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running title: axes of adaptive radiation in Carnivora

# Topographically distinct adaptive landscapes for skulls, skeletons, and size explain the dietary adaptive radiation of Carnivora (Mammalia)

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# Abstract

Models of adaptive radiation were originally developed to explain the early, rapid appearance of distinct modes of life within diversifying clades. Phylogenetic tests of this hypothesis have yielded limited support for temporally declining rates of phenotypic evolution across diverse clades, but the concept of an adaptive landscape that links form to fitness, while also crucial to these models, has received more limited attention. Using methods that assess the temporal accumulation of morphological variation and estimate the topography of the underlying adaptive landscape, I found evidence of an early partitioning of craniodental morphological variation in Carnivora (Mammalia) that occurs on an adaptive landscape with multiple peaks, consistent with classic ideas about adaptive radiation. Although strong support for this mode of adaptive radiation is present in traits related to diet, its signal is not present in body mass data or for traits related to locomotor behavior and substrate use. These findings suggest that adaptive radiations may occur along some axes of ecomorphological variation without leaving a signal in others and that their dynamics are more complex than simple univariate tests might suggest. (Key-words:)

# Introduction

Modern theories of adaptive radiation are implicitly or explicitly predicated on the concept of an adaptive landscape. The topography of the adaptive landscape relates gene frequencies (Wright, 1932) or, less strictly, morphological variation (e.g., Martin and Wainwright, 2013) to fitness, and provides a mechanism for understanding evolutionary change within populations at the generational scale (Lande, 1976; Arnold et al., 2001; Uyeda et al., 2011). G. G. Simpson was the first to make the crucial connection between models of the adaptive landscape taken from population genetics and macroevolutionary patterns observable in the fossil record, leading him to propose that rapid phenotypic evolution in small, peripherally isolated populations (Mayr, 1942) provided a mechanism for the geologically sudden appearance of distinct adaptive types without long-lived intermediate forms via a process he called quantum evolution (Simpson 1944, see also Grant 1963). In later linking quantum evolution to the phenomenon of adaptive radiation (Osborn, 1899, 1902), Simpson (1953) hypothesized that this mode of diversification would likely be concentrated early in clade history when peaks on the adaptive landscape, which he called adaptive zones, were vacant. As adaptive zones fill and ecological opportunity declines, the rate at which novel phenotypes are produced should subsequently slow (Osborn, 1902; Simpson, 1953; Valentine, 1980; Walker and Valentine, 1984), yielding a predictable signal in functional trait data.

The challenge that macroevolutionary biologists face is to infer the topography of the adaptive landscape, and historical dynamics on it, from comparative morphological data. The development of statistical approaches for evaluating tempo and mode in phenotypic evolution on phylogenetic trees has resulted in a rich and diverse toolkit for this task. Some authors, noting that Simpson's model implies that rates of phenotypic evolution should decline over clade history as adaptive zones fill, have used phenomenological (Harmon et al., 2003) or explicit models based on time-varying rates (Blomberg et al., 2003; Freckleton and Harvey, 2006; Harmon et al., 2010) to evaluate support for an "early burst" pattern in comparative data. Relaxing the requirement that shifts to new adaptive zones are concentrated early in clade history has further resulted in models that permit shifts in evolutionary rates as a function of co-occuring species diversity

(Mahler et al., 2010) or along branches of a phylogeny (Venditti et al., 2011; Eastman et al., 2011; Rabosky, 2014) and jumps in trait means independent of evolutionary rate variation (Landis et al., 2013; Landis and Schraiber, 2017; Duchen et al., 2017; Pagel et al., 2022). Other authors have noted that adaptive evolution towards optimal phenotypes implies very different long-term dynamics and covariances between species than a purely diffusive process (Hansen and Martins, 1996a), leading to a variety of methods to infer the presence and location of shifts toward new trait optima or, more precisely, the topography of the underlying adaptive landscape, based on a mean-reverting Ornstein-Uhlenbeck process (Hansen, 1997; Butler and King, 2004; Beaulieu et al., 2012; Mahler et al., 2013; Khabbazian et al., 2016; Bastide et al., 2018). Application of these methods to empirical data has yielded mixed results; True early bursts appear to be rare (Harmon et al., 2010), though challenging to detect (Slater and Pennell, 2014) and not entirely unheard of (Slater et al., 2010; Astudillo-Clavijo et al., 2015; Slater and Friscia, 2019; Stanchak et al., 2019), while support for diversification on a rugged adaptive landscape has been recovered in some clades (e.g., Mahler et al., 2013; Benson et al., 2018; Godoy et al., 2019; Mongiardino Koch, 2021) but not in others (Law et al., 2019).

Conceptual models of adaptive radiation developed by Osborn (1902) and Simpson (1953) focused on the ecological roles that organisms play in their environments and used phenotypes as proxies, with differences in trait values between lineages being interpreted as evidence for meaningful niche differentiation (Givnish, 1997, 2015; Arnold et al., 2001). Similarly, mathematical models of clade dynamics show that traits that are directly associated with resource use evolve more quickly towards their optima and maintain lower levels of variation than other traits, particularly in the face of competition (Gavrilets and Vose, 2005; Doebeli and Ispolatov, 2017). Although this work predicts that early bursts should only occur on a rugged adaptive landscape, comparative methods are data-hungry and traits associated with resource use are labor-intensive to collect. This has led many authors (e.g., Burbrink and Pyron, 2010; Harmon et al., 2010; Slater et al., 2010; Venditti et al., 2011; Burbrink et al., 2012; Godoy et al., 2019; Benson et al., 2018) to use readily available body size data as a proxy for ecology, due to

the presumed correlation between size and many aspects of life history (Peters, 1986). The correlation between body size and axes of ecological diversification is weak in many clades, though, and reliance on it for more general macroevolutionary analyses has been noted to generate misleading results (Jablonski, 1996; Slater, 2015).

Further complications arise as different models of adaptive radiation predict different relationships between evolutionary dynamics along distinct axes of resource use. Osborn's (1902) original formulation of adaptive radiation (Osborn, 1902) was based on the idea of rapid, adaptive evolution across multiple distinct trait complexes within a narrow temporal window (Figure 1 A–C). This "simultaneous radiation" model is often associated with adaptive radiations that result from colonization of a new area or the extinction of competitors, both of which dramatically expand the range of ecological opportunities available to the radiating clade (Valentine, 1980; Walker and Valentine, 1984; Erwin, 1992). Support for time homogeneous evolutionary rates or a flat adaptive landscape associated with one axis of resource use would certainly provide evidence against simultaneous radiation, but it is also possible that adaptive radiations might instead unfold sequentially, or in stages, along distinct axes of resource use (1D–F; Diamond, 1986; Schluter, 2000; Streelman and Danley, 2003; Gavrilets and Vose, 2005; Silvertown et al., 2006b; Glor, 2010). Unfortunately, few studies have simultaneously investigated tempo and mode in phenotypic evolution across distinct ecological axes, and those to have done so have yielded contradictory results regarding the order of niche divergence (Richman and Price, 1992; Ackerly et al., 2006; Silvertown et al., 2006a; Ingram, 2011; Sallan and Friedman, 2012; López-Fernández et al., 2013).

In this paper, I provide quantitative phylogenetic tests of the simultaneous and staged models of adaptive radiation using extant terrestrial members of the mammalian order Carnivora (dogs, cats, bears, weasels, etc.). Carnivorans are ideally suited for such a test as they are numerically diverse ($> 200$ extant species), possess a well-resolved phylogeny, and are ecologically disparate. Carnivorans span a range of dietary specializations, from plant and fruit specialists to obligate faunivores, and also exhibit a diversity of locomotor strategies, from semi-aquatic to

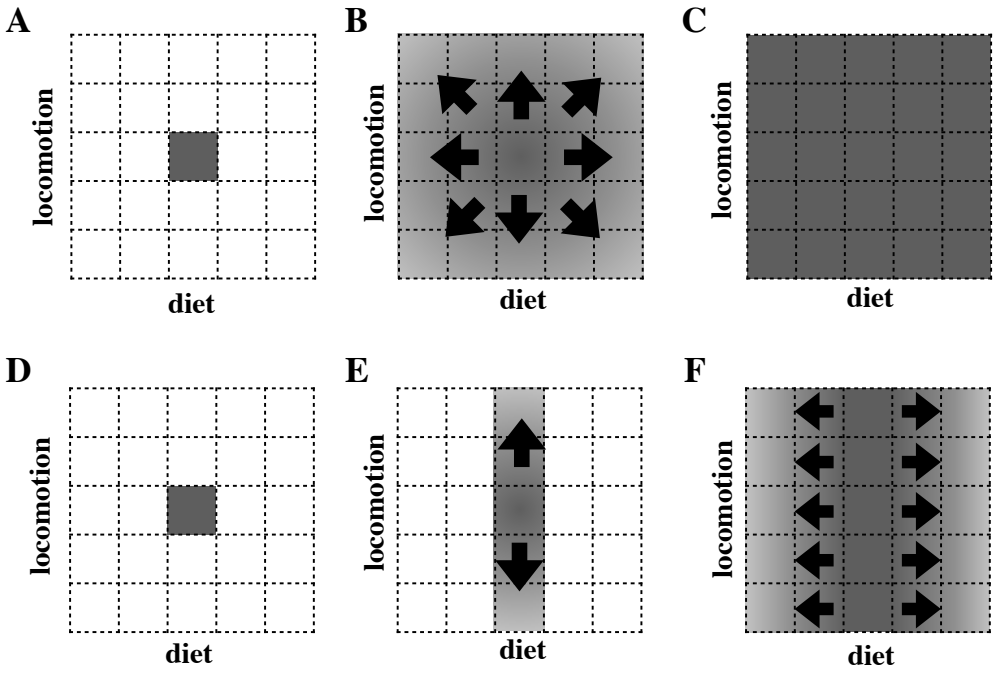


Figure 1: Some theories of adaptive radiation posit that a generalized ancestral form (A) should diversify simultaneously along distinct axes of resource use (here, diet and locomotor mode) (B), establishing complete functional diversity early in clade history with little subsequent change (C). Models of staged adaptive radiation differ from the simultaneous model in suggesting that the same generalized ancestor (D) should first diversify along one axis (frequently substrate-use) (E) and subsequently along another (e.g. resource-use) (F), yielding a sequential pattern of diversification in morphological and ecological data.

arboreal, all of which are reflected in dental and skeletal morphology (Van Valkenburgh, 1987, 1988, 1991; Sacco and Van Valkenburgh, 2004; Friscia et al., 2007; Van Valkenburgh, 2007; Meachen-Samuels and Van Valkenburgh, 2009; Samuels et al., 2013). In an analysis of tempo and mode in craniodental evolution, Slater and Friscia (2019) found strong support for an early phylogenetic partitioning of dental ecomorphological variation in carnivorans, which they interpreted as support for an adaptive radiation along an axes of dietary resource use (see also Meloro and Raia, 2010). This result provides a firm basis for asking similar questions about the evolution of locomotor diversity in the clade, as well as the relationship between macroevolutionary dynamics and the topography of the underlying adaptive landscapes for these traits. Here, I specifically attempt to address three key questions related to the nature of adaptive

radiations and our ability to detect them from comparative data. First, I ask whether carnivoran postcranial functional traits exhibit a signature of early, rapid morphological diversification consistent with traditional models of early-burst adaptive radiation and the signal present in some craniodental metrics. Then, I ask whether traits associated with dietary resource use, locomotor mode, and body size diversify simultaneously or sequentially and, if the latter, in which order do carnivorans diversify. Finally, I quantify the topography of the underlying macroevolutionary adaptive landscapes associated with these traits to ask whether variation in the tempo of trait diversification is associated with presence or absence of distinct adaptive peaks. My results indicate that diet, but not locomotor mode or body mass, was the critical axis of resource use exploited by the radiation of crown-group carnivorans.

## Materials and methods

### *Phylogenetic Framework*

A well-supported, time-scaled phylogenetic framework is essential for testing hypotheses regarding the tempo and mode of morphological diversification. For this study, I used the maximum clade credibility tree for extant and a few recently extinct terrestrial carnivorans generated by Slater and Friscia (2019). The tree topology and its branch lengths were jointly inferred using BEAST v.2.3.2 (Bouckaert et al., 2014) from a supermatrix of 30 nuclear loci and protein-coding mitochondrial genes for 235 taxa under a relaxed uncorrelated log-normal clock (Drummond et al., 2006). The unresolved fossilized birth-death process (Heath et al., 2014; Gavryushkina et al., 2014, 2016) was used as a tree prior, and 250 phylogenetically constrained fossil taxa with associated stratigraphic ages were used to calibrate the relaxed molecular clock. The resulting topology is well-supported (94% of splits have posterior probabilities $> 0.9$) and 95% highest posterior density intervals for node ages are narrow (mean = 2.65 Myr).

### *Ecomorphological Data*

Species mean values for 28 craniodental linear measurements as well as Ln($\sqrt[3]{\text{body mass}}$) for 198 species of extant carnivoran were taken from Slater and Friscia (2019). These were supplemented with 24 new measurements of limbs, scapulae, and pelves from 547 specimens spanning 135 species of extant carnivorans (mean = 4, range = 1-15 specimens per species) housed in the mammalogy collections of the National Museum of Natural History (Smithsonian Institution), Washington D.C., and the Field Museum, Chicago. Measurements were taken using Mitutoyo digital calipers to 0.01mm precision for measurements $<$ 250mm, or with a tape measure to 1mm precision for measurements $>$ 250mm and were selected to allow the computation of 16 ratio-based functional indices (Table 1) that have previously been identified as useful in distinguishing carnivores with distinct locomotor strategies (Davis, 1964; Van Valkenburgh, 1987; Samuels et al., 2013; Gould, 2014). Measurements of the metacarpals and tarsals, though highly informative in distinguishing among mammals with distinct locomotor modes (Samuels et al., 2013; Nations et al., 2019), were not taken here as these elements were infrequently available in osteological preparations of small-bodied taxa and their inclusion would therefore have reduced the number of species that could be sampled for macroevolutionary analyses. I corroborated that postcranial measurements allowed the discrimination of carnivorans with different substrate use preferences by performing a linear discriminant analysis using the `lda` function from the `MASS` library (Venables and Ripley, 2002, Supplementary Information). Each species with available post-cranial measurements was assigned to one of Eisenberg's (1981) substrate use categories (Terrestrial, Scansorial, Arboreal, Natatorial, Semi-Fossorial) following Polly (2010), with some minor edits based on literature review. Leave-one-out cross-validation (Supplementary File A) showed that most taxa can be assigned to their locomotor grouping with relatively high posterior probability, and that where mis-classifications occur, they tended to place taxa into similar locomotor groupings (e.g., scansorial taxa classified as terrestrial).

### *Macroevolutionary models of post-cranial evolution*

Slater and Friscia (2019) recovered strong support for an "early burst" of evolution in carnivoran molar traits but not in other craniodental characteristics or body mass. They considered this

Table 1: Post-cranial functional indices computed for carnivoran species in this study, along with their constituent measurement, functional interpretation, and source(s)

| Index | Interpretation | Reference |
|---|---|---|
| Scapula Index | Scapula shape, described as the ratio of distance across lines parallel to the spine that intersect the anterior and posterior borders of the scapula to the height from the glenoid cavity to the vertebral border, along the spine. Describes the expansion of shoulder musculature versus contribution of scapula to limb elongation | Davis (1964) |
| Glenoid Index | Ratio of glenoid length to glenoid width. Describes shape of shoulder joint, with values closer to 1 suggesting a more mobile shoulder joint | Davis (1964) |
| Brachial Index | Ratio of radius length, measured from the capitulum to inferior scapholunar articular surface, to humerus length, measured from superior margin of head to distal trochlea. Arboreal and natatorial taxa tend to have relatively short distal forelimbs. | Davis (1964), Samuels et al. (2013). |
| Humeral Epicondylar Breadth | Breadth across the humeral epicondyles, divided by humeral length. Provides a measure of the relative size of forearm musculature, which is associated with digging, swimming behavior | Samuels et al. (2013) |
| Capitulum Shape | Ratio of mediolateral to anteroposterior length of radial capitulum. The capitulum is more circular in arboreal taxa but more ovate in semi-fossorial species. | Davis (1964) |
| Fossoriality Index | Length of the olecranon process, measured from the posterior margin of the ulnar notch to the tip of the olecranon, divided by functional length of the ulna. Measures the mechanical advantage of the triceps brachii and therefore the force of elbow extension, which is elevated in fossorial taxa | Samuels et al. (2013) |
| Crural Index | Functional length of Tibia divided by functional length of Femur, measured from femoral head to condyles. Measures the degree of distal elongation of the hindlimb, which is reduced in arboreal, natatorial and fossorial taxa and increased in terrestrial taxa. | Davis (1964), Samuels et al. (2013) |
| Femoral Shaft Shape | Ratio of mediolateral to anterioposterior femoral diameter at the midshaft. Mediolateral expansion of the femoral shaft, relative to anteroposterior dimension, occurs in some natatorial taxa | Samuels et al. (2013) |
| Femoral Epicondylar Width | Bicondylar breadth of the femur divided by functional length. Provides a measure of attachment area for knee and plantar flexors, as well as extensors of the tarsal digits, and therefore of in-force of the distal posterior limb | Samuels et al. (2013) |
| Patella Groove Index | Width of the patellar groove, measured from medial to lateral keel, divided by bicondylar breadth. The tendon of m. quadriceps passes across the patellar groove and so the size of this index provides a measure of in-force of crus extension | Gould (2014) |
| Femoral Epicondylar Index | cranio-caudal depth of the femoral condyles divided by bicondylar breadth. Arboreal mammals tend to have femoral condyles that are wider than they are deep | Gould (2014) |
| Gluteal Index | Greatest distance from the femoral head to the greater trochanter divided by functional length of the femur. The greater trochanter is the site of origin of m. gluteus medius and m. gluteus profundus, and this index therefore provides a measure of the in-lever of these major hip extensors | Samuels et al. (2013) |
| Intermembranal Index | Ratio of the sum of humeral and radial length to the sum of femoral and tibial length. "Cursorial" carnivorans tend to have fore and hind limbs that are more equal in length and therefore possess intermembranal indicies closer to 1 than do other taxa | Davis (1964), Samuels et al. (2013) |
| Ischial Breadth | Bilateral breadth across the ischial tubers divided by maximum length of the pelvis. The Ischial tuberosity is the origin for the hamstring muscles so this metric partially captures information on the mechanical advantage of hip extensors and knee flexors. Terrestrial and cursorial taxa tend to have large values of relative ischial breadth, while fossorial taxa possess low values | Davis (1964) |
| Iliac Breadth | Bilateral breadth at the widest point across the iliac crests divided by maximum length of the pelvis. The ilia provide surface for the origin of the m. gluteus medius and m. sartorius and this metric therefore provides information on the relative mechanical advantage of the hip extensors, flexors, and stabilizers. It is increased in fossorial and large bodied taxa | Davis (1964) |
| Pubic Symphysis Length | Length of the pubic symphisis divided by pelvic length. Shortening of the symphysis has been attributed to increased horizontal thrust on the pelvis, such as in fossorial and natatorial carnivorans | Davis (1964) |

result to be consistent with adaptive radiation along dietary axes and cautioned that different functional indices may provide different macroevolutionary signals. To assess whether locomotor

diversification in carnivorans occurred along one or a few axes of functional post-cranial variation, I evaluated the fit of the same three macroevolutionary models (constant-rates Brownian motion, single-stationary-peak Ornstein-Uhlenbeck model, and early burst) to each of the 16 functional trait indices described above by using the `fitContinuous`() function from the `geiger` library (Pennell et al. 2014, Supplementary File B). To account for measurement error I added sampling variances to the diagonals of the model-specific variance-covariance matrices. Relative model fit was assessed by computing small-sample corrected Akaike Weights, $w_A$, for each model.

### *The Accumulation of Ecomorphological Disparity Through Time*

The simultaneous radiation model predicts that diversification along dietary and substrate-use axes should occur at approximately the same time, while the staged radiation model predicts that locomotor evolution should precede dietary diversification. To differentiate between these two forms of adaptive radiation, it is therefore necessary to assess which axis of trait variation, if any, was exploited first. In the paleobiological literature, weighted average times, often referred to as the Center of Gravity (CG), have long been used as measures of bottom- or top-heaviness in disparity and diversity profiles (Gould et al., 1977; Foote, 1991). Past levels of disparity cannot be inferred from phylogenies of extant taxa, but the partitioning of variation over phylogeny can be evaluated using Disparity Through Time analysis (DTT; Harmon et al., 2003), and this method lends itself well to CG descriptors.

DTT analyses track the standardized average morphological variance of subclades that are extant at time points (=node ages) spanning the root of a phylogeny to the final divergence event in the tree, where the standardization is relative to the total variance of the clade (Figure 2). If $d_i$ is the standardized average subclade disparity at time $t_i$, then the center of gravity of the DTT profile can be computed as

$$CG = \frac{\sum(d_i t_i)}{\sum(d_i)}. \tag{1}$$

Because the average subclade disparity is standardized relative to total clade variance, it

declines from a value of $d = 1$ at relative time $t = 0$ (i.e. along the root edge of the phylogeny) to $d = 0$ at the final branching event on the tree where each extant lineage is an individual species. This conveniently yields an expectation that CG should fall at $t \approx 0.5$ (see Supplementary File D for a simulation-based confirmation), with low CGs representing an early partitioning of variation among subclades and high CGs representing the late maintenance of high within subclade variation. Of course, the exact expected CG for any clade will depend on the shape of the tree (Foote, 1993) and this expectation can be conveniently assessed and compared with the empirical CG via simulation under a constant rates process. This approach is conceptually similar to the Divergence Order Test (DOT) of Ackerly et al. (2006), which calculates the center of gravity for unstandardized independent contrasts (Felsenstein, 1985) to determine whether large divergences in trait values occur early or late in clade history. A potential limitation of the DOT is that contrasts are computed using ancestral state estimates that are, themselves, inferred under a time-homogeneous model of evolution (Sallan and Friedman, 2012). Furthermore, the DOT explicitly assumes that adaptive radiation results from decelerating rates of phenotypic evolution, whereas similar patterns may result from myriad other process, including evolution on a rugged adaptive landscape (Revell et al., 2005; Harmon et al., 2021, e.g.,). Unlike the DOT, the center of gravity does not explicitly assume an underlying evolutionary process but, instead, provides a means of describing and statistically evaluating whether the temporal structure of morphological variation within and among clades is consistent with the hypothesis of early variance partitioning among clades (Foote, 1996).

I calculated CGs for craniodental and post-cranial traits, as well as for body mass, and evaluated their deviation from constant-rates expectations using 9999 datasets of equivalent dimensionality simulated under a constant-rates Brownian motion process (Supplementary File C). The high dimensionality of the craniodental and post-cranial traits pose challenges for efficient and accurate macroevolutionary inference. To reduce data dimensionality, I performed a phylogenetic principal components analysis (Revell, 2009) on the correlation matrices for each dataset using the `phyl.pca` function in the `phytools` library (Revell, 2012). Linear measurements

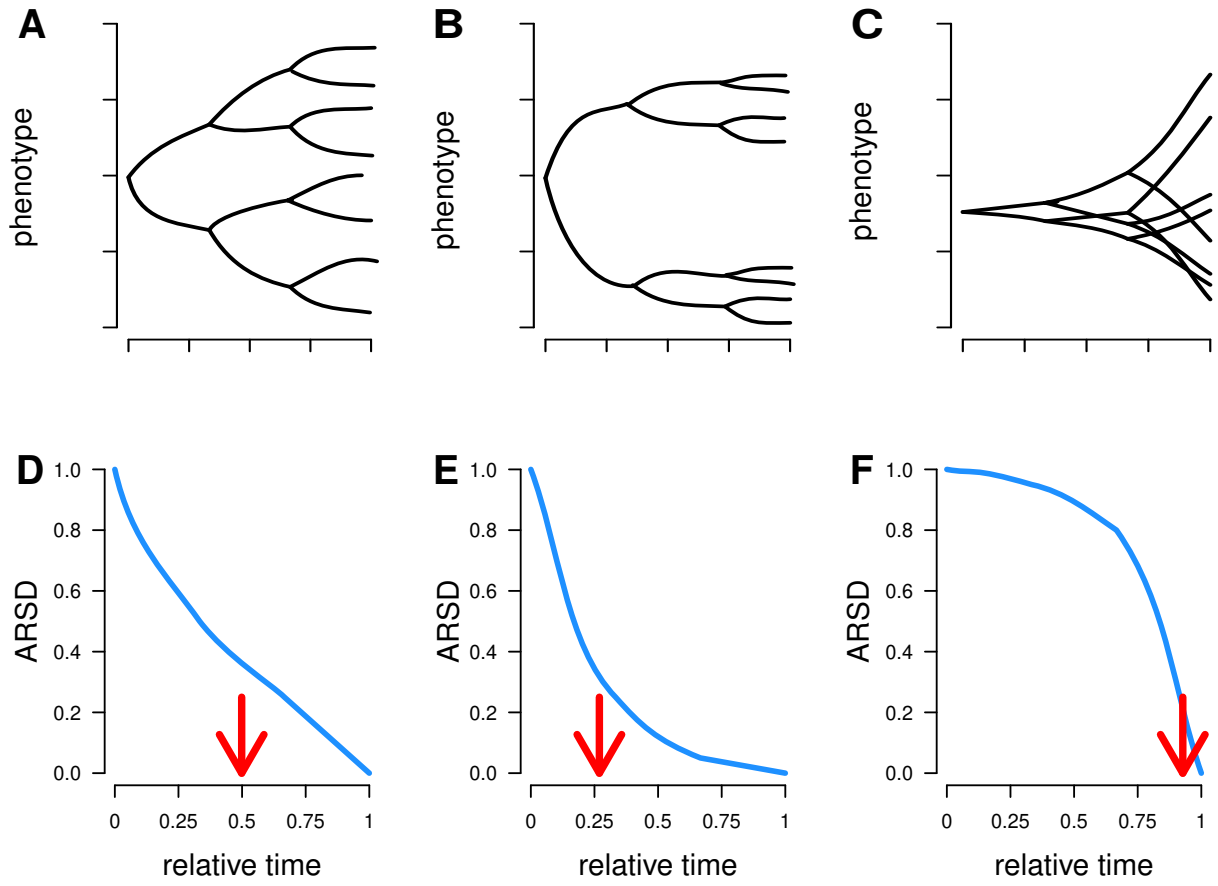


Figure 2: When the mode of phenotypic evolution is consistent with a random walk, phenotypic variation accumulates gradually over phylogeny (A), leading to a pattern in which the average relative subclade disparity through time (ARSD) declines steadily from 1 (i.e. all variance within a single clade) to zero (all clades are single tips) as time progresses from root to tip (D) and a center of gravity (red arrow) that falls at approximately the midpoint. Under an "early burst" scenario, trait variation does not accumulate steadily but rather, seems to accumulate early in the history of the clade (B), yielding an ARSD curve that drops precipitously and then levels out (E), and a center of gravity that falls below the midpoint of clade history. Evolutionary modes such as "late bursts" or time constant rates in a bounded space (e.g., constraints) yield a pattern in which phenotypic variation accumulates towards the tips of the tree (C) and an ARSD curve that declines very slowly until late in clade history (F), with a very high center of gravity.

were transformed into log-shape variables (Mosimann, 1970; Darroch and Mosimann, 1985) prior to principal components analysis by dividing each species' measurements by its geometric mean and taking the natural log, in order to remove consideration of overall size and to focus on ecomorphological shape. I retained all pPCs that explained more than 5% of the total variation in each multivariate dataset. CGs were finally compared across sets of traits to determine the

relative order of divergence.

*The Adaptive Landscape of Carnivoran Ecomorphological Diversificaton*

Simple macroevolutionary models and centers of gravity provide insights into the phylogenetic partitioning of morphological variation and hint at the kinds of evolutionary processes that might be responsible, but they do not allow us to discriminate between modes of adaptive radiation based purely on declining rates and those resulting from adaptive evolution on a rugged landscape. To understand the context for carnivoran ecomorphological evolution, I therefore estimated the macroevolutionary landscapes for craniodental and post-cranial traits, as well as body mass, using the phylogenetic expectation-maximization approach implemented in the `PhylogeneticEM` library (Bastide et al., 2018). This approach assumes that trait evolution follows an Ornstein-Uhlenbeck process in which traits evolve towards a primary optimum or, in the case of multivariate trait evolution, a vector of primary optima ($\theta$). The method then attempts to identify the presence and location of shifts in the vector of primary optima. Univariate traits evolve according to a standard Ornstein-Uhlenbeck process (Hansen and Martins, 1996b; Hansen, 1997) but traits can also be modeled in a true multivariate framework, with variances and covariances specified by an evolutionary rate matrix $\mathbf{R}$, though a single strength of attraction, $\alpha$, must then be shared by all traits.

As with DTT analyses, I used pPC axes explaining more than 5% of the total variation for each multivariate dataset. The maximum number of shifts allowed, `K_max`, was set to 30, based on preliminary trials, the `nbr_alpha` argument, which determines the resolution of the grid of $\alpha$ values evaluated, was set to 100, and the LINselect option used for model selection. Aristide et al. (2018) provided a proof that shows the most commonly assumed form of early burst (that is, exponentially declining evolutionary rates with respect to time) can be identified in this framework by allowing for inference of negative $\alpha$ values (see also Uyeda et al. 2015). I therefore set the `allow_negative` argument to `TRUE`. For convenience of interpretation, positive $\alpha$ values were converted into phylogenetic half-lives ($t_{1/2}$), which correspond to the time taken for a trait to move half way from its ancestral value to a new primary optimum after a regime shift.

# Results

## *Macroevolutionary model fitting*

Contrary to predictions of both the simultaneous and staged models of adaptive radiation, I found no evidence for early bursts of locomotor adaptation within Carnivora. Brownian motion or SSP models were uniformly recovered as best-fitting across the 16 functional indices, with support for the early burst model never exceeding that of BM or SSP (Table 2) and maximum likelihood estimates of the early burst exponential rate decline parameter never large (maximum $r$=-0.0016, equivalent to a rate half-life of 433myr). Maximum likelihood estimates of the $\alpha$ parameter of the OU process are relatively small, at most corresponding to a phylogenetic half-life of 6.3 myr (Femoral Shape), and more typically in the range of 23-34myr.

Table 2: Akaike Weights for the three models (BM: Brownian motion; SSP: single stationary peak; EB: early burst) fitted to each Functional Index. The weight corresponding to the best fitting model for each index is bolded. Parameter estimates are provided for the best fitting model; note that the $\alpha$ parameter is only relevent to SSP models.

| Functional Index | BM | SSP | EB | Root | Rate | $\alpha$ |
|---|---|---|---|---|---|---|
| Scapula Index | **0.59** | 0.21 | 0.21 | 0.85 | $2.9*10^{-4}$ | - |
| Glenoid Shape | 0.01 | **0.99** | 0.00 | 0.69 | $2.1*10^{-4}$ | 0.05 |
| Brachial Index | 0.12 | **0.83** | 0.04 | **0**.84 | $6.3*10^{-4}$ | 0.03 |
| Humeral Epicondylar Breadth | **0.52** | 0.29 | 0.18 | 0.25 | $9.6*10^{-5}$ | - |
| Capitulum Shape | 0.38 | **0.49** | 0.13 | 1.46 | $4.9*10^{-4}$ | 0.03 |
| Fossoriality Index | 0.16 | **0.78** | 0.06 | 0.14 | $7.1*10^{-5}$ | 0.03 |
| Crural Index | 0.37 | **0.50** | 0.13 | 0.93 | $5.2*10^{-4}$ | 0.02 |
| Femoral Shaft Shape | 0.00 | **1.00** | 0.00 | 1.12 | $1.0*10^{-3}$ | 0.11 |
| Femoral Epicondylar.width | **0.52** | 0.30 | 0.18 | 0.19 | $3.0*10^{-5}$ | - |
| Patella Groove Index | **0.44** | 0.4.0 | 0.16 | 0.43 | $6.6*10^{-5}$ | - |
| Femoral Epicondylar Index | 0.23 | **0.69** | 0.08 | 0.01 | $1.0*10^{-6}$ | 0.03 |
| Gluteal Index | **0.44** | 0.4.0 | 0.16 | 0.18 | $2.9*10^{-5}$ | - |
| Intermembranal Index | 0.39 | **0.47** | 0.14 | 0.84 | $2.0*10^{-4}$ | 0.02 |
| Ischial Breadth | 0.12 | **0.83** | 0.04 | 0.58 | $4.6*10^{-4}$ | 0.03 |
| Iliac Breadth | **0.58** | 0.21 | 0.21 | 0.64 | $6.0*10^{-4}$ | - |
| Pubic Symphysis Length | **0.57** | 0.23 | 0.2.0 | 0.27 | $1.5*10^{-4}$ | - |

## *The Accumulation of Ecomorphological Disparity Through Time*

Phylogenetic principal components analysis of the craniodental log-shape variables yielded 4 pcs that explained more than 5% of the variation. PC1 explained 44% of the variance and

separates hypercarnivores, defined by a combination of strong jaws and canines but with small or absent second and third molars (negative scores) from more mesocarnivorous and omnivorous/herbivorous taxa with positive scores. PC2, which explained 9.09% of the variation, separates taxa with large posterior molars (positive scores) from taxa with smaller posterior molars and larger anterior molars (negative scores). PC loadings are provided in Supplementary Table C1. A plot of PC1 and PC2 shows a generally obvious phylogenetic partitioning (Fig. 3A), with more mesocarnivorous clades (e.g, Canidae Mephitidae), occupying a high PC1/low PC2 postion, more carnivorous clades (e.g., Felidae, Hyaenidae) occupying low PC1/low PC2 positions, and more omnivorous/herbivorous clades (e.g., Ailuridae, Ursidae) occupying high PC1, high PC2 positions. The upper left quandrant of this bivariate morphospace, which corresponds to the impossible combination of simultaneously small and large posterior molars, is unoccupied.

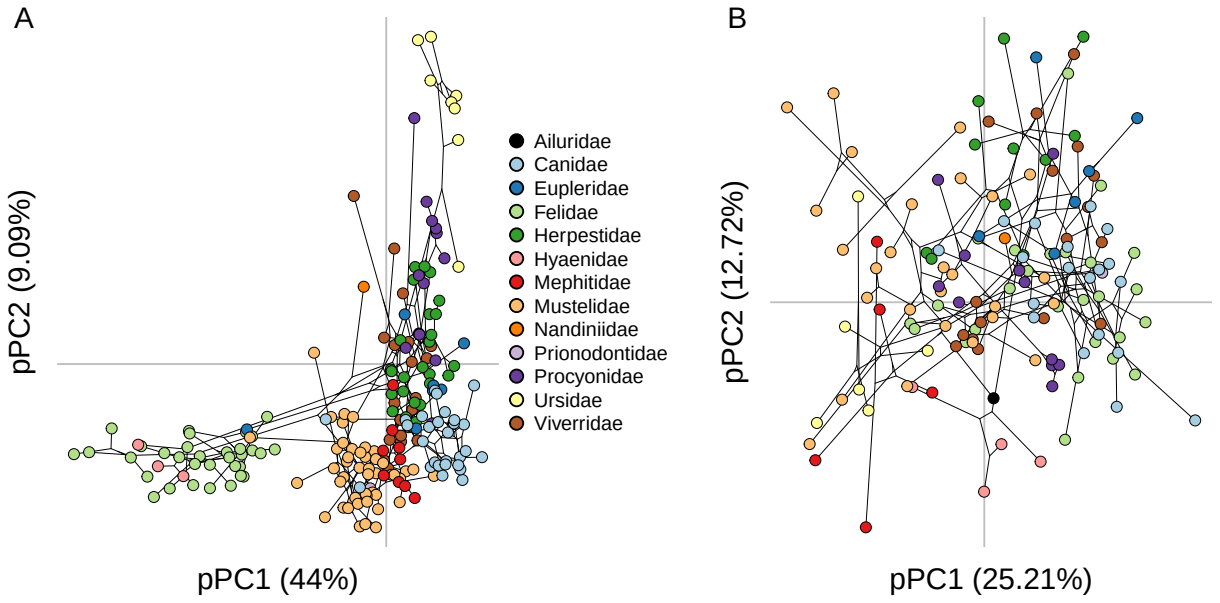


Figure 3: Phylogenetic principal components analysis of craniodental log-shape variables (A) yields a clear phylogenetic and ecological signal. This signal is less apparent in a plot of the first two pPC axes derived from post-cranial measurements (B)

Six phylogenetic principal components explained more than 5% of the variation in post-cranial log-shape variables. The first component (Fig. 3B), explaining 25.21% of the variation, separates long-limbed terrestrial taxa (positive scores) from natatorial and

semi-fossorial taxa with short broad limbs (negative scores). Patterns along subsequent PCs are less obvious. The second principal component accounts for 12.7% of the variation in post-cranial measurements but neither it, nor a plot of the space defined by the first 2 PCs (Figure 3B) are amenable to clear ecological interpretations. PC loadings is provided in Supplementary Table C2 .

The average subclade disparity through time profile for craniodental traits is broadly consistent with constant-rates expectation for the first 15 million years of carnivoran history, as indicated by a curve (solid line) that tracks the mean of the Brownian motion simulations (dashed line; Figure 4A). However, craniodental subclade disparity shows a substantial drop in the mid-Oligocene and lies at the lower bound of the constant-rates expectation (shaded area) for the rest of the Cenozoic (Figure 4A). The Center of Gravity for craniodental average subclade disparity appears slightly top-heavy (CG=0.60); however, the expected CG is dependent on the structure of the phylogeny (see SI) and is, in fact, significantly lower than expected under a constant rates process (95% quantiles under BM = 0.61-0.71 ; $P$=0.01;Fig. 4D). As suggested by the disparity through time curve (Figure 4B) the Center of Gravity for post-cranial traits (Fig 4C) is much higher than that for craniodental traits and is significantly higher than expected under a constant-rates process (CG = 0.72, $P < 0.001$; Figure 4E). The partitioning of body mass variation among and within clades is entirely consistent with a constant rates process (Fig 4C), with a CG that is virtually indistinguishable from Brownian expectation (CG = 0.699, Expectation = 0.669, $P = 0.167$; Figure 4F). The order of divergence, from earliest to most recent, therefore appears to be craniodental traits, body mass, post-cranial traits.

*The Adaptive Landscape of Carnivoran Ecomorphological Diversificaton.—*

The dietary adaptive landscape estimated from the first four craniodental pPC axes by the `PhylogeneticEM` algorithm contains 25 peaks that are distinct from the ancestral regime. Note that `PhylogeneticEM` does not identify and collapse so-called convergent shifts (shifts to similar optimal morphologies) ands so many of these peaks overlap one another (see below). The optimal configuration is shown in Figure 5; 16704 equivalent configurations were recovered and, although not all could be visually evaluated, branch shift frequencies showed that alternative configurations

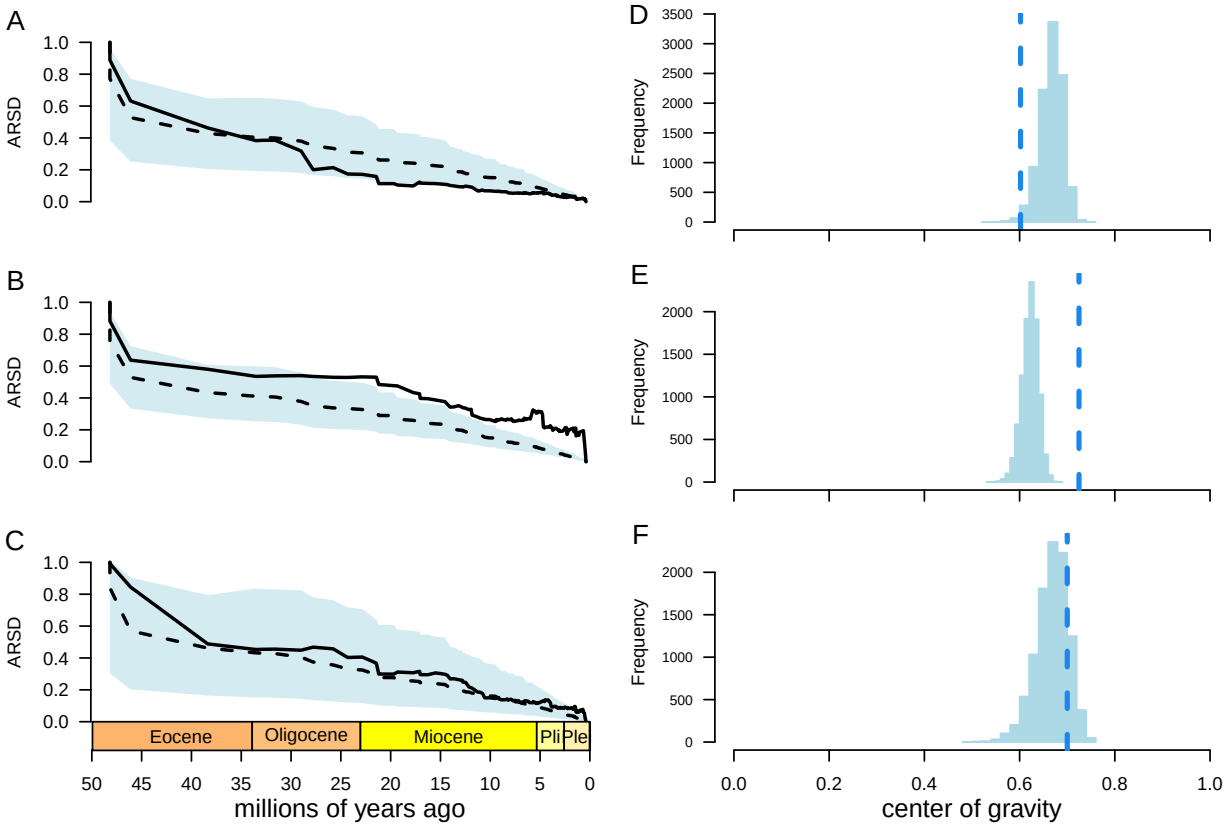


Figure 4: Disparity through time plots for carnivoran craniodental (A), post-cranial (B) and body mass (C) data. The solid line is the average relative sub-clade disparity for the data set, the dashed line is the median from 9999 datasets simulated under a constant rates process, and the shaded area corresponds to the 95% quantiles of the simulated data. Shown on the right (D-F) are the corresponding centers of gravity for the simulated datasets (solid bars) and the center of gravity for the trait data (dashed vertical line).

differ in the local arrangement of shifts (Supplementary Materials). For example, shifts may be swapped between sister taxa (sequential vs independently acquired). The strength of the pull to these optima is inconsistent with an early burst, *sensu* Harmon et al. (2010); it is positive and relatively strong ($\alpha = 0.26$), corresponding to a phylogenetic half-life of $\sim t_{1/2} = 2.7$ myr.

Within feliform carnivorans, peak shifts are recovered along the branches leading to an unnamed clade comprising Prionodontidae + Felidae, Felidae, Pantherinae, Hyaenidae, and terminal branches leading to the spotted hyaena *Crocuta crocuta* and the Malagasy Fossa *Cryptoprocta ferox*. All of these taxa are hypercarnivorous, relative to other members of the suborder. Additional shifts are found in the common ancestor of hemigalinine and paradoxurine

viverrids, mungotine herpestids, and the Malagasy falanouc *Eupleres goudotii*, representing a diversity of more frugivorous, omnivorous and potentially vermivorous taxa. Other feliforms most commonly fall in the ancestral regime. Among caniform carnivores, shifts are recovered along the branch leading to Canidae and within the family on terminal branches corresponding to the hypercarnivores *Speothos venaticus* and *Cuon alpinus*, Ursidae, Tremarctinae + Ursinae (i.e., Ursidae minus the giant panda *Ailuropoda*), Musteloidea, Mephitidae, the kinkajou *Potos flavus*, *Nasua* + *Nasuella* + *Bassaricyon*, Mustelidae, Melinae, the honey badger *Mellivora capensis*, Mustelinae, Lutrinae, Ictonychinae, and the lesser grison *Galictis cuja*. These shifts represent a more diverse set of dietary ecologies, ranging from more carnivorous (mustelids) to more omnivorous (ursids) and even frugivorous (*Potos*).

The adaptive landscape for post-cranial traits is apparently much flatter than that for craniodental traits and no shifts are identified. The strength of the pull to the ancestral regime is positive ($\alpha = 0.07$) but translates to a phylogenetic half-life of $t_{1/2} = 9.9$ myr, which implies slightly constrained macroevolutionary dynamics. A much flatter adaptive landscape emerges for body mass, with no shifts detected and a positive but very small $\alpha$ (0.02) corresponding to a phylogenetic half-life of $t_{1/2} = 34.7$ myr.

## Discussion

Models of adaptive radiation were originally developed to explain the early, rapid appearance of fundamentally distinct ("essentially discontinuous"; Simpson, 1953, p.223) modes of life within diversifying clades in the fossil record (Osborn, 1902). A modern focus on the "early rapid" component of these models has led to the development of numerous methods for assessing temporal variation in macroevolutionary rates (Blomberg et al., 2003; Harmon et al., 2003; Freckleton and Jetz, 2009; Harmon et al., 2010; Venditti et al., 2011) and yielded limited support for this mode of diversification in body size and shape data. The concept of an underlying adaptive landscape that links form to fitness, while also crucial to these models, has received less attention in modern phylogenetic tests of the early burst adaptive radiation hypothesis (but see

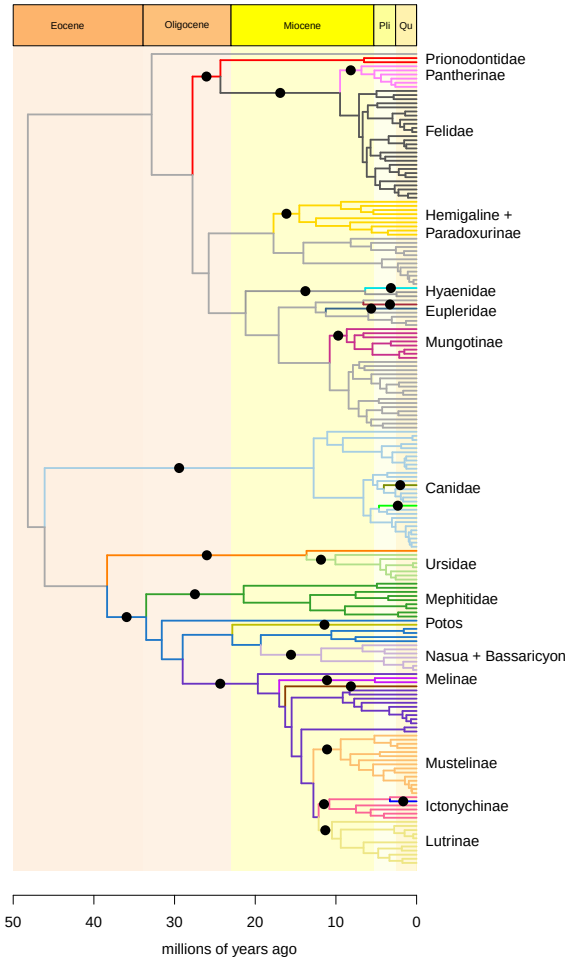


Figure 5: Carnivoran phylogeny showing the 25 adaptive peak shifts identified by the `phyloEM` approach. Black circles are placed at the midpoint of each branch along which a peak shift is inferred to have occurred, with branches inheriting and retaining that peak colored distinctly. Clade names are provided to orient the reader to shifts described in the results and are not intended to be exhaustive.

Mahler et al., 2013; Aristide et al., 2018; Mongiardino Koch, 2021), and it therefore remains unclear whether adaptive radiations unfold simultaneously across distinct axes of resource use, or sequentially with some axes being exploited before others. Using methods that focus on the temporal accumulation of morphological variation (Harmon et al., 2003; Slater and Pennell, 2014) and the topography of the underlying adaptive landscape (Bastide et al., 2018), rather than variation in rates, I found that significant early partitioning of craniodental morphological variation across carnivoran phylogeny occurs on an adaptive landscape with multiple peaks,

consistent with classic ideas about adaptive radiation (Osborn, 1902; Simpson, 1953; Valentine, 1969). Although strong support for this mode of adaptive radiation is present in traits related to diet, its signal is not present in body mass data or for traits related to locomotor behavior and substrate use. These findings suggest that the nature of adaptive radiation is more complex that simple univariate tests might suggest, and provide some hints regarding fruitful directions that future work might explore.

### *Carnivorans Adaptively Radiated on a Rugged Dietary Landscape*

Competition for dietary resources has long been viewed as a critical factor promoting the evolution of morphological innovations in some of the most iconic examples of adaptive radiation (Darwin, 1845; Lack, 1947; Grant, 1981; Schluter and Grant, 1984; Osborn, 1902). Theoretical models lend support to this hypothesis by predicting that early rapid evolution along axes of resource use should promote speciation and stable coexistence (Gavrilets and Vose, 2005; Doebeli and Ispolatov, 2017), while genomic evidence has started to accumulate that indicates relatively simple, and sometimes repeatable, genetic or transcriptomic "key innovations" can produce morphological features associated with distinct dietary specializations (Berenbaum et al., 1996; Lamichhaney et al., 2015; Vizueta et al., 2019; McGee et al., 2020). Carnivorans and their extinct stem lineages (Carnivoramorpha), are characterized by the presence of a carnassial pair, a modified upper fourth premolar and lower first molar that form a scissor-like pair of blades for efficiently cutting tough materials such as skin and connective tissue, that first appeared in the fossil record during the latest Paleocene (Solé et al., 2016). Although carnassials have evolved multiple times in mammalian evolutionary history, the true innovation in carnivoramorphans, relative to extinct mammalian clades such as creodonts and borhyaenids or the extant dasyurid marsupials, is that carnassialization is restricted to a single locus and that the basin-like posterior part of the lower carnassial tooth is free to occlude with the non-carnassial upper first molar (Van Valkenburgh, 1999, 2007). By varying the proportion of the lower carnassial given to slicing (the anterior trigonid) versus grinding (the posterior talonid), carnivorans can therefore optimize

efficiency at processing different types of food, ranging from vertebrate flesh to fruits or even bamboo stems (Wesley-Hunt, 2005; Van Valkenburgh, 2007). Ecomorphological (Van Valkenburgh, 1988, 1991, 2007), and behavioral (Van Valkenburgh, 1996) evidence supports a prominent role for molar morphology in determining dietary resource use, and comparative evidence for early burst-like dynamics in carnassial shape has been previously recovered (Meloro and Raia, 2010; Slater and Friscia, 2019). My results corroborate these findings using multivariate data encompassing a suite of craniodental functional systems (carnassial form, jaw muscle in-levers, mandibular bending strength). As noted by Slater and Friscia (2019), support for early-burst dynamics in datasets comprising only extant taxa could potentially arise due to selective pruning of phylogeny by extinction, yielding a phylogenetically conservative distribution of traits that only the incorporation of fossil evidence could overturn (Slater et al., 2012). Although the distribution of multivariate craniodental trait values is phylogenetically conservative for carnivorans, the large, positive $\alpha$ value estimated by `phylogeneticEM` indicates that this result is not due to temporally declining rates but, rather, that the evolution of craniodental disparity in carnivorans occurred on a rugged adaptive landscape as predicted by qualitative (Osborn, 1902; Simpson, 1944, 1953) and quantitative (Gavrilets and Vose, 2005) models of adaptive radiation. The rich carnivoran fossil record could and should be leveraged to further interrogate this result, but it is unclear whether this would result in a significant overturning of it, as selective extinction should increase, rather than decrease phylogenetic signal in comparative data. It also remains unknown whether this mode of diversification is likely to be unique to carnivorans among mammalian orders due to their novel dental anatomy, or whether it represents a more general pattern of ecomorphological diversification (Van Valen, 1971). Fulwood et al. (2021) found no support for early burst patterns in molar topographic complexity data across lemuriform primates, but Aristide et al. (2018) found evidence for distinct adaptive peaks in platyrrhine cranial shape data, driven largely by variation in the craniofacial skeleton and which is associated with multidimensional niche membership. Outside of Primates, much comparative macroevolutionary work has relied on body mass, which is only weakly predictive of broad dietary niche (Price and

Hopkins, 2015), and there remains much potential for rigorously evaluating hypotheses regarding modes of evolutionary diversification across mammalian phylogeny using ecomorphological data.

*The Locomotor Landscape is Flat ... At Least for Carnivora*

Conceptual and theoretical models of staged adaptive radiation have tended to assume that divergence along habitat-use axes should precede divergence along axes of dietary resource use (Diamond, 1986; Streelman and Danley, 2003; Gavrilets and Losos, 2009). Empirical evidence in favor of this form of staged radiation is mixed (Richman and Price, 1992; Ackerly et al., 2006; Silvertown et al., 2006a; Sallan and Friedman, 2012; Ingram, 2011), but has been unclear whether this lack of support reflects real underlying evolutionary dynamics or limiting assumptions regarding rate constancy or the estimation of ancestral states (Glor, 2010). Based on the methods employed here, there is no evidence for an early partitioning of post-cranial morphological variation among carnivoran clades. Strikingly, I also find no evidence for the presence of distinct peaks on the post-cranial adaptive landscape, despite the fact that post-cranial morphology is broadly predictive of locomotor behavior and substrate use in carnivorans (Van Valkenburgh 1987, Samuels et al. 2013; but see Martín-Serra et al. 2014). It is possible, of course, that the lack of signal recovered here reflects a lack of measurements from ecologically important post-cranial elements, rather than a lack of peaks on the locomotor adaptive landscape; among unmeasured elements within my dataset, high phylogenetic signal in calcaneal gear ratio, associated with foot posture and open versus closed habitat use, has been found for North American carnivorans (Polly et al., 2017), the lengths and shapes of metapodials and phalanges have been found to be highly predictive of arboreality in carnivorans (Van Valkenburgh, 1987), as well as mammals more generally (e.g., Nations et al., 2019), and body shape diversity, as defined by relative measures of the axial skeleton, is consistent with evolution on an adaptive landscape defined by clade specific peaks, albeit peaks that are not obviously associated with ecology (Law, 2021). Further tests of this finding using an expanded ecomorphological dataset are needed to corroborate the lack of early-burst dynamics, but on some level the distinction between craniodental and postcranial

evolutionary dynamics is also unsurprising. While relative sizes and shapes of teeth intuitively relate to food acquisition and processing, the post-cranial skeleton is composed of many moving parts that must work together to facilitate locomotor performance. The post-cranial skeleton therefore tends to exhibit a high degree of inter-element covariance (Young and Hallgrímsson, 2005; Goswami et al., 2009), which may frustrate the production of discontinuous morphological variation that is maximally optimized for a given locomotor demand (Niklas, 1997, 1999, 2004; Marshall, 2014). Scaling of limb proportions in response to changes in body size can also affect functional indices, meaning that more diverse locomotor behaviors can be achieved for a given morphology at small body sizes (Jenkins et al., 1974; Janis and Martín-Serra, 2020; Weaver and Grossnickle, 2020; Wimberly et al., 2021), or that allometric patterns dominate shape change independent of locomotor behavior at larger sizes (Martín-Serra et al., 2014). Finally, while locomotor diversity in Carnivora is striking for a mammalian order, it does not span the full breadth of substrate use, locomotor specialization, or morphological diversity encompassed by sequentially higher-level groupings of mammals, such as Laurasiatheria, Boreoeutheria, or Placentalia, where patterns of shape variation associated with substrate use or behavior may be more discontinuous (Chen and Wilson, 2015; Janis and Martín-Serra, 2020; Weaver and Grossnickle, 2020). In other words, failure to detect early-burst like patterns at a given level of the phylogenetic hierarchy does not preclude the possibility that a burst occurred at a higher level than the one sampled (Foote, 1996; Jablonski, 2017). The lack of support for partitioning of post-cranial variation among carnivoran clades may well be due to carnivorans themselves sitting on a peak on a broader mammalian adaptive landscape. A more comprehensive analysis of carnivoran post-cranial morphological evolution is required to refute or confirm the my findings, which suggest that extant carnivore locomotor diversity reflects evolution along a continuum, rather than a set of discrete life history modes. However, my findings are silent with respect to the hypothesis that mammalian evolution more broadly is characterized by adaptive radiation along an axis of substrate use (Osborn, 1902; Van Valen, 1971), and higher-level tests of this hypothesis are urgently required.

*The Unpredictable Role of Body Size in Macroevolution*

Body mass has long been a focal trait for comparative biologists, partly due to its wide availability and ease of access in the literature, but also due to its supposed strong relationship with multiple aspects of life history and ecology (Bonner, 1965; Calder, 1984; Peters, 1986; LaBarbera, 1989). Macroevolutionary studies of diverse clades have yielded support for dynamics that are consistent (Slater et al., 2010; Derryberry et al., 2011; Pyron and Burbrink, 2012) and inconsistent (Harmon et al., 2010; Venditti et al., 2011) with adaptive radiation along an axis of body size variation, but few have explicitly related variation in size to variation in ecological role and, therefore, to macroevolutionary dynamics on the adaptive landscape; indeed, some authors have used the apparently stochastic nature of body mass evolution to argue more generally that trait optima are too ephemeral over macroevolutionary timescales to be a useful paradigm at all in comparative research (Pagel et al., 2022). My results would initially seem to strengthen this conclusion by not only demonstrating that the accumulation of body size disparity within and among carnivoran clades is consistent with a null Brownian motion model (figure 4C; see also Roycroft et al. 2020 for a spatial demonstration of this phenomenon using Australian rodent body mass), but also by showing that there are no pronounced peaks on the body size adaptive landscape. I stress that, just as for post-cranial traits, this result should not be taken to mean that body mass evolution is not adaptive in carnivorans, nor that selection on body mass may be strong and directional over microevolutionary timescales (Schluter 1988, Kingsolver et al. 2001, Kingsolver and Pfennig 2004, Hereford et al. 2004; but see Rollinson and Rowe 2015). Rather, despite the importance of body mass for many aspects of organismal ecology, microevolutionary patterns need not scale to macroevolutionary levels (Jablonski, 1996), and adaptive peaks associated with body size variation are likely not stable at geographic (Diniz-Filho and Tôrres, 2002; Diniz-Filho et al., 2009; Roycroft et al., 2020) or temporal scales ranging from seasonal (Powell and King, 1997) to geologic (Finarelli, 2007; Slater, 2015; Law, 2019). Still, it is striking that the ephemeral nature of these body mass peaks contrasts strongly with the stable peaks associated with dietary resource that have persisted for over 50 million years in this clade (Slater,

2015). This result should not be surprising, as the material properties of muscle, keratin, and cellulose that influence tooth shape and size are unlikely to have undergone dramatic shifts over this period, even if the climatic and environmental factors or the composition and body size distribution of the prey base that influence body mass have systematically varied (Van Valkenburgh, 2007; Slater, 2015). The decoupling of tempo and mode in craniodental and body size evolution recovered here (see also Meloro and Raia, 2010; Slater, 2015; Slater and Friscia, 2019) suggests that these traits have played fundamentally different roles in facilitating ecological interactions over macroevolutionary timescales, leading to distinct signals in these comparative data. Instead of providing evidence against the utility of the adaptive landscape metaphor (Pagel et al., 2022), these results together suggest that body size is, in general, likely to be a poor substitute for ecomorphological traits when attempting to understand clade macroevolutionary dynamics (Jablonski, 1996; Slater, 2015).

## Conclusion

Adaptive radiation is a provocative term and has been used to describe a range of macroevolutionary scenarios (Givnish, 1997, 2015; Olson and Arroyo-Santos, 2009; Losos et al., 2010), from replicated ecomorph origins in isolated populations of a single species (Schluter, 1993, 1995) to rapid rates of speciation (Slowinski and Guyer, 1989) or phenotypic evolution (Harmon et al., 2010). Despite this diversity of perspectives, using the original formulations of adaptive radiation (Osborn, 1902; Simpson, 1953) we are able to make clear predictions about the structure of ecomorphological variation across phylogeny and the topography of the underlying adaptive landscape on which this variation evolves (Arnold et al., 2001). Evaluating these hypotheses across trait complexes in a single clade can yield novel insights into whether adaptive radiations tend to occur simultaneously across trait complexes (Osborn, 1902), sequentially along distinct axes of resource use (Diamond, 1986; Streelman and Danley, 2003), or, as I have found here, whether some ecological axes are more accessible to diversifying clades than others. Importantly, while the phylogenetic comparative methods toolkit continues to expand, it is

mature enough now that the limitations to addressing questions about the frequency and form of adaptive radiation lie not in the availability of methods but, rather, in the availability of suitable data. My results confirm that body size, while widely accessible and intrinsically interesting in its own right, is an axis of trait variation that evolution is able to exploit rapidly in response to ephemeral shifts in the topography of the adaptive landscape, and there is no guarantee that variation in size is related to niche dynamics that are important over macroevolutionary timescales (Uyeda et al., 2011). I suggest that the most fruitful inference of adaptive radiation dynamics will emerge from analyses of morphological traits that can be directly and explicitly related to the distinct ecological roles that organisms play in their environments. It is time for comparative biologists to move beyond body size and to employ a richer suite of ecomorphological data to more directly evaluate hypotheses about the nature of adaptive radiation.

## Data Availability

All data and scripts associated with this article are accessible through the Dryad Digital Data Repository at doi:10.5061/dryad.tdz08kq24 (link to become active upon acceptance).

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