, while no carnivorans in our data set primarily consume roots, the probability of consuming some roots does robustly increase with increased lower grinding area, particularly in larger species. The effect of carrion consumption on OPCr m1 and m2 is not strong, though the interaction between mass and m2 OPCr suggests that carrion consumption may be highest in small-bodied carnivores with complex m2s, and lowest in large carnivores with complex m2s. Eggs are an unimportant component of carnivoran diet, but relief of the m2 predicts an increased consumption, particularly in small-bodied carnivores.

Predicting Dietary Importance in Data-deficient Extant and Fossil Carnivorans

Dietary importance predictions for the 11 data-deficient extant taxa are consistent with limited knowledge regarding their diets. Most data-deficient taxa are small-bodied members of clades that are traditionally considered to exhibit more generalized diets (Herpestidae, Viverridae) and our predictions reflect this, with non-negligible contributions of hard invertebrates, fruits and herptiles inferred for most (figure 3). Carrion, eggs, fish plants, roots, and seeds are identified as relatively low importance foods across these taxa, and while most are likely to at least occasionally consume small mammals, large mammals are unlikely to be ever consumed. Among more

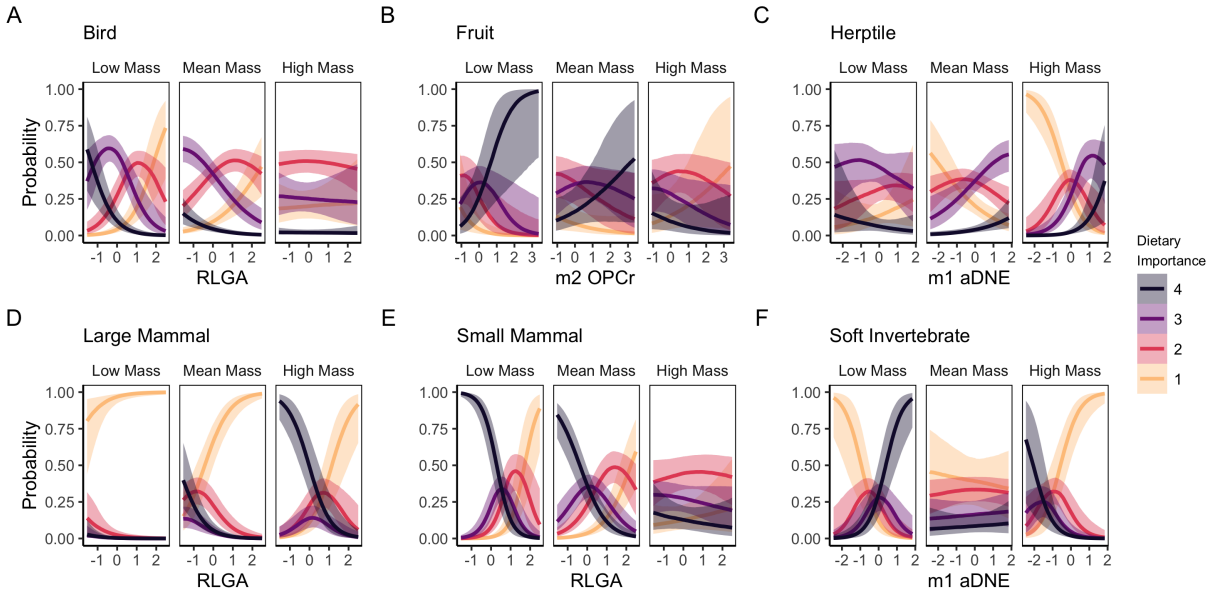

Figure 2: The influence of dental morphology, mass, and their interaction on dietary prediction strongly varies between dietary items. Plots depict the 80% prediction intervals for each of the 4 dietary ranks at low mass, average mass, and high mass. RLGA measurements can effectively predict the amount of bird (**1A**) and small mammal (**1E**) in the diet of small-bodied carnivorans, however these predictions become much less effective for large bodied species. However, RLGA can effectively predict the amount of large mammal consumed across all body sizes (**1D**). m1 aDNE effectively predicts herptiles and soft invertebrates in the diet of large carnivorans, however it is more difficult soft invertebrates for average-sized species and herptiles for smaller species (**1C**, and **1F**). A high m2 OPCr value in small carnivorans means a high probability of eating fruit, though the predictive power decreases with increasing mass. (**1B**).

specialized taxa, the bay cat *Catopuma badia* and marbled cat *Pardofelis marmorata* are confidently predicted to be obligate small mammal feeders and to include a large proportion of birds in their diet. These are the only two taxa for which large mammals have non-negligible probability of being occasionally consumed. The cat-like linsang *Prionodon linsang* is predicted to be similarly carnivorous but, unlike the cats, invertebrates, particularly hard invertebrates, also form a critical component of its diet. Soft invertebrates are predicted to feature heavily in the diets of banded palm civet *Hemigalus derbyanus* and Sunda stink badger *Mydaus javanensis*, as well as the short-tailed mongoose *Herpestes brachyurus*. Due to the small body size of many of these data-deficient taxa, predictions of some food items, herptiles in particular, were uninformative.

Projecting data-deficient extant species into the multivariate diet space for data-rich species

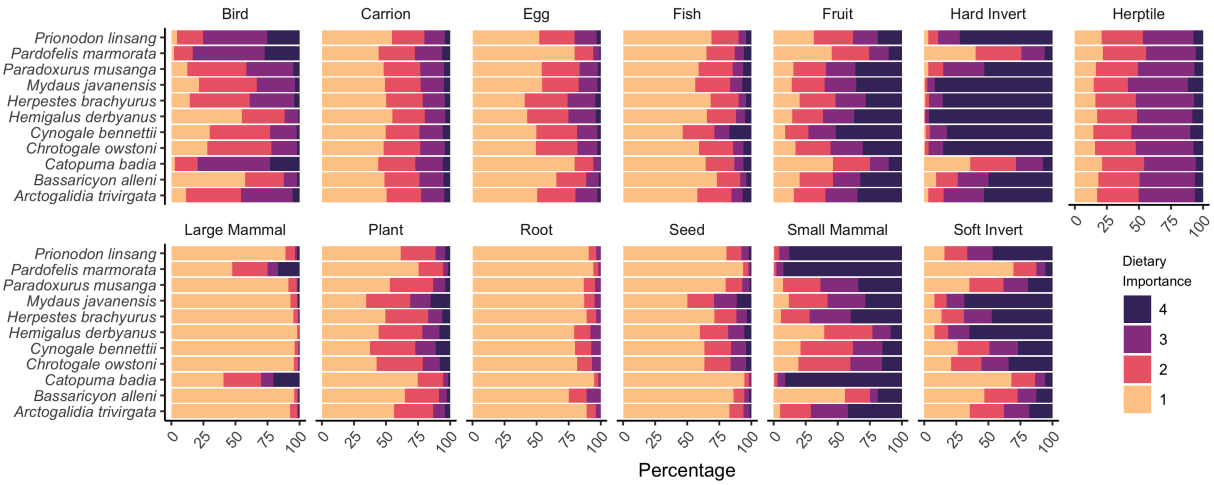

Figure 3: Ordinal models of dietary items can be used to predict the diet of understudied species. Estimates of the diet rankings of these 11 species with cryptic dietary data use the models for each dietary item, weighted by the LOO stacking scores, and the cryptic species' dental metrics and mass as input. Some dietary items, such as bird, small mammal, and soft invertebrate, have heterogeneous predictions across species, demonstrating that molars and mass influence these predictions. Other diet items such as root, carrion, and herptile, have similar and ambiguous predictions across all species, suggesting a low predictive power for these taxa.

shows that both cats cluster exclusively with other members of Felidae, and particularly with small to medium-sized species (Table 4). The "cat-like" linsang does not cluster with felids at all, but rather is closest to the North American mink, as well as a selection of mustelids, canids, euplerids, and mephitids (latter two not shown in Table 4) that are united in placing high importance on small vertebrate and invertebrate prey. Among other results, it is notable that the nearest neighbors of the three Southeast Asian hemigaline viverrids all come from the American Procyonidae (*Procyon* spp. in the case of *Chrotogale* and *Cynogale*, and *Nasua* and *Nasuella* for *Hemigalus*).

Predictions for the relative importance of different food items in the diet of many extinct carnivorans (Figure 4) are also consistent with previous work. We infer that large mammals were an extremely important component of the diet of the machairodont felid *Smilodon fatalis* and the nimravids *Dinictis* and *Hoplophoneus primaevus*. Small mammals and, to a lesser extent, birds are also inferred to have been an important component of diet in the two smaller nimravids, while the probability that *Smilodon* at least occasionally consumed carrion is greater than 50%. Animal-

Table 4: Nearest Neighbors 1-3 for Data Deficient Extant Taxa and Fossil Taxa in Multivariate Diet Space.

Taxon	Family	Neighbor 1	Neighbor 2	Neighbor 3
Catopuma badia	Felidae	*Felis silvestris*	*Leptailurus serval*	*Leopardus wiedii*
Pardofelis marmorata	Felidae	*Leptailurus serval*	*Leopardus wiedii*	*Felis silvestris*
Herpestes brachyurus	Herpestidae	*Mephitis mephitis*	*Viverricula indica*	*Spilogale putorius*
Mydaus javanensis	Mephitidae	*Ichneumia albicauda*	*Fossa fossana*	*Bassariscus astutus*
Prionodon linsang	Prionodontidae	*Neogale vison*	*Galictis cuja*	*Vulpes zerda*
Bassaricyon alleni	Procyonidae	*Potos flavus*	*Bdeogale jacksoni*	*Nasua nasua*
Arctogalidia trivirgata	Viverridae	*Lycalopex vetulus*	*Conepatus mesoleucus*	*Paguma larvata*
Chrotogale owstoni	Viverridae	*Procyon lotor*	*Procyon cancrivorus*	*Ichneumia albicauda*
Cynogale bennettii	Viverridae	*Procyon lotor*	*Procyon cancrivorus*	*Ailurus fulgens*
Hemigalus derbyanus	Viverridae	*Nasuella olivacea*	*Nasua nasua*	*Bdeogale jacksoni*
Paradoxurus musanga	Viverridae	*Conepatus mesoleucus*	*Paguma larvata*	*Lycalopex vetulus*
Daphoenus	Amphicyonidae	*Canis aureus*	*Arctictis binturong*	*Canis latrans*
Tomarctus	Canidae	*Canis simensis*	*Canis latrans*	*Chrysocyon brachyurus*
Smilodon fatalis	Felidae	*Panthera leo*	*Panthera onca*	*Crocuta crocuta*
"Miacis" latidens	"Miacidae"	*Conepatus mesoleucus*	*Lycalopex vetulus*	*Paguma larvata*
Promartes lepidus	?Mustelidae	*Vulpes velox*	*Nandinia binotata*	*Vulpes macrotis*
Dinictis	Nimravidae	*Uncia uncia*	*Neofelis nebulosa*	*Panthera pardus*
Hoplophoneus primaevus	Nimravidae	*Neofelis nebulosa*	*Caracal caracal*	*Uncia uncia*
Ursus spelaeus	Ursidae	*Ursus maritimus*	*Ursus arctos*	*Tremarctos ornatus*

NOTE.- Neighbors are listed in order of increasing distance, such that Neighbor 1 is closest to the taxon in question followed by Neighbor 2 then Neighbor 3.

derived protein sources, such as fish and herptiles, receive high probabilities for occasional consumption in these taxa, but they are generally inferred to be unimportant. Less obviously, our models also place a relatively high probability (>0.75) on the occasional consumption of fruits by the cat-like predators.

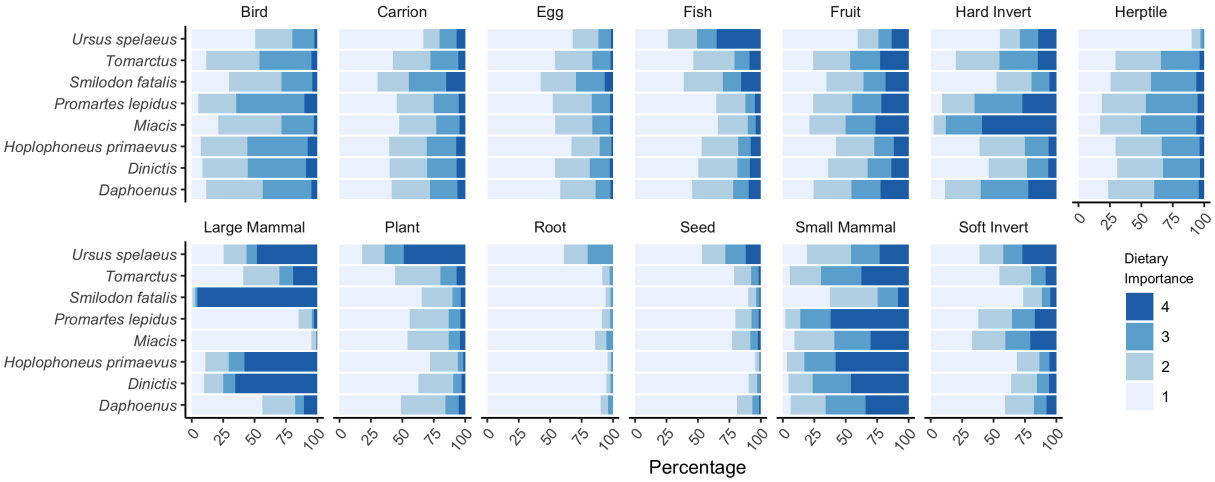

Figure 4: Ordinal modeling can also provide detailed information on the importance of dietary items for extinct species. As in figure 3, model-averaged item importance scores are generated from dental metrics and estimated body mass for each species, with 1 indicating an item is predicted to be never consumed and 4 indicating that is of primary importance to the diet of that species.

The borophagine canid *Tomarctus* and the amphicyonid *Daphoenus* are both inferred to have had relatively generalized diets, with no food items strongly (> 90% frequency) recovered as belonging to groups 3 or 4 but with fruits, small mammals, and, in the case of *Daphoenus*, hard invertebrates cumulatively achieving more than 50% posterior probability. *Tomarctus* is inferred to at least occasional take large mammal prey with relatively high probability (~ 0.75). Although plants are inferred to contribute to the diet of the cave bear *Ursus speleaus*, we find no evidence that it was a plant specialist; rather, plants, fish, and large and small mammals all contributed regularly to overall diet.

The paleodiet of the two other taxa in our sample have not been as thoroughly studied. We infer that *"Miacis" latidens*, a small-bodied stem carnivoran from the Eocene of North America, relied on hard-bodied invertebrates, with fruit and small vertebrates also contributing to its diet. *Promartes lepidus* is inferred to have primarily consumed small mammals, though herptiles, birds,

fruit and invertebrates all yield non-negligible probabilities of featuring at least occasionally in its diet.

Projecting fossil species in the mulitvariate diet space of extant taxa again yields a mix of intuitive and surprising results. The sabertoothed taxa unsurprisingly cluster close to larger extant cats, with the spotted hyaena *Crocuta crocuta* also close to *Smilodon* due to its strong reliance on large mammal prey. The cave bear falls closest to the most carnivorous extant bear, the polar bear, but the more omnivorous brown and Andean bears are also found among its three nearest neighbors, suggesting that a more generalized diet is plausible for the extinct taxon. *Daphoenus* and *Tomarctus*, despite their distinct phylogenetic affinities, cluster closest to extant canids. *Tomarctus* is closest to the Ethiopian wolf, coyote, and maned wolf, all of which tend to rely on small mammals and birds, rather than large mammalian prey, while the amphicyonid falls close to the golden jackal as well as a viverrid (the binturong *Arctictis binurong*), suggesting that it may have been more of a dietary generalist. "*Miacis*" *latidens* and *Promartes lepidus* fall closest to a suite of small-bodied carnivorans spanning the families Canidae, Mephitidae, Nandiniidae, and Viverridae. However, as indicated by the model-averaged importance scores, "*M.*" *latidens* clusters closer to taxa that are generally considered more insectivorous, such as the hog-nosed skunk and hoary fox, while *P. lepidus* falls closer to more carnivorous species including the kit and swift foxes.

Discussion

Diet is a fundamental life history trait, defining an organism's basic biology as well as its role in a community. However, diet is also a complex, multidimensional trait and efforts to condense the diversity and frequency of food consumption into discrete dietary categories necessarily omit critical information regarding the realized dietary composition of a given species. We have demonstrated that dietary item importance rankings, phenotypic traits associated with food processing, and multilevel ordinal modeling can be leveraged to validate the relationship between

traits and food item importance, and to predict the dietary composition of extinct and understudied extant taxa without the need to condense multivariate dietary data into one of a few discrete categories. Our findings illuminate a nuanced perspective on dietary diversity by demonstrating the true multivariate nature of individual species' diets, while simultaneously revealing the loss of important ecological and biological information that follows the discrete categorization of complex traits. Additionally, our results highlight how the complex interactions between focal dietary traits, such as molar shape and structure, and peripheral traits, such as body mass, are critical to fully understanding a species' dietary structure.

Diet is a Multivariate Trait

The question of how to best quantify or categorize mammalian diet has lived long in the literature. Simple classification schemes that crudely reflect trophic level (carnivore, omnivore, herbivore) continue to be widely used in comparative studies (e.g., Evans et al., 2007; Fabre et al., 2017; Price and Hopkins, 2015; Price et al., 2012; Rowe et al., 2016; Santana et al., 2011), despite an awareness that two species in the same category may use dietary items of very different sizes, material properties, nutritional qualities, and phylogenetic status (Pineda-Munoz and Alroy, 2014). Eisenberg (1981) provided one of the first attempts to more finely describe the full range of diversity in mammalian feeding behavior using a classification scheme with 16 states, each of which was based on a dominant food item (i.e. a specialization). These categorical states have been further refined over time by workers specializing on more restricted clades, each of which may exhibit their own range of unique predatory and dietary behaviors (Boyer, 2008; Fulwood et al., 2021; Kienle et al., 2017; Slater, 2015; Slater et al., 2010; Toljagić et al., 2018; Van Valkenburgh, 1988; Verde Arregoitia and D'Elía, 2021; Williams and Kay, 2001). Still, it is apparent that most mammals make use of a mixture of food types and that dietary variation is more continuously distributed than the most complicated categorical classifications are able to permit (Pineda-Munoz and Alroy, 2014). Indeed, our ordination of dietary importance data for carnivorans revealed that even species traditionally categorized as "carnivores" occupy a broad

swath of dietary space, and do not cluster into natural groupings (Figure 1B). Attempts to project dietary variation into a single univariate, quantitative trait (e.g., López-Aguirre et al., 2022; Rojas et al., 2018) may also lead to information loss; although the first principal component of our importance scores appears to represent a carnivory-herbivory continuum, as in Rojas et al. (2018), finer-scale patterns of dietary variation, such as a dominant use of invertebrate prey or fish, occur on subsequent axes and are missed if we focus only on a the first or the set of "significant" PCs.

Characterizing diet in a more natural, quantitative fashion still poses considerable challenges, particularly when expanding consideration to taxa that lack detailed ecological data. In one attempt to address this problem, Grundler and Rabosky (2020) proposed a novel comparative method in which the proportional utilization of a finite suite of resource types is modeled as a multinomial distribution that can evolve over the branches of a phylogenetic tree. Under this model, observational data on the frequency with which resources are used by a given species do not represent the diet itself, but rather are draws from the multinomial distribution (i.e. the diet) allocated to that branch of the phylogeny, which is, in turn, estimated by the model. Using a large database of dietary observations (Grundler, 2020), Grundler and Rabosky (2021) found evidence that snakes rapidly expanded in dietary diversity and complexity during the early Cenozoic from a likely insectivorous ancestor. While this approach holds much promise for modeling the evolution of complex traits on phylogenies of extant taxa, it appears to be of more restricted applicability to extinct lineages, where observational data on dietary item use are not typically available and "diet" must be estimated from proxies. Data-deficient extant taxa may also pose considerable problems for this method; although variation in sampling quality can be explicitly accommodated (Grundler and Rabosky, 2020), usable observational data are simply lacking for a large number of taxa (Gainsbury et al., 2018). In this respect, the more qualitative but widely applicable approach of Rojas et al. (2011) and Kissling et al. (2014) that we use here is the one that we think holds particular promise. We acknowledge that the use of keywords to rank the importance of food items is not without problems of its own, and in particular that the use of appropriate literature resources is paramount for quality control of

data (Gainsbury et al., 2018). It is also likely that the items listed by Rojas et al. (2011) and Kissling et al. (2014) are too broad for describing dietary variation within some subclades, while perhaps not broad enough to capture fine-scale patterns of dietary niche partitioning within more ecologically homogenous clades or communities (McNaughton et al., 1986; Pineda-Munoz and Alroy, 2014; Machado, 2020). Nonetheless, this coding scheme captures major patterns of dietary variation without the need to pigeon-hole taxa into arbitrary specialist groupings while, critically, providing a means for estimating dietary item importance in taxa of unknown ecology, including fossils. This particular flexibility is paramount in making informed macroevolutionary and paleoecological inferences (Finarelli and Flynn, 2006; Slater et al., 2012).

Predicting Multivariate Diet from Multivariate Morphology: Challenges and Future Potential

Predicting dietary item importance rankings from ecomorphological data presents novel challenges, but the flexibility of Bayesian multi-level modeling suggests that these methods hold much promise for future work in functional ecology. Past efforts to link ecomorphology and diet have relied on multivariate classification methods, such as discriminant function analysis, to identify combinations of traits that maximally distinguish among groups and to classify species of unknown ecology (Boyer, 2008; Friscia et al., 2007; Hopkins et al., 2021; Sacco and Van Valkenburgh, 2004). However, accommodating phylogenetic autocorrelation in discriminant function analysis is challenging (but see Schmitz and Motani, 2011) and it can be difficult to explicitly model covariates, particularly where the magnitude and sign of the effect varies as a function of predictor value. Multinomial Bayesian regressions that allow for the joint estimation and incorporation of phylogenetic signal in residual error have been recently employed for dietary prediction in fossil primates (Fulwood et al., 2021), and we have extended this approach by treating importance ranks as ordered variables and by including body size as a covariate. Body size is poor predictor of mammalian dietary categories in comparison to ecomorphological metrics

(Grossnickle, 2020), but our results suggest that body size may still contain an important signal for predicting dietary item importance ranks. Fulwood et al. (2021) did not include size as a covariate in their multinomial models but did note that, among primates in general, the teeth of folivores and insectivores resemble one another so closely that body mass must typically be used to discriminate between them (Kay, 1975). Similar effects are apparent in our carnivoran data. For example, lower grinding area (RLGA) effectively predicts the relative importance of large mammals, small mammals and birds, food items with similar mechanical properties. However, large mammals appear to be a less important component of small and medium bodied carnivoran diets, regardless of RLGA value (figure 1D), while RLGA is a poor predictor of the importance of birds and small mammals in the diets of large carnivorans (figure 1A,E), consistent with the idea that energetic constraints enforce a strong effect on prey size in mammals (Carbone et al., 1999, 2007). More strikingly, high values of DNE for the lower first molar, suggestive of a tooth with multiple tall cusps, predict a high importance of soft invertebrates in the diet of small bodied carnivorans, while the exact opposite relationship is recovered for large bodied taxa, driven largely by the low profile but more complex (high OPCr) first molars of the sea otter, raccoon, and the bears. If importance rankings are to provide a fruitful avenue for future investigations of ecological diversity and evolution, then the flexible framework provided by Bayesian multilevel modeling will play a critical role in untangling phylogenetic and allometric relationships between form and function.

Using predictive ordinal modeling to estimate dietary rankings from phenotypic data can help reconstruct dietary partitioning within a community, determine community dietary breadth, and enable explicit tests of ecological redundancies in a probabilistic manner. For example, a persistent question in evolutionary ecology is the role of limiting similarity in community structure (MacArthur and Levins, 1967). Briefly, limiting similarity postulates that two individuals that occupy an identical niche space should not co-occur in space and time. Support of limiting similarity has been equivocal, leading to the emergence of null hypotheses that place no emphasis on species' adaptations or ecological niche in the formation of communities (Hubbell,

2001; MacArthur and Wilson, 1963). Partitioning of food types is a fundamental aspect of community assembly and maintenance (Grant, 1986; MacArthur and Levins, 1967), and the ranking method presented here holds promise for quantifying diet in both poorly studied extant communities and paleo communities. Generating food consumption probabilities for species within a community naturally segues to comparisons of dietary structure across communities. Examples include comparing dietary structure between communities that occupy similar habitat but vary in species richness or taxonomic structure, or identifying changes in community dietary structure that occur with faunal turnover across space or time. For example, the dietary similarity that we identify between extant hemigaline viverrids of Southeast Asia and procyonids of the Americas suggests incumbency of the latter clade as a potential explanation for why viverrids failed to colonize the New World despite repeated opportunity and an otherwise geographically unconstrained distribution (Hunt, 1996). Baskin (2003) noted that procyonids only became the dominant hypocarnivorous carnivorans in North America after the extinction of phlaocyonine and cynarctine canids (subfamily Borophagine) in the early Hemingfordian and Clarendonian land mammal stages (Early through Middle Miocene), respectively. We can hypothesize that dietary item importance prediction for these canids might yield further similarities to hemigaline viverrids and procyonids, providing additional evidence for the long-term exclusion of feliform hypocarnivores from North America. The approaches outlined in this paper provide a straightforward way of testing this hypothesis.

The relationship between carnivoran diet and molar structure is well-documented, with numerous examples of how variation in this simple, functional toolkit influences the processing of various food items (Crusafont-Pairó and Truyols-Santonja, 1956; Friscia et al., 2007; Smits and Evans, 2012; Van Valkenburgh, 2007), and serves as a good starting point for building and testing ordinal models of dietary rankings. However, we believe our methodology can be adapted to virtually any system that has sufficient dietary composition data available. One well-studied example is the avian beak, a tool used for both food acquisition and processing (Grant, 1986; Pigot et al., 2020). In this case, different metrics of beak shape, such as length, width, curvature,

or keratin thickness, along with other phenotypic traits such as mass or tarsus length, may vary in their ability to predict the quantity of different food types obtained and consumed. Moreover, the method of ordered ranking need not be restricted to diet composition; with importance rankings of locomotor modes, such as swimming, climbing, digging, or flying, models could be constructed to evaluate which phenotypic traits are associated with different foraging strata or microhabitat use. Testing the effect of phenotypic traits on ranked features of diet, behavior, locomotion, microhabitat, or other commonly discretized environmental or biological variables, rather than forcing data into discrete categories, holds great potential for identifying the traits that best predict life history, interactions between multiple traits that are otherwise unobserved, or presence of correlated traits that may generate noise in categorical analyses.

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