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# A Novel Multiscale Assessment of Community Assembly across Time, Space, and Functional Niche

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**ABSTRACT:** A basic ecological tenet is that organisms in a community occupy different niches and have different traits, but how consistently competition, selection, and phylogenetic effects structure communities remains uncertain. Are all communities created equal? We examine how mammalian carnivorous communities are assembled with regard to mass, diet, and locomotion. Here, we use a multivariate nearest-neighbor framework to examine multiple North American localities spanning 3 million years to determine whether community assembly is consistent through time and four modern localities around the world to assess the effects of habitat. Additionally, we examined how trait patterns differ among families and how family-level evolutionary effects affect them. We found some broadly consistent patterns, although differences are more pronounced than similarities. Diet is more affected by evolutionary constraints than by time or place. Locomotion is most affected by habitat, and the ability to partition niches is related to habitat heterogeneity. Mass is influenced by family, but also by habitat and the mass-selective extinction events at the end-Pleistocene. These findings indicate that assembly patterns are not largely determined by within-community interactions but instead show that each community is a product of its independent variables.

**Keywords:** mass, diet, locomotion, guild, Carnivora.

## Introduction

How and why traits vary among species in a community may be the most important step to understanding community assembly, and interspecific competition and niche differentiation play a large role in this process. In mammals, examples of niche differentiation in closely related groups might include differences in dietary and/or locomotor specialization (Hutchinson 1959; Shiels et al. 2013). Competition can also result in size segregation, and in extreme cases, this phenomenon could result in traits that

are evenly dispersed from each other (Rosenzweig 1966). Evenly spaced mass distributions seem to be a community-dependent phenomenon and have been found in some studies (Ben-Moshe et al. 2001; García and Virgós 2007) but not others (Kiltie 1984).

Phylogeny also affects which ecological processes are most important for shaping communities (Kembel and Hubbell 2006), and some degree of evolutionary relationships must be considered in assessing assembly patterns (Webb et al. 2002). Phylogeny, size, and niche differentiation work in conjunction to shape communities where traits can show up as clustered, random, or evenly dispersed (uniform).

For example, North American mammal masses are relatively uniform across spatial scales and habitats (Brown and Nicoletto 1991). But there is a bimodal size distribution in African mammals that is more pronounced than in North or South American mammal assemblages (Kelt and Meyer 2009). Each of these ecosystems has a different combination of habitats and phylogenetic histories, which ultimately leads to differences in overall distributions.

Additionally, different processes can also affect the same community at different scales. Belmaker and Jetz (2013) examined bird and mammal assemblages from around the world and found that different patterns of community assembly were shaping communities on regional scales versus those shaping communities on local scales.

A paleontological perspective can help us understand the evolutionary patterns responsible for these differences and how modern communities have developed into their present state. Paleoecologists ask the same questions and focus on the same variables (e.g., masses, diet, phylogeny) as ecologists who work exclusively in modern systems, except paleoecologists examine communities through time at a wide range of temporal scales (DiMichele et al. 2004). This deep-time perspective can reveal patterns that appear over longer periods than seen in even long-term studies of modern communities. Multiple studies have made use

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of vertebrate fossils to reconstruct past habitats and ecosystem interactions among extinct species (Andrews et al. 1979; Janis et al. 2000; García and Virgós 2007; Lawing et al. 2012). Additionally, it is important to note that vertebrate species diversity can be reliably determined from the fossil record, but species abundances cannot (Damuth 1982).

Both modern and paleontological ecologists can make use of ecometrics, the study of taxon-free trait analysis and how morphological traits can be correlated with environment (Eronen et al. 2010). These traits can be any morphological trait that reflects how an organism interacts with its environment, for example, leaf shape, tooth structure, body mass, or limb proportions. These traits must be easily measured, their structure must be closely related to their function, and they must directly interact with their environment (Eronen et al. 2010). Ecometrics has come into the spotlight as a way to measure both biodiversity (Roberts and Moore 1997; Alfaro et al. 2007; Anderson 2009) and effects of climate change in many different types of organisms (Eronen et al. 2010; Polly et al. 2011). Ecometrics can also be used to examine how morphology shapes ecological communities and how niches are partitioned in closely related sympatric species.

Since morphology can be objectively measured, it is a metric that can be statistically quantified rather than subjectively qualified. In this study, we use a morphological approach to examine mammalian communities using the order Carnivora, as an exemplar, to determine whether carnivoran communities show consistent patterns of trait clustering and dispersion over (1) different habitats: Serengeti, Africa, tree savanna and subtropical rain forest; Kanha, India, monsoon forest; Pantanal, Brazil, tropical rain forest; and Yellowstone National Park, United States, temperate steppe and mountain forest; and (2) different temporal zones: Hagerman Fossil Beds National Monument (4–3.2 million years [myr] BP), Rancho La Brea Tar Pits (40–10 thousand years [kyr] BP), Middle Butte Cave (5 kyr BP), and Moonshiner Cave (3.5 kyr BP). We ask these questions using three parameters of functional morphology—mass, dietary indices, and locomotor indices—to investigate what roles factors such as phylogenetic effects and interspecific competition play in community composition within a closely related group of mammals and how much those roles vary across sites and through time.

We build on previous work (Hertel and Lehman 1998; Ingram and Shurin 2009) by extending a nearest-neighbor framework to include information on the full set of neighbor interactions among measurements. Neighbor methods, derived from approaches common in spatial statistics, analyze the distribution of distances between measurements rather than the measurements themselves; this distribution differs depending on the degree to which points

are clustered, evenly dispersed, or scattered at random. Extending the analysis from only nearest neighbors to include all pairs of points (all neighbors) allows us to identify patterns of clustering or repulsion among measurements at multiple scales. This is a critical element of understanding niche differentiation, as it is possible that different factors structure diversity at different scales of morphology. Size, diet, and locomotion are not the only important functional descriptors of species in a community, but they capture important parts of the variation involved in niche differentiation in mammals (Hutchinson 1959; Hutchinson and MacArthur 1959; Morlo 1999; Smith et al. 2004; Abello et al. 2012), and when diet and locomotor variables are analyzed in a multivariate framework, they give information about species interactions that may not be apparent from only one of these variables. Including the fossil record allows us to examine the changes that have taken place in North America over 3 million years, such as climate changes and faunal turnover as well as an extinction event, and how these changes affect morphology and trait spacing in carnivoran communities.

If trait spacing is mostly determined by within-community interactions, then we would expect to see the same trends through time and across space, which may be affected by the human-caused extinction in the late Pleistocene but not by the gradual climate changes from the early to late Quaternary. If trait spacing is caused by independent factors in each community (e.g., habitat, climate, phylogenetic composition), then we expect that trends will be different across communities in both space and time. For example, if trait spacing is mediated by habitat, then locomotor indices should be evenly spaced in heterogeneous habitats and clumped in homogeneous habitats, and masses may also be clumped if a habitat necessitates certain masses for certain tasks, for example, climbing or jumping.

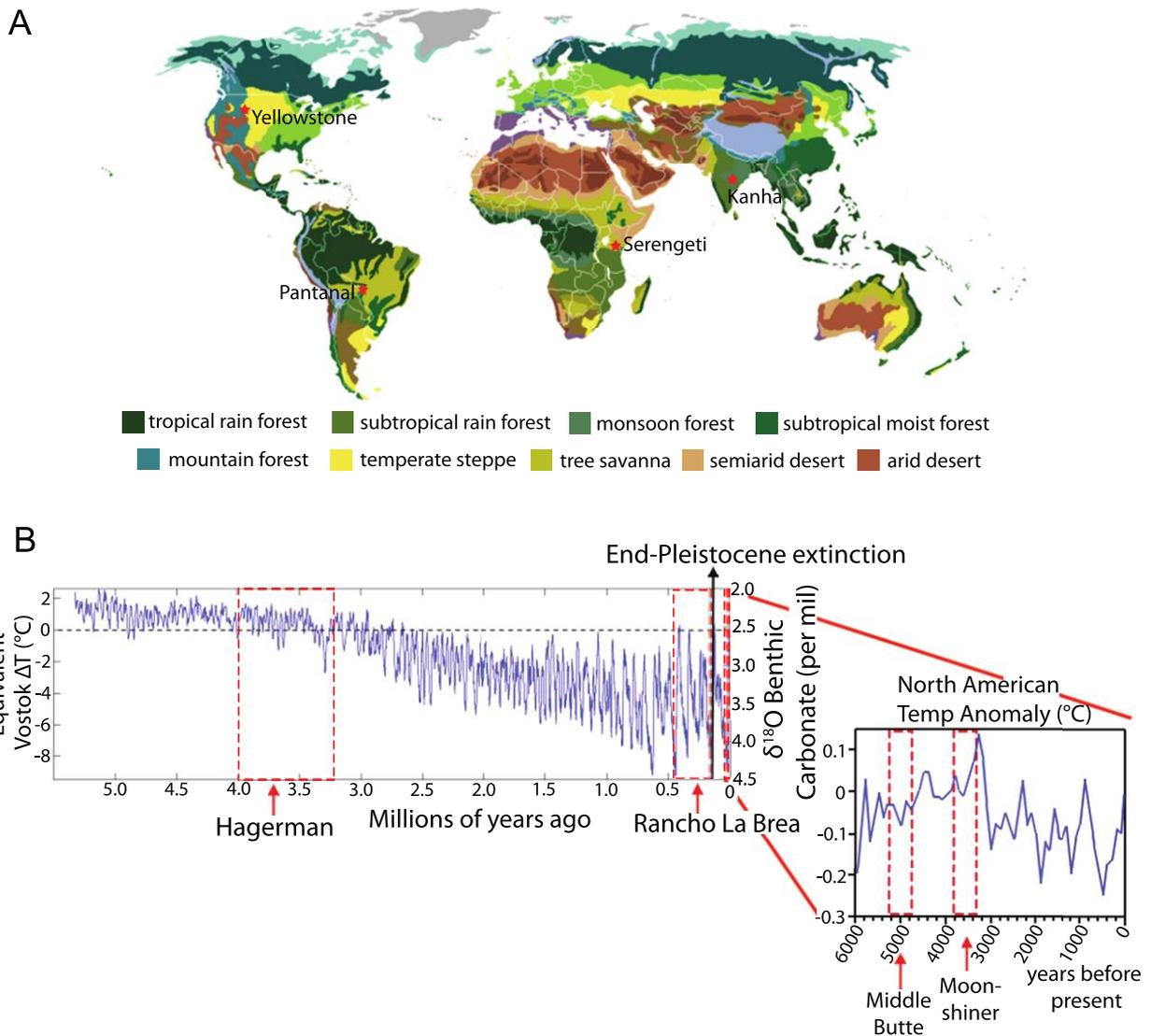
A secondary goal is to ask how groups of closely related species coexist at a single location and whether competition structures their niches within the range allowed by phylogenetic effects. To address this, we examine how morphometric traits are structured among species within individual families, where phylogenetic effects are expected to be strongest, as prior studies have shown the importance of phylogeny in community assembly rules (Webb et al. 2002; Kembel and Hubbell 2006; Kraft et al. 2007). By examining mammalian carnivore assemblages through time using multiple dimensions of functional diversity, we can obtain a better understanding of what processes structure extant and past carnivoran communities over the last 3 million years.

Material and Methods

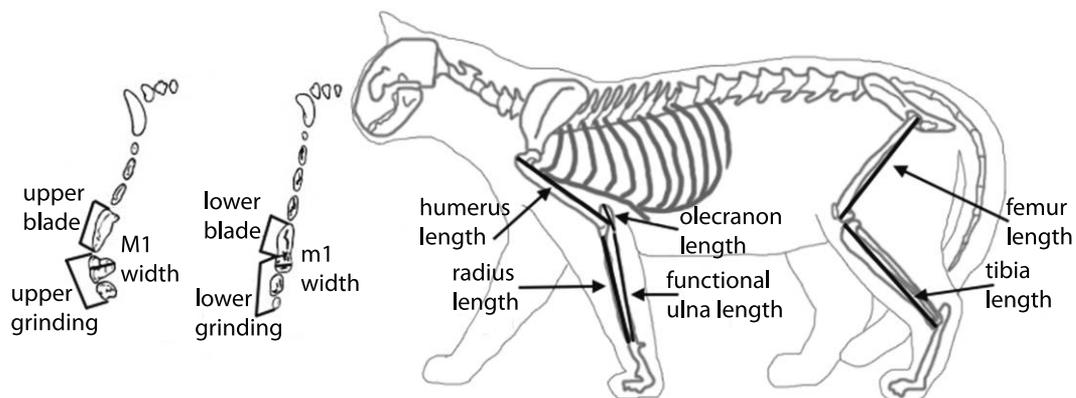
Data Collection

We chose four extant assemblages that are rich with carnivoran species and representative of the diversity of climatic environments (see fig. 1A for biome assignments): Kanha National Park in India, a monsoon and subtropical rain forest with heterogeneous habitat; Pantanal tropical wetland in Brazil and surrounding areas; Serengeti National Park in Tanzania and Kenya, a semiarid grassland habitat that is

broadly representative of the Pliocene environments at the Hagerman fossil site; and Yellowstone National Park in Idaho, Wyoming, and Montana, which is representative of the Holocene fossil sites in Idaho. A database was compiled from these four localities with carnivoran species present, but abundances *sensu stricto* (Schleuter et al. 2010) were not calculated because of comparisons with fossil localities where abundances cannot be accurately calculated. Body sizes were extracted from Smith et al. (2003) and also from mammalian species accounts (table A1, available online) for



**Figure 1:** A, Earth’s biomes with our four modern sites shown as red stars to indicate their locations; only relevant biomes are labeled. Locations are approximate. B, Time and climate for the last 5.5 million years showing the temporal range of Hagerman Fossil Beds National Monument, Rancho La Brea Tar Pits, Middle Butte Cave, and Moonshiner Cave (red dashed boxes) along with an estimation of difference in climate ( $\Delta^{\circ}C$ : blue line) from the present. The end-Pleistocene extinction event is marked with a black line. A and B are modified from Wikipedia Creative Commons. Holocene inset is adapted from Wanner et al. (2008).



**Figure 2:** Diagram showing cranial and postcranial measurements used to make the functional indices in this study; equations for calculating functional indices can be found in table 1.

locality-specific masses. We considered analyzing male and female mass separately because of the high degree of sexual dimorphism in carnivorans (Gittleman and Van Valkenburgh 1997; Jones 1997). However, since we are comparing modern assemblages to fossil assemblages, we could not use sex-specific masses because sex cannot be assigned for fossil species. Therefore, only locality-specific species averages were used.

Additionally, we chose four North American fossil localities representative of important moments in the origin of the modern Quaternary climate and biome system: Hagerman (4.0–3.2 myr BP), a late Pliocene site representative of a grassy, riparian, pre-Quaternary environment; Rancho La Brea (40–10 kyr BP), a Late Pleistocene site representative of the temperate biomes during the last glacial maximum, just prior to the end-Pleistocene extinction; Middle Butte (5 kyr BP), a preclimatic optimum, postextinction fauna; and Moonshiner (3.5 kyr BP), a postextinction fauna that occurred at the Holocene climatic optimum, a period moderately warmer than today (if anthropogenic climate changes in the last decade are excluded; fig. 1B).

There may be some biases in the fossil record that make a complete species list from fossil localities difficult to obtain. We are not claiming here to have an all-inclusive list for these fossil localities; however, it has been shown that species richness can be accurately obtained from the fossil record even though species abundances usually cannot (Damuth 1982). Additionally there may be some question of whether species actually coexisted at the same locality or were separated by thousands of years. At Hagerman, this may be a real issue as precise dating has not been done on most of the fossils. But we think that this fossil site has much to offer and that chances are high

that many of the organisms found at Hagerman coexisted at least at some point in time. At Rancho La Brea, this is less of a concern as the timing is on a much smaller scale within a pit (a few thousand years), and all species used in this study have been found in a single pit, 61–67, with the possible exception of *Homotherium*.

Body mass estimates for extinct species were gleaned from the Paleobiology database (accessed 2011; <http://www.pdb.org>) and references therein (see table A1).  $\log_2$  body mass was analyzed as in prior studies of mass to separate body size into easily distinguishable categories (Preston 1962; Brown and Nicoletto 1991).

Morphological measurements comprising three dental and three postcranial indices were measured directly from museum specimens or taken from the literature for both extant and extinct assemblages (fig. 2). These measurements are known to be good indicators of diet (Van Valkenburgh and Koepfli 1993; Friscia et al. 2007) and locomotor habits respectively (Van Valkenburgh 1987; Lewis 1997; Samuels and Van Valkenburgh 2008). Measurements were taken from specimens at the Natural History Museum of Los Angeles County (LACM); George C. Page La Brea Tar Pits Museum (LACMHC); Donald R. Dickey collection at UCLA (UCLA); US National Museum of Natural History (USNM); Idaho Museum of Natural History (IMNH); Hagerman Fossil Beds National Monument (HAFO), and from the primary literature (Bjork 1970; Wayne 1986; Van Valkenburgh and Koepfli 1993; Friscia et al. 2007).

All of our analyses used these functional indices (e.g., brachial index), not the measurements from which they were calculated (e.g., humerus length). For diet and locomotion, three indices were examined multivariately, while mass was analyzed univariately. For multivariate

analyses of diet and locomotion, each of the three individual variables was rescaled to have a minimum of 0 and a maximum of 1, so each contributes approximately equally to distance measurements in three dimensions. Full descriptions of all indices are in table 1. All functional indices analyzed in this study can be accessed via Dryad digital repository (<http://dx.doi.org/10.5061/dryad.j16p2>; Meachen and Roberts 2014). No locomotor analyses were performed for Hagerman because insufficient postcranial data were available.

### Data Analysis

*Neighbor Statistics and Neighbor Identities.* For each assemblage, we calculated and graphed two sets of neighbor statistics. These statistics use the distribution of distances between measurements, rather than the distribution of the measurements, to test for deviation from an expected distribution. This shows whether measurements of a variable are more clumped (smaller distances) or more evenly spread out (larger distances) in the measurement space than expected. This is a question of clustering in a given space (a one-dimensional space for mass and three-dimensional spaces for locomotion and diet) and using neighbor distributions similar to those used in spatial statistics provides a more detailed view than single summary statistics.

First, we plotted the cumulative distribution of nearest-neighbor distances. For each point in a measurement data set there is one nearest-neighbor distance, the distance to the closest other point. The nearest-neighbor function  $G$  counts the proportion of those nearest-neighbor distances that are less than or equal to a given distance  $d$ ; as  $d$  increases, the proportion of nearest-neighbor distances within that range increases until all of them have been counted. Second, the all-neighbors function  $K_s$  counts the proportion of all distances to other points that are less than or equal to a given distance  $d$  (this is very closely related to Ripley's  $K$  [Ripley 1976]), but the expectation is different because our data are not actually a realization of a homogeneous point process), increasing  $d$  until all neighbors have been counted.

For each of the three functional sets (locomotion [3 variables], mass, [1 variable], diet [3 variables]) in each of the eight assemblages, we evaluated these two functions at a range of distances. This means we are calculating distances in a three-dimensional space for locomotion and diet and in a one-dimensional space for mass. We compared each empirical neighbor function with a background expected distribution generated by calculating the same statistic on 100 simulated data sets with the same sample sizes as the empirical data. Simulated data for each functional variable was generated from a normal distribution

(for  $\log_2$  mass) or a normal distribution truncated at 0 (for all other indices) whose mean and standard deviation matched that of the full modern or fossil data set for that variable (see supplementary information and figures A1, B1–B3, available online, for an illustrated explanation and for comparisons of the empirical distributions with those used for simulations). These simulated data sets provide replicates of the functional indices (e.g., olecranon index [OLI] or brachial index [BI]), not of the raw measurements from which those indices were calculated (e.g., humerus length).

*Clustering within Families.* In addition to analyzing entire assemblages, we examined clustering within individual families to identify phylogenetic effects. For example, the seven musteloid species that coexist in the modern Yellowstone Park ecosystem are all small- to medium-sized long-bodied, short-legged species, features they share because they are closely related. Viewing a group with a shared body form, we can ask whether they are more clumped or more dispersed than expected within the bounds of their phylogenetic group. For this analysis we used only the five modern and four fossil families for which sample sizes for a single location were relatively large ( $>5$ ): felids, canids, and herpestids in the Serengeti; felids in the Pantanal and at Rancho La Brea; and mustelids at Yellowstone, Hagerman, Middle Butte, and Moonshiner.

*Nearest-neighbor identities.* First, we determined whether the nearest neighbors for species in a family were in the same family more or less often than would be expected by chance. This is a measure of how clumped individual families are for a given measurement, compared to other families; species frequently having nearest neighbors from the same family might indicate phylogenetic effects, while species rarely having nearest neighbors from their own family suggests substantial overlap with other families and possibly competition within a family. We counted the proportion of nearest neighbors that were in the same family for each point and compared that proportion to the distribution of 1,000 replicates of the same statistic with families relabeled at random.

*Family space.* Second, we examined the dispersion of closely related species within the range of a measurement occupied by a single family, which provides information about the degree to which competition structures a family within the range dictated by constraints. For example, if mustelids occupy only a subset of the morphological space occupied by carnivores as a whole, their measurements might be significantly dispersed within this “weasel-space” if competition among them is an important factor. We tested for this effect with a single-dimension summary statistic, the standard deviation of neighbor distances (Ingram and Shurin 2009), because sample sizes for single

Table 1: Dietary and locomotor functional indices measured in this study

Acronym	Functional index	Calculation	Functional significance	Index reference
RBL	Relative carnassial blade length (dental)	Length trigonid m1/length total m1	More carnivorous sp. have relatively longer blades.	Van Valkenburgh and Koepfli 1993; Friscia et al. 2007
RLGA	Relative lower grinding area (dental)	$\frac{\{(length\ m1\ talonid \times width\ m1) + (length\ m2 \times width\ m2)^{1/2}\}}{length\ of\ m1\ trigonid}$	More herbivorous sp. have relatively more grinding area.	Van Valkenburgh and Koepfli 1993; Friscia et al. 2007
RUGA	Relative upper grinding area (dental)	$\frac{\{(length\ M1 \times width\ M1) + (length\ M2 \times width\ M2)^{1/2}\}}{length\ of\ the\ P4}$	More herbivorous sp. have relatively more grinding area.	Van Valkenburgh and Koepfli 1993; Friscia et al. 2007
BI	Brachial index	Radius length (RL)/humerus length (HL)	Low values indicate mechanical advantage, high values velocity advantage; ecological role is separated on a continuum. Runners have high values, climbers have intermediate values, and swimmers and diggers have low values.	Samuels and Van Valkenburgh 2008; Meachen-Samuels and Van Valkenburgh 2009
OLI	Olecranon length (of the ulna) index	Olecranon length (OL)/functional ulna length (FUL) (ulna length – olecranon length)	Higher values indicate mechanical advantage in forearm extension—diggers, swimmers, and prey grapplers.	Samuels and Van Valkenburgh 2008; Meachen-Samuels and Van Valkenburgh 2009
CI	Crural index	Tibia length (TL)/femur length (FL)	Low values indicate mechanical advantage, high values velocity advantage; separates climbers and diggers from runners and jumpers.	Samuels and Van Valkenburgh 2008

families are smaller than for the entire assemblage. This statistic tests whether the standard deviation of distances between adjacent ordered points is greater than or less than expected; a low standard deviation indicates evenly spaced points, while a high standard deviation can indicate clustering. We compared the empirical test statistic for each of these samples to the distribution of the same statistic calculated from a sample of the same size generated from a uniform distribution with the same maximum and minimum as the extremes in the empirical sample. This treats the empirical extremes as boundaries, but allows the range to change in each simulated sample. We chose one diet variable (RLGA; see table 1) and one locomotor variable (BI) for this analysis, which depends on ordering points in a single dimension. For an illustrated description of our methods, see appendix B, available online.

We did all calculations and simulations of these statistics in R (R Development Core Team 2009) using our own code, some of which was based on code by Travis Ingram (Ingram and Shurin 2009). In addition to common probability distributions in the base R installation, we used functions for the truncated normal distribution in the package *msm* (Jackson 2011). Our R code can be accessed via Dryad digital repository: <http://dx.doi.org/10.5061/dryad.j16p2> (Meachen and Roberts 2014).<sup>1</sup>

## Results

The *G* and *K<sub>s</sub>* statistics must be interpreted as distributions rather than as simple indices. In general, if measurements are randomly distributed through morphological space, the neighbor distances between points will include a predictable and highly variable distribution of short and long values. As the evaluation distance *d* increases, the number of neighbor pairs that have been counted increases smoothly (see fig. B2 for the behavior of the statistics in some specific random cases). When measurements are more clustered than expected for a given random pattern at a given spatial scale, there is an overabundance of small distances (effectively the definition of a cluster). Neighbor pairs are counted faster than expected, making the curve rise steeply around the values of *d* at that spatial scale. Conversely, when measurements are more dispersed than expected, neighbor distances are relatively large; there are fewer short distances, and the curve is lower and flatter than expected. When points are maximally dispersed, all nearest-neighbor distances are very even, giving the curve a characteristically steep slope or a sudden rise at higher distance values after an initial low or flat period.

Our empirical distributions are compared to expectation

<sup>1</sup> Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

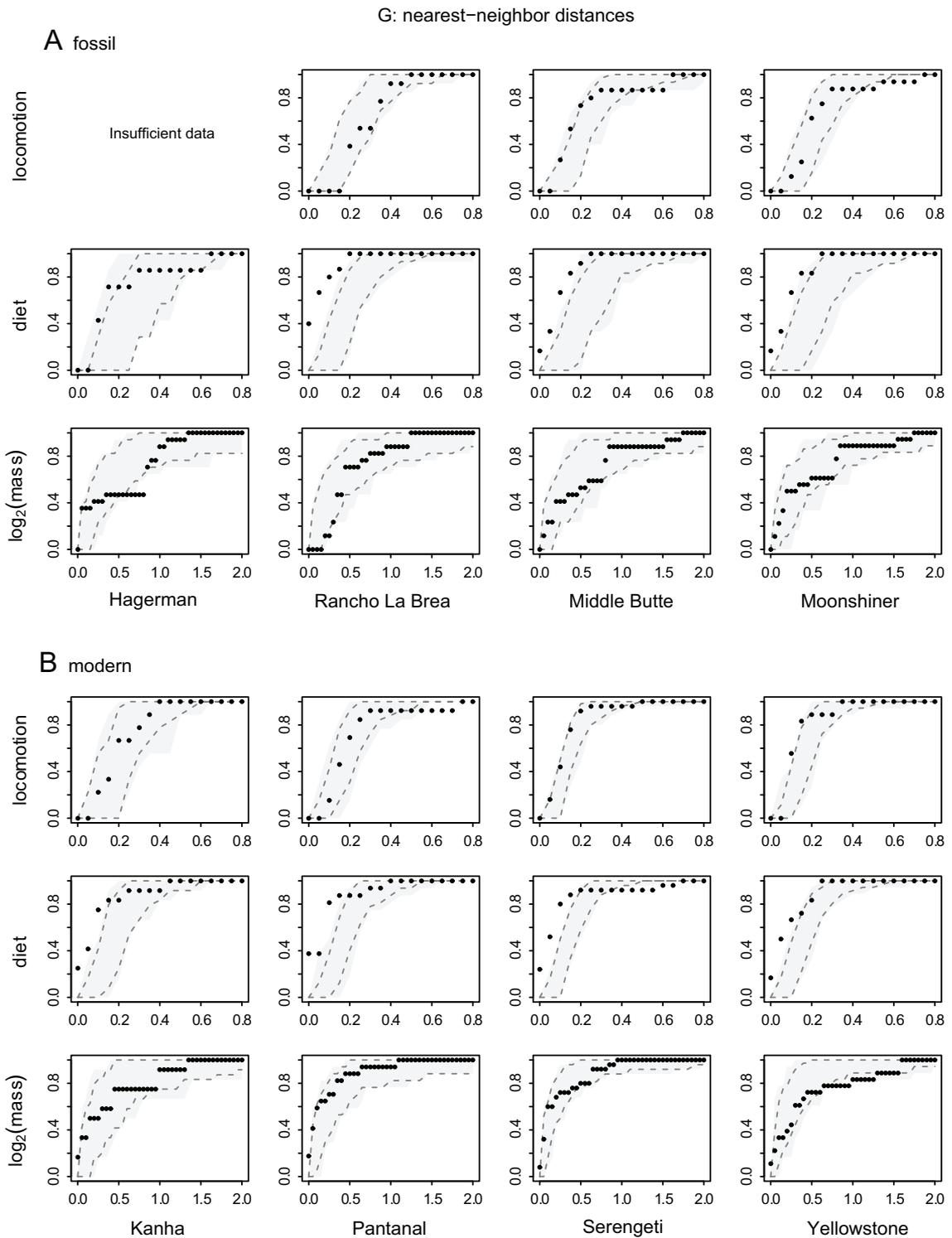
envelopes generated by calculating the same statistic on 100 random samples of the same size chosen from a particular probability distribution (normal or truncated-normal). Results of these tests are therefore significant in the specific context of a particular expectation distribution. It is also important to remember that different patterns and degrees of deviation from the expected distribution can emerge at small and large scales—for example, a set of points could have multiple tight clusters that are themselves evenly spaced. This would result in many short nearest-neighbor distances (because all nearest-neighbors would be within tight clusters) and a *G* graph that rose more steeply than expected. But it would also result in a more complex pattern of distances for all neighbors (*K<sub>s</sub>*), in which there might be within-cluster distances, between-close-cluster distances, and between-distant-distances, but no distances outside these categories. Such a graph for *K<sub>s</sub>* might rise, plateau, rise, plateau, rise, and plateau, showing significant clustering at small scales and significant dispersion at larger scales.

## Mass

*Fossil Localities.* All sites appear to have a random distribution for *K<sub>s</sub>*, but subtle differences appear when we examine *G* (figures 3A and 4A). For Hagerman we see a sharp slope, followed by a flattening of points that repeats twice. This pattern may indicate the presence of several tight pairs or clusters of points with very small nearest-neighbor distances within an otherwise evenly spaced distribution. This pattern may also be present at Middle Butte and Moonshiner, although not strongly enough to be clearly different than expected. Rancho La Brea has an initially uniform distribution of nearest neighbors with a random distribution overall, suggesting that points are slightly overdispersed at small distances.

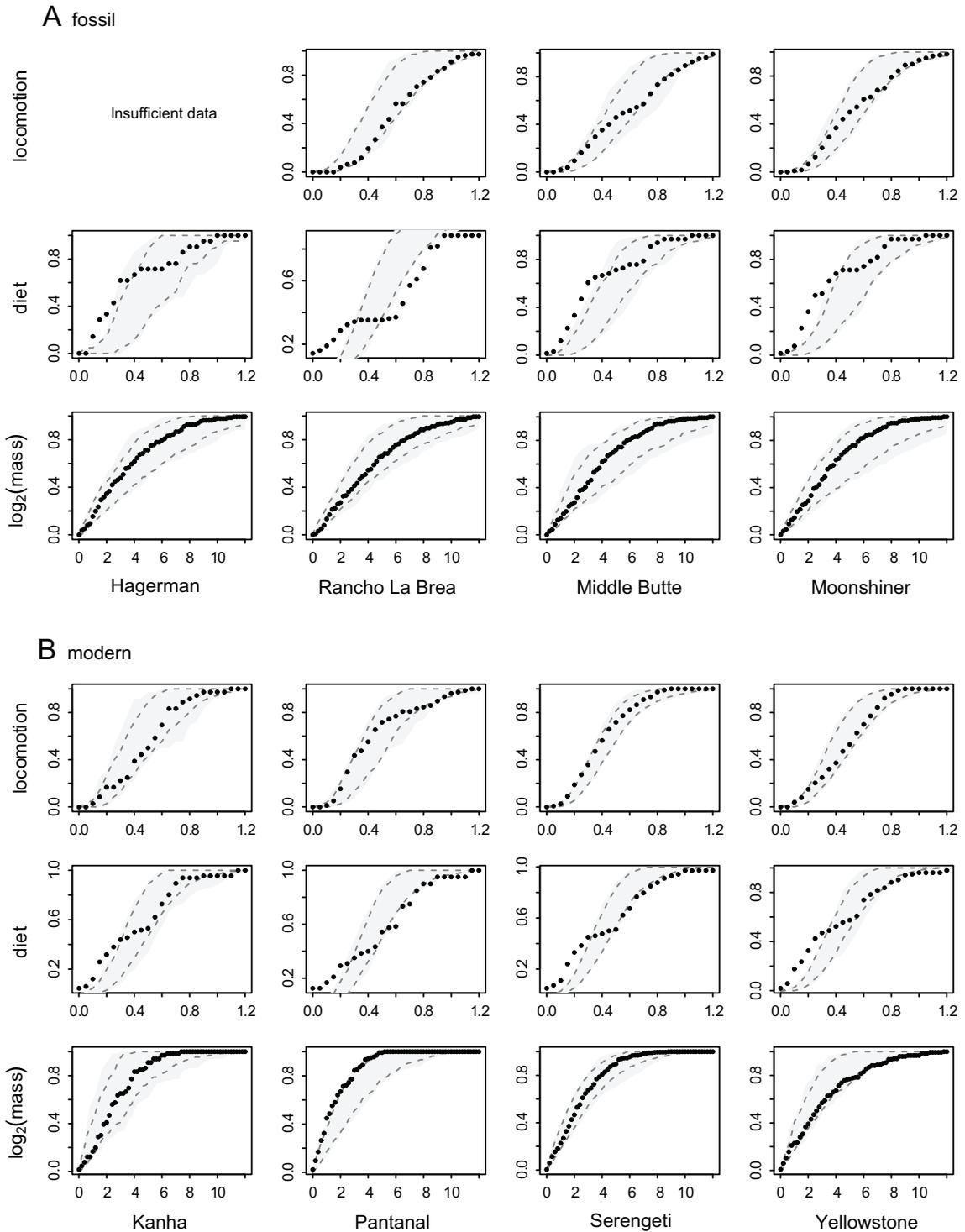
The two preextinction fossil sites displayed a wider range of masses than all modern sites except Yellowstone. Masses at Rancho La Brea were highly left skewed with higher masses compared to other sites, including other fossil sites (fig. A2).

*Modern Localities.* Results for both nearest-neighbor (*G*) and all-neighbor distances (*K<sub>s</sub>*) indicate the Pantanal and Yellowstone assemblages are not randomly assorted (figs. 3B and 4B). Pantanal has a more clumped distribution of masses than expected, an overabundance of short distances. Masses in Yellowstone are overdispersed, with fewer short and more long distances than expected, and with a lack of medium-length nearest-neighbor distances indicating some pairs or small clusters within an otherwise even distribution. Kanha and Serengeti both appear to have an overall random distribution of masses for both *G* and *K<sub>s</sub>*.



**Figure 3:** G (nearest-neighbor distances) plots for all measurements for fossil localities (A) and modern localities (B). For all plots the X-axis is  $d$  (the evaluation distance) and the Y-axis is the percentage of neighbor distances less than  $d$ . Hagerman had insufficient data for the brachial index and was not included in this analysis. Shaded areas indicate the region containing all the curves generated from the simulated data; dotted lines outline the middle 95% of that region.

Ks: all-neighbor distances



**Figure 4:** Ks (all neighbor distances) plots for all measurements for fossil localities (A) and modern localities (B). For all plots the X-axis is  $d$  (the evaluation distance) and the Y-axis is the percentage of neighbor distances less than  $d$ . Hagerman had insufficient data for the brachial index and was not included in this analysis. Shaded areas indicate the region containing all the curves generated from the simulated data; dotted lines outline the middle 95% of that region.

*Diet (RLGA, Relative Upper Grinding Area, Relative Carnassial Blade Length)*

*Fossil Localities.* In G (fig. 3A), all fossil sites have sharp initial slopes, indicating significant small-scale clumping across localities, with Hagerman shifting to random at the end of the curve. From Ks (fig. 4A) for Hagerman, Middle Butte, and Moonshiner caves, we see an initial clumped distribution outside of the 95% simulation envelope followed by a switch to a random pattern when the percentage of neighbors distances less than  $d = 0.6$ . This indicates that while there are more very short distances than expected (clumps at small scales); overall the distribution is consistent with the expectation. Rancho La Brea shows a different pattern with the same initial clumpedness but with a switch to overdispersion around  $d = 0.5$ . At this locality, there is a complex pattern in which very short distances and very long distances are overabundant, with relatively few medium distances. This can indicate multiple evenly spaced clumps with all distances either intraclump (short) or interclump (long), in this corresponding to three clumps: bears, cats, and other taxa.

*Modern Localities.* Modern locale G graphs (fig. 3B) show that approximately 80% of the nearest-neighbor distances are very short, in all cases more than expected. From Ks (fig. 4B), all modern sites again show a similar pattern with a clumped all-neighbor distribution (above the 95% confidence interval) until the percentage of neighbors distances less than  $d = 0.5$ , and then a switch to an overdispersed distribution of all-neighbor distances thereafter. This is very consistent with the pattern observed for fossil localities.

*Locomotion (BI, Crural Index, OLI)*

*Fossil Localities.* For nearest-neighbor distances (fig. 3A) Rancho La Brea shows a random pattern, whereas Middle Butte and Moonshiner caves show slight overdispersion at medium to long distances (around  $d = 0.6$ ). For all-neighbor distance (fig. 4A) Rancho La Brea shows a pattern of very slight overdispersion for almost the entire curve. Middle Butte and Moonshiner both have random Ks distributions, with slight overdispersion at longer distances (after the percentage of neighbors distances less than  $d = 0.6$ ). Hagerman had insufficient postcranial data to run any analyses.

*Modern Localities.* Kanha and Pantanal show random distribution of nearest-neighbor distances (fig. 3B); whereas Serengeti and Yellowstone show clumped nearest-neighbor distributions. For all-neighbor distances (fig. 4B), Kanha and Yellowstone both show a random pattern leaning to-

ward overdispersal. Pantanal and Serengeti both show a clumped all-neighbor distribution.

*Single-Family Analyses*

*Nearest-Neighbor Identities.* There were no cases in which the average number of same-family nearest neighbors was lower than expected ( $P_{\text{low}} \leq 0.05$  based on 1,000 permuted samples; table 2), but many cases in which the average was higher than expected ( $P_{\text{high}} \leq 0.05$ ). For mass, this was true only for herpestids at Serengeti (nearest-neighbor identity [NNID] = 0.833;  $P_{\text{low}} = 1.000$ ,  $P_{\text{high}} = 0.006$ ). For diet, felids were always clumped, with all nearest neighbors also being felids for all sites—Pantanal ( $P_{\text{low}} = 1.000$ ,  $P_{\text{high}} = 0.003$ ), Serengeti ( $P_{\text{low}} = 1.000$ ,  $P_{\text{high}} = 0.000$ ), and Rancho La Brea ( $P_{\text{low}} = 1.000$ ,  $P_{\text{high}} = 0.003$ ). Canids were also clumped at Serengeti (NNID = 0.800;  $P_{\text{low}} = 0.999$ ,  $P_{\text{high}} = 0.010$ .) Mustelids were more likely than expected to be each other's nearest neighbors at Middle Butte (NNID = 0.833,  $P_{\text{low}} = 0.978$ ,  $P_{\text{high}} = 0.022$ ). For locomotor indices, felids from Pantanal were highly clumped (NNID = 1.00,  $P_{\text{low}} = 1.000$ ,  $P_{\text{high}} = 0.009$ ), as were canids at Serengeti (NNID = 1.00,  $P_{\text{low}} = 0.999$ ,  $P_{\text{high}} = 0.000$ ).

In general, when a large number of canids, felids, or herpestids coexist at a site, at least one functional measurement group had a significantly large value of the test statistic. These families often seem to occupy their own regions of morphometric space for these functional indices. For mustelids, significant clumping was found at only one site (diet at Middle Butte) of the four at which five or more species co-occur.

*Family Space.* The family space analyses show how evenly spread measurements are within a given family's range. A significantly small value of the test statistic indicates even spreading (even neighbor distances; low standard deviation), while a significantly high value of the test statistic indicates uneven neighbor distances and some degree of clumping. We found several cases of significant ( $P \leq 0.05$  based on 1,000 simulations) high or low values (table 3). We found low values for brachial index for felids at Pantanal (test statistic = 0.0128,  $P_{\text{low}} = 0.016$ ) and significantly high values for brachial index for herpestids at Serengeti (0.2218,  $P_{\text{low}} = 0.031$ ) and mustelids at Moonshiner (0.1462,  $P_{\text{low}} = 0.049$ ). For RLGA, we found significantly low values for Mustelidae at Middle Butte (0.0210,  $P_{\text{low}} = 0.045$ ) and significantly high values for canids at Serengeti (0.3559,  $P_{\text{high}} = 0.000$ ) and mustelids at Yellowstone (0.1516,  $P_{\text{high}} = 0.016$ ). The presence of both significantly high and significantly low values suggests that there is no single strong pattern acting within families.

Table 2: Results of family analyses, nearest-neighbor identities

Site	Family	Functional index	Nearest-neighbor identity	$P_{\text{low}}$	$P_{\text{high}}$
Pantanal	Felidae	Log <sub>2</sub> (mass)	.222	.348	.702
		Diet	1.000	1.000	.003*
		Locomotion	1.000	1.000	.009*
Serengeti	Canidae	Log <sub>2</sub> (mass)	.400	.936	.288
		Diet	.800	.999	.010*
		Locomotion	1.000	1.000	.000*
Serengeti	Felidae	Log <sub>2</sub> (mass)	.333	.858	.399
		Diet	1.000	1.000	.000*
		Locomotion	.500	.956	.168
Serengeti	Herpestidae	Log <sub>2</sub> (mass)	.833	1.000	.006*
		Diet	1.000	1.000	.000*
		Locomotion	.333	.863	.396
Yellowstone Park	Mustelidae	Log <sub>2</sub> (mass)	.625	.900	.227
		Diet	.750	.984	.073
		Locomotion	.625	.923	.214
Hagerman	Mustelidae	Log <sub>2</sub> (mass)	.750	.984	.085
		Diet	.750	.916	.084
Rancho La Brea	Felidae	Log <sub>2</sub> (mass)	.333	.714	.658
		Diet	1.000	1.000	.003*
		Locomotion	.400	.748	.525
Middle Butte	Mustelidae	Log <sub>2</sub> (mass)	.625	.926	.213
		Diet	.833	.978	.022*
		Locomotion	.667	.949	.164
Moonshiner	Mustelidae	Log <sub>2</sub> (mass)	.556	.788	.439
		Diet	.750	.906	.094
		Locomotion	.714	.974	.125

Note: Mean percentage of nearest neighbors from the same family. Term  $P_{\text{low}}$ : percentage of permutation values less than or equal to the empirical value  $P_{\text{high}}$ : percentage of permutation values greater than or equal to the empirical value. Terms  $P_{\text{high}} + P_{\text{low}}$  may be greater than 1 if some permutations are exactly equal to the empirical test statistic.

\* Significant values ( $P \leq .05$ ).

## Discussion

Our results show that the patterns we see are not largely determined by within-community interactions but instead show that each community is a product of its independent variables (e.g., habitat, phylogeny, temporal range). Our modern community results show that habitat plays a large role in trait spacing for locomotor indices; whereas dietary indices remain more constant across localities. Mass differed somewhat across modern localities, and correlated with habitat heterogeneity. Our fossil localities show that the same locomotor patterns hold across time—habitat heterogeneity dictates locomotor spacing. Dietary index seems likely to be a product of phylogenetic effects in both modern and fossil communities. But we find that the Pleistocene extinction events played a role in the reduction of mass diversity in modern communities compared with preextinction communities.

## Mass

*Importance of Body Mass.* The importance of mass has been specifically demonstrated in the mammalian order Carnivora with regard to partitioning of resources in an ecosystem. Mass is integrally related to prey size preference in carnivorans. Previous studies show that energetic scaling dictates carnivorans above 21 kg will not be able to make a living catching only small prey (Carbone et al. 1999).

Body size in carnivorans is also intimately related to carnivore-carnivore interactions (Rosenzweig 1966; Dayan and Simberloff 1996; Ben-Moshe et al. 2001; García and Virgós 2007). Size structuring in niche partitioning has been shown in many extant carnivore assemblages (Dayan et al. 1990, 1992; Dayan and Simberloff 1994, 2005), and in extinct hypercarnivore assemblages of Europe (García and Virgós 2007); indicating that size in carnivorans is important for both predator-prey interactions and competitive interactions with other carnivorans.

**Table 3:** Results of family analyses, family space

Site	Family	Functional index	Test statistic	$P_{\text{low}}$	$P_{\text{high}}$
Pantanal	Felidae	Log <sub>2</sub> (mass)	.0642	.391	.609
		BI	.0128	.016*	.984 <sup>†</sup>
Serengeti	Canidae	Log <sub>2</sub> (mass)	.1254	.705	.295
		RLGA	.3559	1.000	.000* <sup>†</sup>
		BI	.0188	.097	.903 <sup>†</sup>
Serengeti	Felidae	Log <sub>2</sub> (mass)	.1176	.804	.196
		BI	.1338	.853	.147
Serengeti	Herpestidae	Log <sub>2</sub> (mass)	.0780	.516	.484 <sup>†</sup>
		RLGA	.0893	.621	.379
		BI	.2218	.969	.031*
Yellowstone Park	Mustelidae	Log <sub>2</sub> (mass)	.0826	.746	.254
		RLGA	.1516	.984	.016*
		BI	.0532	.417	.583
Hagerman	Mustelidae	Log <sub>2</sub> (mass)	.0252	.076	.924
		RLGA	.1036	.891	.109
Rancho La Brea	Felidae	Log <sub>2</sub> (mass)	.0869	.572	.428
		BI	.2069	.943	.057
Middle Butte	Mustelidae	Log <sub>2</sub> (mass)	.0572	.477	.523
		RLGA	.0210	.045*	.955 <sup>†</sup>
		BI	.0520	.261	.739
Moonshiner	Mustelidae	Log <sub>2</sub> (mass)	.0544	.509	.491
		RLGA	.0346	.156	.844
		BI	.1462	.951	.049*

Note: Family space test statistic. SDNDR, the standard deviation of next-neighbor distances within the family divided by the family range  $P_{\text{low}}$ ; percentage of simulation values less than or equal to the empirical value  $P_{\text{high}}$ ; percentage of simulation values greater than or equal to the empirical value brachial index (BI) at Hagerman was not used due to missing data. Field relative lower grinding area (RLGA) could not be calculated in some cases because the range is 0 and the test statistic is undefined.

\* Significant values ( $P \leq .05$ ).

<sup>†</sup>  $P_{\text{low}} < .05$  in the nearest-neighbor identity analysis.

*Preextinction World.* Both preextinction fossil communities have a wide range of body masses skewed toward larger sizes, meaning body sizes were larger pre-Pleistocene extinction. For both the Pliocene and the Pleistocene locality there is a danger, especially with body mass that some species may they have not been found yet. Although this concern is real, studies that have examined taphonomic process between fossil sites and modern sites have shown that most species will be fossilized, even if they are not fossilized in realistic relative abundances, and undiscovered species will have been relatively rare to begin with (Damuth 1982). Additionally, preservational biases should show less, not more diversity at fossil localities than at modern sites; the opposite of what we find here.

*Modern World.* Mass distributions are different between modern and fossil localities. All fossil sites, including post-extinction, pre-European colonization localities, show similar Ks distributions; whereas modern communities show more heterogeneous patterns. Sizes of smaller taxa

are similar between fossil sites and modern sites. But our data also suggest that a wider diversity of both smaller and larger animals existed pre-Holocene; concordant with a recent study on diversity loss in small mammals at the Pleistocene/Holocene boundary (Blois et al. 2010). There were mass distribution similarities found between Yellowstone and fossil communities, which may be attributable to the geographic proximity and shared phylogenetic histories of these sites.

Our results from Yellowstone support Brown and Nicoletto's (1991) finding that North American mammalian body masses are uniformly distributed. However, carnivore assemblages from other localities did not show this same pattern. Results from Pantanal show a clumping pattern among all carnivorans. Our results concur with those of Kiltie (1984), who found that cats in the Neotropics do not show uniform size distributions. Size distributions in carnivorans appear to be dependent on both locality and species present. Additionally, habitat type seems to be affecting mass distributions in the Pantanal. This locality is

composed mostly of forested and riparian habitats. Carnivores that live in these two environments must be able to deal with the physical limitations of a closed habitat, affecting both body size and locomotor habits. Our findings support those of Bakker and Kelt (2000), that habitat heterogeneity plays a role in the size-structuring of mammal communities.

Importantly, our results from North America and South America show that carnivores are a good proxy for all mammals in these two environments (Brown and Nicoletto 1991; Bakker and Kelt 2000). However, we did not find a bimodal size distribution of African carnivores that was seen in all African mammals (Kelt and Meyer 2009). We found uniform mass distributions at only one out of eight localities: Yellowstone Park. Therefore, we propose that uniform spacing of masses is the exception rather than the rule.

*Diet.* Diet is structured the same in carnivores through time. This is likely the product of phylogenetic similarity, as evidenced by our results. This may imply that dental characters are relatively static and evolve more slowly within families, than prior to when the families emerged. We see some evidence for this with a strong pattern of family level clumping for diet variables. It is very common for members of a given family to have nearest neighbors from the same family, suggesting that individual families occupy their own regions of diet space. Carnivory is a highly successful dietary strategy and is likely maintained regardless of time, space, and habitat. This is the case more for diet than it is for locomotion or mass, for which there is broader overlap among families and nearest neighbors are frequently from different families. Additionally, it is important to note that the use of ratios in this analysis may produce a clumping artifact. However, we do not see this same effect in locomotor indices.

#### *Locomotion or Habitat Usage*

*Preextinction World.* Our findings indicate that locomotor adaptations were varied at Rancho La Brea, and this may have been a successful strategy by which carnivores partitioned their niches at this site. Unfortunately, Hagerman did not offer us postcranial data to test the hypothesis whether this was normative before the Pleistocene extinction events. The two early Holocene cave sites show similar patterns to Rancho La Brea.

*Modern World.* When we examine each locomotor index individually we see that carnivores from Pantanal are clumped and skewed toward arboreality or swimming adaptations, with robust bones that have short out-levers for increased power to swim and climb (Cartmill 1985). Con-

versely, Serengeti carnivores are clumped and skewed more toward cursoriality, a mode of locomotion better adapted to more open and arid habitats with long gracile bones for a velocity advantage (Hildebrand 1985). Although Serengeti habitats are more heterogeneous than those of Pantanal, a large portion of the Serengeti is savanna ecosystem (McNaughton 1985), a relatively open habitat. Yellowstone shows even dispersal, as did Rancho La Brea, suggesting that temperate North America has had a relatively heterogeneous habitat for the last 50 kyr.

Locomotor indices seem to be dictated by environment, although there is also a phylogenetic signal (see Dryad Digital Repository for individual dietary and locomotor indices: <http://dx.doi.org/10.5061/dryad.j16p2>; Meachen and Roberts 2014). This dissimilar pattern compared with diet may suggest that tooth morphology is more constrained than postcranial morphology. It may also suggest that postcranial morphology is subject to more selection depending on the environment.

#### *Family-Level Analyses*

Our analyses indicate that phylogeny has an effect on niche partitioning in carnivores; however, the effect is neither eminently predictable nor consistent. It depends on a unique combination of variables that differs between families from locality to locality. Some families are consistently the same, that is, cats for diet. This proclivity toward a hypercarnivorous diet with no grinding area is clearly a phylogenetic constraint of the family Felidae; however, mass and locomotion are not as conserved in felids as evidenced by the cats of the Serengeti. Many of these phylogenetic similarities are time and place specific. For instance, cats show a much broader range of locomotor habits in Serengeti than in Pantanal. Families are not constrained to one particular strategy, and some families show more variation than others. There is clearly a strong effect of evolutionary history (family-level taxonomy) on diet in particular, causing characteristic patterns of clumping and dispersion at multiple scales.

Mustelidae, which show the greatest variation in locomotor mode (Baskin 1998; Schutz and Guralnick 2007), show a lack of phylogenetic clumping with regard to locomotion at Yellowstone, with substantial overlap with other families. The coexistence of a large number of mustelids at this site may therefore be in part due to their ability to overcome phylogenetic effects and spread into new niche space, reducing the effects of intrafamily competition. Of the eight Yellowstone mustelids, three are terrestrial, two are semiaquatic, two are climbers, and one is fossorial. Digging and swimming may share similar morphological signals such as a pronounced olecranon process,

a robust humerus (flared deltopectoral crest), and shared features in the manus.

The factors that determine how communities are assembled are labile with regard to time, habitat, and taxonomic group. In Carnivora, dietary indices seem to be more affected by phylogeny than by time or place. Locomotion is most affected by habitat, and the ability to partition niches by habitat is related to habitat heterogeneity at a specific site. The importance of mass has been shown repeatedly and mass can successfully be used to partition niches in animal communities, but it is not without its limitations. Mass is tied not only to phylogeny but also to habitat and to past events, such as the megafaunal extinction.

It is clear that the balance among historical, ecological, and competitive forces changes through time and across habitats and that it also varies among functional traits. Future hypotheses that come from our results include: the distribution of dietary traits will be unaffected by future environmental reorganization or extinction events, unless changes are severe enough to cause entire families to become extinct; locomotor trait spacing is linked to habitat, so it will likely be affected by environmental changes, and associated with habitat heterogeneity; and mass spacing is sensitive to environmental changes (habitat) and extinction events, which can be caused by both climate change and anthropogenic effects.

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