

Clade sorting has a greater effect than local adaptation on ecometric patterns in Carnivora

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ABSTRACT

Background: Ecometric patterning is the sorting of mean values of functional traits in communities in space through time at continental scales. Ecometric patterns can emerge from intraspecific population-level processes (selection along an environmental gradient), species-level processes (geographic sorting of species based on functional trait differences), or clade-level processes (geographic sorting based on phylogenetically shared traits). We analysed a hind limb ratio related to locomotion in carnivores (Mammalia, Carnivora) to determine (1) whether its ecometric patterning involves intraspecific population-level evolutionary processes; (2) whether ecometric patterning is produced by clade sorting processes; and (3) how ecometric patterns are altered by species turnover during glacial–interglacial cycles.

Data: We analysed (1) intraspecific variation in hind limb ratio in five species to evaluate the importance of population-level processes in ecometric patterning; (2) the distributions of ratios within and among communities to evaluate the importance of clade sorting; and (3) the distributions of ratios of seven glacial fossil assemblages to evaluate temporal dynamics in ecometric patterns. We also analysed three-dimensional calcaneum shape to assess the strength of phylogenetic and functional components of hind limb variation.

Analytical methods: Geometric morphometrics, phylogenetic comparative methods, and phylogenetic community assembly methods were used to evaluate trait-based clade sorting; RLQ analysis was used to measure the correlation between vegetation openness, spatial scale, species occurrences, phylogeny, and hind limb traits; and trait space was used to analyse turnover between glacial and extant carnivore communities.

Results: Population-level selection is either too weak or ineffective to produce hind limb trait gradients within carnivore species; however, clade-level trait-based sorting has a strong impact on community-level trait distributions. RLQ analysis demonstrates that clade membership interacts with hind limb ratios and vegetation openness in carnivore community assembly. Glacial–interglacial cycles produced turnover in faunas and hind limb trait distributions regardless of location or biome.

Keywords: clade sorting, ecometrics, functional traits, geographic variation, limb proportions, locomotor morphology, spatial patterning.

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INTRODUCTION

Gradients in morphology and community membership are produced by historical processes that involve the interaction between functional traits and environments in the assembly of regional species pools and local communities (Diamond, 1973, 1975; Ricklefs and Travis, 1980; Miles *et al.*, 1987; Westoby *et al.*, 1995; Poff, 1997; Weiher and Keddy, 1999; Ackerly, 2003; McGill *et al.*, 2006; Westoby and Wright, 2006; Webb *et al.*, 2010). Gradients in community assembly can operate at any spatial scale, but here we focus specifically on regional and continental scales where the processes involved could, in principle, include evolution by natural selection, biogeographic sorting, or extinction (either local or global), often in the context of global-scale environmental changes. Examples of community-level trait–environment sorting at continental scales include plant leaf, stem, and root traits (Box, 1981; Wolfe, 1993; Westoby and Wright, 2006), mammalian body size (Eisenberg, 1981; Brown and Nicoletto, 1991), terrestrial poikilotherm body size (Makarieva *et al.*, 2005a, 2005b; Head *et al.*, 2009), mammalian herbivore tooth crown height (Fortelius *et al.*, 2002; Eronen *et al.*, 2010b, 2010c), snake tail length (Lawing *et al.*, 2012), carnivore hind limb mechanics (Polly, 2010; Polly and Sarwar, 2014), and number of litters per year in mammals (Lawing *et al.*, 2016a). Throughout this paper, we refer to these continental-scale patterns in community functional trait means as ecometric patterning (Eronen *et al.*, 2010a; Polly *et al.*, 2011; Polly and Head, 2015; Fortelius *et al.*, 2016).

The mechanisms by which ecometric patterns are produced, which logically could include natural selection on local populations or biogeographic sorting of species or clades, are poorly understood, as is the time scale over which the gradients originate, which could arguably be as short as tens or hundreds of years or as long as hundreds of thousands or even millions of years. For a diversity of perspectives on the mechanisms and temporal scales that produce trait–environment correlations, see Simpson (1944), Bock and Von Wahlert (1965), Levins (1968), Lynch and Lande (1993), Rosenzweig (1995), Jablonski and Sepkoski (1996), Ackerly (2003), Lister (2004), Ackerly *et al.* (2006), Millien *et al.* (2006), Ricklefs (2006), Raia (2010), McPeck (2008), Kraft and Ackerly (2010), and Jönsson *et al.* (2015). Here, we test the roles that intraspecific population-level processes (local trait selection along an environmental gradient), species-level processes (geographic sorting of species based on functional trait differences), and clade-level processes (geographic sorting based on phylogenetically shared traits) play in establishing a community-level gradient in functional locomotor traits in mammalian carnivores.

Our previous research has shown that sorting of living Carnivora into major vegetative and physiographic environments involves their hind limb locomotor morphology (Polly, 2010) (Fig. 1). This ecometric relationship is functionally related to stance and lever mechanics. Carnivores range from plantigrade, in which the entire foot is placed on the substrate during resting stance, to digitigrade, in which only the distal ends of the toes touch the substrate and the metatarsals and tarsals function as an additional limb segment (reviewed by Taylor, 1989; Polly, 2007). Bears are typical plantigrades; canids and felids are typical digitigrades. The mechanical lever proportions affect behavioural and ecological performance (Biewener, 2003). Digitigrade animals have long distal feet and are capable of long strides, fast paces, and powerful leaps because they achieve more foot extension from the same muscular contraction length than do plantigrade animals (Fig. 1A). Plantigrade animals, in contrast, are able to generate a proportionally larger out force for the same muscular input. These lever proportions can be described by a simple gear ratio of two measurements taken from the calcaneum, the bone that forms the heel (Polly, 2008) (Fig. 1B). The gear ratio arranges carnivore species on a spectrum from the lowest values in plantigrade bears to the highest

values in digitigrade felids (Fig. 1C). Hind limb gear ratio thus has an effect on performance in different environments and affects community assembly in carnivores, which is seen in the geographic sorting of average ratios in communities of North American carnivores (Polly, 2010) (Fig. 1D). On average, carnivores in the rugged, dry, or open landscapes of Mexico and the desert southwest have a larger calcaneum gear ratio, indicating they are on average more digitigrade than carnivores in the boreal forests and tundra of Canada and Alaska. Not only does the mean gear ratio vary geographically, but so too does the variation in gear ratio within communities. For example, carnivore assemblages in the Midwest, which was historically covered by dense Eastern deciduous forest, have little variety in the ratio because many of them are scansorial (terrestrial animals with good climbing abilities), but carnivore assemblages in the boreal forests and tundra of Canada and Alaska have a lot of variation because they form mixed communities of plantigrade bears, digitigrade canids and felids, and intermediate mustelids. Mean gear ratio strongly correlated with vegetation cover ($R^2 = 0.49$) (Fig. 1E), ecological province ($R^2 = 0.70$), and mean annual temperature ($R^2 = 0.48$), but not with species richness ($R^2 = 0.05$) or elevation ($R^2 = 0.07$) (Polly, 2010; Polly and Sarwar, 2014). The statistical and spatial significance of these correlations has been demonstrated with randomization tests (Polly, 2010; Polly and Sarwar, 2014). The ecometric relationship is driven by locomotor strategy rather than by peculiarities of the calcaneum gear ratio trait because snakes, which fill the same terrestrial carnivore guild, but which have a grossly different locomotor system, have locomotor traits (tail/body ratio) with similar correlations with vegetation cover and ecological province (Lawing *et al.*, 2012).

We test three hypotheses that collectively address the questions of whether trait-based sorting is at the population, species, or clade level and whether the current ecometric pattern extends deep in time. We start with the Gleasonian null hypothesis that community assembly in carnivores is the product of the independent sorting of species and with the hypothesis from our previous results that hind limb ratios influence their sorting based on performance interactions with vegetation and physiography. From there, we test hypotheses that trait-based sorting might occur at lower or higher hierarchical levels and whether evolutionary change in hind limb traits is an ongoing phylogeographic process that promotes differentiation within species today.

Our first test is whether the same environmental gradient in hind limb ratios at the community level also occurs within species. This test determines whether the environmental gradient that produces the community-level pattern is capable of causing traits to evolve by natural selection to optimize local performance. Environmental heterogeneity commonly creates selection gradients that produce intraspecific clines in functional morphology (e.g. Endler, 1973; Caumul and Polly, 2005; Cardini *et al.*, 2007; Zamudio *et al.*, 2016). This test indicates whether the environmental selection that sorts community trait means also produces within-species clines. Lack of intraspecific clines would indicate that parallel adaptation among all species in a local community is not the process responsible for the community-level ecometric pattern. A negative result would therefore also suggest that species (or clades) are biogeographically sorted by traits they already possessed from deeper in their evolutionary histories. The existence of intraspecific clines would indicate that trait adaptations to the environmental gradient have occurred more recently than the establishment of current geographic ranges and the divergence of the species and clades making up communities (although it would not by itself preclude trait adaptations that predate the assembly of modern communities).

Our second test is whether hind limb ratios and community membership are phylogenetically structured within carnivores. This test determines whether trait-based sorting is independent in each species or whether it occurs at the level of clades that share traits by common ancestry. This is a phylogenetic community assembly question (e.g. Webb, 2000; Webb *et al.*, 2002; Ackerly, 2003; Kraft *et al.*, 2007; Emerson and Gillespie, 2008; Kraft and Ackerly, 2010; Raia, 2010; Webb *et al.*, 2010; Pavoine *et al.*, 2011) and we use community assembly and phylogenetic comparative methods to test it. Not only is phylogenetic community sorting an interesting question for functional trait macroecology, but it is important for palaeontology because it is closely linked to clade sorting as a macroevolutionary process that affects taxonomic diversity and trait disparity through time (e.g. Vrba, 1984; Jablonski, 2008a). If clades are sorted along environmental gradients by their functional traits in the modern world, it may imply that the origins of traits and clades were correlated responses to the origins of new environments in the past and have tracked them since (cf. Simpson, 1944).

And our third test is whether the modern geography of hind limb ecometric patterns in carnivores is geologically recent. To do this, we make a site-by-site comparison between community-level trait distributions between the last glacial maximum (22,000 years ago) and now. This test has two purposes. First, it simply indicates whether ecometric patterns change over geologically short periods of time. However, temporal turnover in ecometric distributions also relates to the mechanism of clade sorting. Geologically recent turnover in the trait distributions within communities would indicate that they have not evolved *in situ* as one might expect if a community is composed of closely related species that share similar traits by common ancestry, an assumption that forms the null hypothesis of some methods for reconstructing the biogeographic centres of origins for clades (e.g. Bremer, 1992; Koepfli *et al.*, 2008; Davies *et al.*, 2008) and estimations of ancient climates (e.g. Vieites *et al.*, 2009; Lawing *et al.*, 2016b). Confirming with the fossil record whether ecometric patterns turned over with the environmental changes associated with glacial–interglacial cycles is thus important, especially since the divergences between carnivore species and clades, and thus their hind limb traits, predate these cycles.

DATA AND METHODS

Trait data

Two kinds of trait data were collected from the calcaneum bone of living and fossil carnivores. We scanned bones from 37 extant carnivores to study the correlation between calcaneum shape with phylogeny and with the gear ratio index (Fig. 2). This sample of 3D scans includes non-North American taxa. Using either the *NextEngine Ultra HD Scanner*TM or the *FARO Edge ScanArm*TM, we produced 3D point clouds that were processed into closed meshes using *ScanStudio Pro*TM or *Geomagic*TM software respectively. The coordinates of thirteen 3D landmarks were collected from down-sampled and reoriented meshes using *Rhinoceros*TM and *Meshlab*TM (Fig. 2). We Procrustes superimposed the landmarks (Rohlf and Slice, 1990) and ordinated them with a covariance-based principal components analysis to produce shape variables for further analysis (Dryden and Mardia, 1998). We also collected linear caliper measurements from 1861 museum specimens from all 47 extant North American Carnivora and selected extinct Pleistocene species. We calculated gear ratio from the maximum length of the calcaneum over the distance between the distal base of the sustentacular process and the proximal tuber (Polly, 2010) (Fig. 1B). This ratio is always

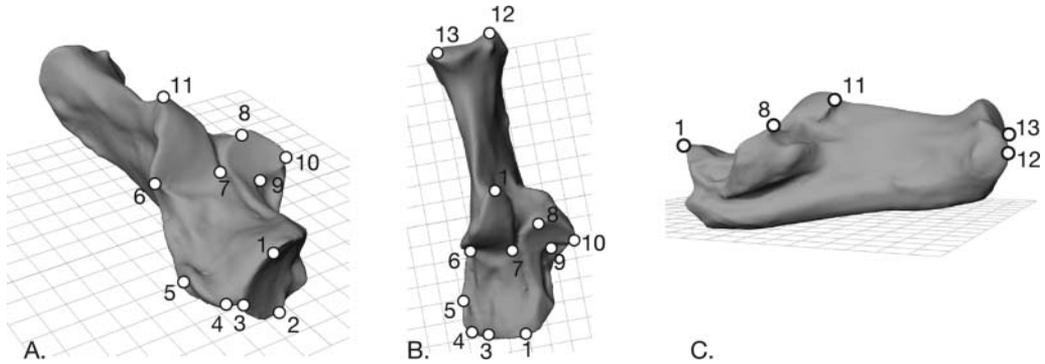


Fig. 2. 3D landmarks shown on the calcaneum of a mountain lion (*Puma concolor*) in laterodistal view (A), dorsal view (B), and medial view (C).

greater than 1.0 and it is larger in digitigrade taxa. Gear ratio and sample size for the extant North American species are reported in Appendix 1 (www.evolutionary-ecology.com/data/3011Appendix.pdf). The ratio data are an expanded version of those analysed by Polly (2010) and Polly and Sarwar (2014). For most analyses, data were pooled by species, which entails the assumption that the species' mean is representative of its morphology at all geographic locations. This assumption was relaxed for the intraspecific analyses in which data were analysed at the level of individuals as described below.

Specimens are housed in the American Museum of Natural History (New York, NY), Denver Museum of Science and Nature (Denver, CO), Field Museum of Natural History (Chicago, IL), Indiana State Museum (Indianapolis, IN), William R. Adams Zooarchaeology Collection (Bloomington, IN), Universidad de Valladolid (Valladolid, Spain), Museum of Southwestern Biology (Albuquerque, NM), North Carolina State Museum of Natural Sciences (Raleigh, NC), Oklahoma Museum of Natural History (Oklahoma City, OK), Smithsonian Institution (Washington, DC), University of California Museum of Vertebrate Zoology (Berkeley, CA), University of Missouri (Columbia, MO), University of Texas Vertebrate Paleontology Lab (Austin, TX), and the Utah Museum of Natural History (Salt Lake City, UT).

Geographic and environmental data

Geographic ranges for North American carnivores were resampled from shape files available in Digital Distribution Maps of Mammals of the Western Hemisphere (Patterson *et al.*, 2007) using a grid of 50 km equidistant points (Polly, 2010). The geographic ranges in these shape files are updated from the ones published by Hall (1981). The data are historical, representing carnivore ranges as they were around 1900 AD. Contemporaneous historical vegetation cover data were resampled using the same 50 km grid points from Matthews' compilation of Global Vegetation Types, which was based on a combination of historical sources and remote sensing data (Matthews, 1983, 1984). Vegetation cover is classified in that data set into 28 types that are linked to UNESCO's vegetation classification scheme, which indexes them into the six progressive categories from open to closed canopy that we used here (UNESCO, 1973). We used Bailey's (1983, 1998) ecological regions as geographic units of analysis for

the intraspecific study. Bailey used a hierarchical system of ecological domains, divisions, provinces, and sections, which he defined based on macroclimate at the higher levels and vegetation, topography, and seasonality at the lower levels. For our intraspecific analyses, we used Bailey's division-level regions, the boundaries of which are illustrated below.

Phylogenetic tree

A composite phylogenetic tree for North American carnivores (Fig. 3) was based on a number of phylogenetic studies (Erdbrink, 1953; Van Valkenburgh *et al.*, 1990; Mazza and Rustioni, 1993; Baskin, 1998a, 1998b; Hunt, 1998; Mattern and McLennan, 2000; Wesley-Hunt and Flynn, 2003; Flynn and Wesley-Hunt, 2005; Wesley-Hunt, 2005; Johnson *et al.*, 2006; Polly *et al.*, 2006; Fulton and Strobeck, 2007; Yu *et al.*, 2007; Sato *et al.*, 2009; Tedford *et al.*, 2009; Agnarsson *et al.*, 2010; Eizirik *et al.*, 2010; Flynn *et al.*, 2010; Wolsan and Sato, 2010; Fuentes-González and Muñoz-Durán, 2012; Spaulding and Flynn, 2012; Tseng *et al.*, 2013). Divergence dates for the tree's nodes are based on fossils that have been subjected to rigorous phylogenetic analyses in the above

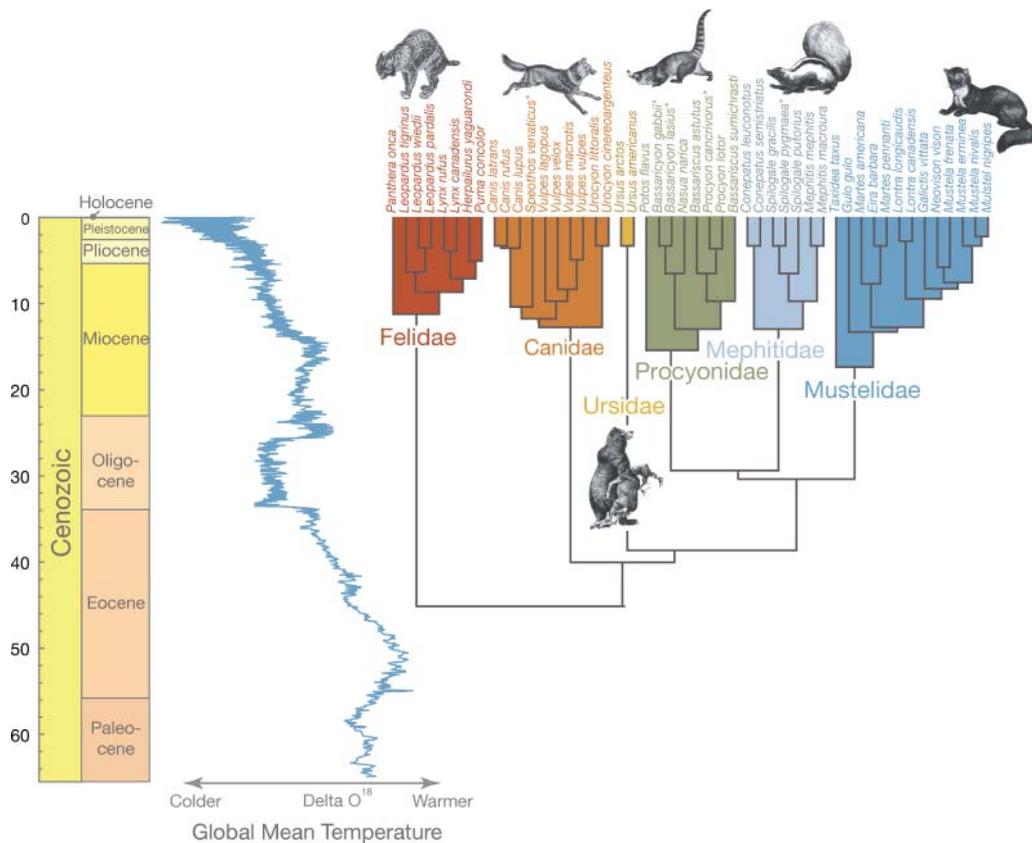


Fig. 3. Phylogeny of living North American Carnivora with divergence times calibrated with key fossil occurrences. The global temperature curve is from oxygen isotope data (Zachos *et al.*, 2001). Family-level clades are highlighted with coloured blocks. *Species not included in the RLQ analysis because of their limited North American range. [Animal pictures are copyright-free illustrations from Large and Weller (2004).]

works. The tree was pruned to match the two data sets, one for the 37 species with calcanea and one for the 47 extant North American Carnivora.

Analysis of intraspecific trait patterns and comparison with community-level patterns

To analyse intraspecific variation in hind limb ratios, we chose five widespread species: bobcat, *Lynx rufus* ($N = 45$); coyote, *Canis latrans* ($N = 105$); grey fox, *Urocyon cinereoargenteus* ($N = 135$); raccoon, *Procyon lotor* ($N = 133$); and long-tailed weasel, *Mustela frenata* ($N = 57$). These species are good representatives for this analysis because they have large geographic ranges, each of which spans much of North America and thus a wide variety of vegetative and physiographic environments, and they vary in their locomotor systems (bobcat, coyote, and grey fox are digitigrade, long-tailed weasels are semi-digitigrade, and raccoons are plantigrade to semi-digitigrade), and they are phylogenetically diverse (bobcats belong to Felidae, coyote and grey fox to Canidae, long-tailed weasels to Mustelidae, and raccoons to Procyonidae).

We characterized intraspecific variation with histograms and geographic heat maps to evaluate the range and pattern of hind limb ratios in each species. We tested whether geographic variation within the five species was correlated with ecometric means in order to evaluate whether the environmental gradient has the same effect on within-species as they do on community mean values. We were unable to sample intraspecific population means at the same granularity as community-level means. Geographic patterns in hind limb ratio within species are necessarily derived from measurements on individual museum specimens. Estimating local population means therefore requires a reasonable sample size from each location, and it is impossible to assemble independent samples for each of these species at every 50 km grid point. Instead, we obtained as many specimen measurements from across the entire geographic range of the species and then binned them into subregional samples using ecological divisions (Bailey, 1983, 1998). We chose ecological divisions as our bins because previous work has shown that the community-level means are strongly correlated with these ecoregions (Polly, 2010), so if within-species variation is structured the same way, these units of analysis should reveal it. Ecometric community-level means were recalculated using the same divisions. The correlation between the intraspecific and community-level patterns was then tested using randomization methods. Spatial autocorrelation has the potential to introduce spurious correlations into this analysis, but, as described below, there was no significant correlation between intraspecific and community-level trait patterns, so no further autocorrelation adjustments were made.

Analysis of phylogenetic structure in hind limb traits

Phylogenetic structuring in calcaneum shape was partially analysed by Polly (2008). Additional analyses were performed here to establish the statistical relationship between gross calcaneum morphology and calcaneum gear ratio and between both of these data sets and phylogeny. Morphometric shape variables and gear ratios each were mapped onto phylogeny using the generalized linear model (GLM) algorithm and assuming a Brownian motion model of evolution (Martins and Hansen, 1997). Phylogenetic correlation was measured with Blomberg's K ($kappa$) and Adams' K_{multi} (Blomberg *et al.*, 2003; Adams, 2014). K is the ratio of observed MSE_0/MSE to the MSE_0/MSE expected under a Brownian motion model of evolution, where MSE_0 is the mean squared error of the raw trait data around the value of the base node and MSE is the mean squared error of the trait data using the phylogenetic

covariance matrix of the tree (Blomberg *et al.*, 2003). K takes on a value of 1 when the tree explains as much trait variance as expected under Brownian motion and it approaches 0 when the tree explains none of it. Note that K can be larger than 1 if trait covariances have greater fidelity with the tree than expected under Brownian motion, which can happen under directional or diversifying models of evolution. We used Blomberg's K for univariate hind limb gear ratio, and Adams' K_{multi} for multivariate calcaneum shape.

K takes on the same range of values as Pagel's λ (lambda), another commonly used measure of phylogenetic structure (Pagel, 1999), but only the former can be interpreted as the proportion of variance explained by phylogeny. Pagel's λ differs from K in that it is a scaling factor applied to branch lengths (technically to the trace of the phylogenetic covariance matrix) with the effect of progressively pushing the tree's nodes to the root to form a star phylogeny as λ changes from 1 to 0 (Pagel, 1999; Freckleton *et al.*, 2002). λ thus also takes on a value of 1 when trait variance is fully explained by a Brownian motion model of evolution and a value of 0 when none of it is explained, but it is a parameter related to the model of evolution rather than the proportion of variance explained by phylogeny.

Analysis of community-level trait structure

Extensive analyses of the community-level ecometric patterns in these carnivore hind limb traits have been presented by us elsewhere (Polly, 2010; Polly and Sarwar, 2014; Polly and Head, 2015), including the correlation between hind limb gear ratio and several environmental variables and tests against a series of null models. Here, we tested whether community mean gear ratios were higher or lower than expected by chance using standardized effect size (SES) and a related randomization test. SES is a measure in standard deviations of how trait values in a local community compare to the distribution of values in random communities of the same size assembled from a species pool (Gotelli and McCabe, 2002; Gotelli and Rhode, 2002). SES is calculated as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} is the observed mean trait value in the community, I_{sim} is the mean value of randomly assembled communities of the same size (note that the expectation of random mean values is simply the mean trait value of the species pool regardless of the size of the community), and S_{sim} is the standard deviation of the mean values of randomly assembled communities of the same size. We drew 10,000 random communities from the North American carnivore species pool. If the random distributions were normal, one could interpret SES values higher than 1.96 or lower than -1.96 as significantly different from random given $\alpha = 0.05$; however, the random distribution is not always normal (especially with the SES application to community-level phylogenetic structure described below), so we also calculated a P -value directly from the random distribution itself (Manly, 2006). The observed trait mean was considered significant if it was higher or lower than the upper and lower 95th percentiles of the random assemblages.

Analysis of community-level phylogenetic structure

We measured phylogenetic relatedness of local communities using mean time since common ancestry for all pairs of species occupying each 50 km grid point. This metric is similar to Webb's mean pairwise nodal distance (Webb, 2000; Webb *et al.*, 2002), except that ours is measured in absolute divergence time (millions of years) instead of the number of intervening nodes. Webb applied a correction factor to his mean nodal distance (the Net Relatedness Index, or NRI) because some subclades have more nodes than others, thus introducing a bias in

the estimation of the mean nodal distance. Webb's correction is unnecessary for our data because absolute times since common ancestry are unaffected by differences in species richness in subclades. We did, however, use standardized effect size (SES) to evaluate whether closeness of phylogenetic relationship departs from a null model of random community assembly (see above). The distribution of mean time since common ancestry in random communities is decidedly non-normal (it is skewed strongly towards deeper divergences), so we again calculated *P*-values for each community directly from the random distributions rather than from the number of standard deviations. As above, we drew 10,000 random species assemblages of the same size from the pool of living North American carnivores for each 50 km grid sample. The observed relatedness index was considered significant if it was higher or lower than the upper and lower 95th percentiles of the random assemblages. Note that the mean time since common ancestry index has little power to detect small differences in phylogenetic structure because any fauna that contains a felid and at least one species from another family will have pairs of taxa whose last common ancestor was the last common ancestor of all crown Carnivora, which skews mean relatedness towards the bottom of the tree.

Knowing whether community membership is phylogenetically over- or under-dispersed only indirectly addresses the hypothesis that carnivore communities are sorted by clade rather than by species. We therefore used another permutation test to determine whether one or more family-level clades are over-represented in communities across the continent. For each 50 km grid point, we drew 10,000 random communities of the same size from the pool of living species, from which we determined whether the representation of any family-level clade was statistically greater in the real community than in the random ones. This test is similar to the one recently proposed by Hoehn *et al.* (2015), except that ours only tests for over-representation of subclades and does not directly take trait values into account, nor does it test for emergent clade properties.

RLQ analysis of the correlation between vegetation cover, spatial scale, phylogeny, and hind limb ratios

We directly assessed the relationship between vegetation cover and hind limb ratio while simultaneously taking into account spatial scale and phylogeny using RLQ analysis (Dolédéc *et al.*, 1996; Pavoine *et al.*, 2011). RLQ is an ordination technique that finds the major axes of covariation between two matrices (**R** and **Q**) that are linked by a matrix of species occurrences by sites (**L**) (Dolédéc *et al.*, 1996). Following Pavoine *et al.* (2011), a matrix of environmental variables (in this case vegetation openness) can be juxtaposed with a matrix of spatial variables (in this case a nearest-neighbour matrix) to create a matrix with sites in the rows and environment and space in the columns. Our study has 8436 relevant sampling sites. The vegetation matrix consists of a single column with 1 to 6 based on the openness of the site's vegetation cover. These data were standardized to have a mean of 0 and variance of 1. The spatial matrix provides a mechanism to assess the geographic scale of spatial sorting. In our analysis, the spatial matrix had 8436 rows and columns, which contained a 1 if the two sampling points were within 55 km of one another and a 0 otherwise. After centred principal components ordination, the first 25 axes were retained. They were standardized to have a mean of 0 and total variance of 1, which gives equal weight to the vegetation and spatial matrices. The **Q** matrix has species in the rows and consists of juxtaposed trait and phylogenetic matrices. We used 42 species for this analysis, excluding

five whose distribution is primarily South American and therefore are too limited to evaluate their trait–environment relationship in an analysis of North America. These species were *Speothos venaticus* (represented at only 2 of the sampling points), *Bassaricyon lasius* (1 point), *B. gabbii* (30 points), *Procyon cancrivorus* (30 points), and *Spilogale pygmaea* (35 points). The excluded taxa are marked with asterisks on the phylogeny in Fig. 3. The trait matrix had one column with the mean hind limb gear ratio for each species, which was standardized as above. The phylogenetic matrix is the phylogenetic covariance matrix typically used in phylogenetic comparative methods (e.g. Martins and Hansen, 1997; Revell, 2010). It is a 42×42 matrix with time since common ancestry in the off-diagonal elements and time between the tip and the base of the tree in the diagonal elements. As with the spatial matrix, this matrix was ordinated using centred principal components analysis, standardized, and juxtaposed with the trait matrix. Singular value decomposition was then used to obtain paired right- and left-hand eigenvector matrices (**U** and **V**). The eigenvectors are the major axes that maximize the joint correlation between all the data sets and thus reveal the interaction between vegetation, spatial scale, community structure, phylogeny, and traits. Scores for the vegetation and spatial data were obtained by multiplying them by **V** and scores for hind limb ratio and phylogeny were obtained by multiplying them by **U**.

Comparison of carnivore communities through time

To measure mean hind limb ratio turnover in carnivore assemblages since the last glacial maximum, we selected seven vertebrate fossil sites from 18,500 radiocarbon years ago (22,000 calendar years ago) in which the carnivore fauna was well represented: New Trout Cave, West Virginia (Grady, 1986); Anderson Pit, Indiana (Richards, 1972); Brynjulfson Cave I, Missouri (Parmalee and Oesch, 1972); Friesenhahn Cave, Texas (Graham, 1976); January Cave, Alberta (Burns, 1991); Little Box Elder Cave, Wyoming (Anderson, 1968; Long, 1971); and McKittrick, California (Jefferson, 1991). While the fossil faunas were not precisely contemporaneous with the last glacial maximum, they all occurred within a geologically short window when ice sheets would have been extensive (see Appendix 2 for minimum and maximum age estimates for each site; [3011Appendix](#)). Faunal lists were obtained from the Neotoma Paleocology Database (<http://www.neotomadb.org>) and crosschecked against the literature cited here. Calcaneum measurements were collected from museum specimens housed at the University of California Museum of Paleontology, the Vertebrate Paleontology Laboratory of the University of Texas at Austin, and the American Museum of Natural History. For each assemblage, the mean and standard deviation of the gear ratios of the constituent species of the fossil assemblages and the extant carnivore faunas from the same locations were compared as a measure of the amount of trait change that occurred at each location between the time of the last ice sheets and today [for similar comparisons of trait turnover at single locations, see Lawing *et al.* (2012) and Polly and Head (2015)]. Species lists and gear ratios for each fossil site are reported in [3011Appendix 2](#).

Except as noted above, all analyses were performed in *Mathematica*TM with the packages *Phylogenetics for Mathematica* v.3.0 and *Morphometrics for Mathematica* v.12.0 (Polly, 2014, 2016).

RESULTS

Intraspecific variation does not follow ecometric clines

In no species was there a significant correlation between intraspecific variation and the pattern in mean gear ratio at the community level. The mean trait value of each species varied predictably with limb posture, the highest means in the digitigrade taxa and lowest ones in the semi-digitigrade to plantigrade taxa: *Lynx rufus* ($\bar{x} = 1.37$, $SD = 0.036$), *Canis latrans* ($\bar{x} = 1.26$, $SD = 0.031$), *Urocyon cinereoargenteus* ($\bar{x} = 1.25$, $SD = 0.039$), *Procyon lotor* ($\bar{x} = 1.21$, $SD = 0.035$), and *Mustela frenata* ($\bar{x} = 1.21$, $SD = 0.062$) (Fig. 4). Variation within each species was about half as much, on average, as the variation among the mean values of North American carnivores ($SD = 0.04$ and 0.07 respectively) and was almost twice as high in *M. frenata* than the other four species. The broad range of intraspecific variation in hind limb ratio indicates that the raw material for sorting along the vegetation gradient is available, but there was only partial evidence for spatial structuring of trait values within species and no evidence for spatial correlation with community-level means in the same trait. To test the significance of spatial trait sorting within species, individuals were binned by ecological division and the mean within-species gear ratio was calculated for each bin (see maps in Fig. 4). Binning was necessary because geographic sampling of individuals was necessarily scattered as discussed above. One-way analyses of variance (ANOVA) found significant differences in one species, *L. rufus* ($P = 0.01$), but not in *P. lotor* ($P = 0.10$), *U. cinereoargenteus* ($P = 0.08$), *C. latrans* ($P = 0.96$), or *M. frenata* ($P = 0.53$). None of the observed correlations between within-species and ecometric means was significant based on 10,000 random permutations of the gear ratio means among the divisions as follows: *L. rufus* ($R = -0.32$, $P = 0.34$), *C. latrans* ($R = 0.45$, $P = 0.19$), *U. cinereoargenteus* ($R = -0.24$, $P = 0.48$), *P. lotor* ($R = -0.12$, $P = 0.73$), and *M. frenata* ($R = 0.21$, $P = 0.53$). Thus, the geographic differentiation within species does not parallel the ecometric pattern in community means.

Calcaneum shape and gear ratio are strongly correlated with phylogeny

Geometric morphometric analysis shows that calcaneum shape is closely linked to gear ratio. The first two axes of principal component morphospace, which collectively account for 52% of the shape variation, roughly separate the family-level clades (Fig. 5). PC1 is driven by the position of the sustentacular process and therefore is strongly correlated with gear ratio ($R^2 = 0.60$, Fig. 5 inset). The shape of the calcaneum is also significantly correlated with the gear ratio index when the relationship is tested with all PC axes ($R^2 = 0.21$, $P = 0.00$). These results reconfirm previous findings based on eigenshape analysis that shape variation in the calcaneum is closely linked to the position of the astragalus and thus to limb posture and gear ratio (Polly, 2008).

Between-species variation in calcaneum shape and gear ratio are both strongly linked to phylogeny (Fig. 5). The phylogenetic component of shape variance is more than 30% for calcaneum shape as a whole (Adams' $K_{multi} = 0.32$), 100% for PC1 of calcaneum shape (Blomberg's $K = 1.01$), and about 60% for the hind limb gear ratio (Blomberg's $K = 0.58$). A projection of the phylogenetic tree into morphospace shows substantial parallel and convergent evolution in calcaneum shape, especially between canids and felids. These two clades have independently evolved a digitigrade calcaneum shape that is towards the

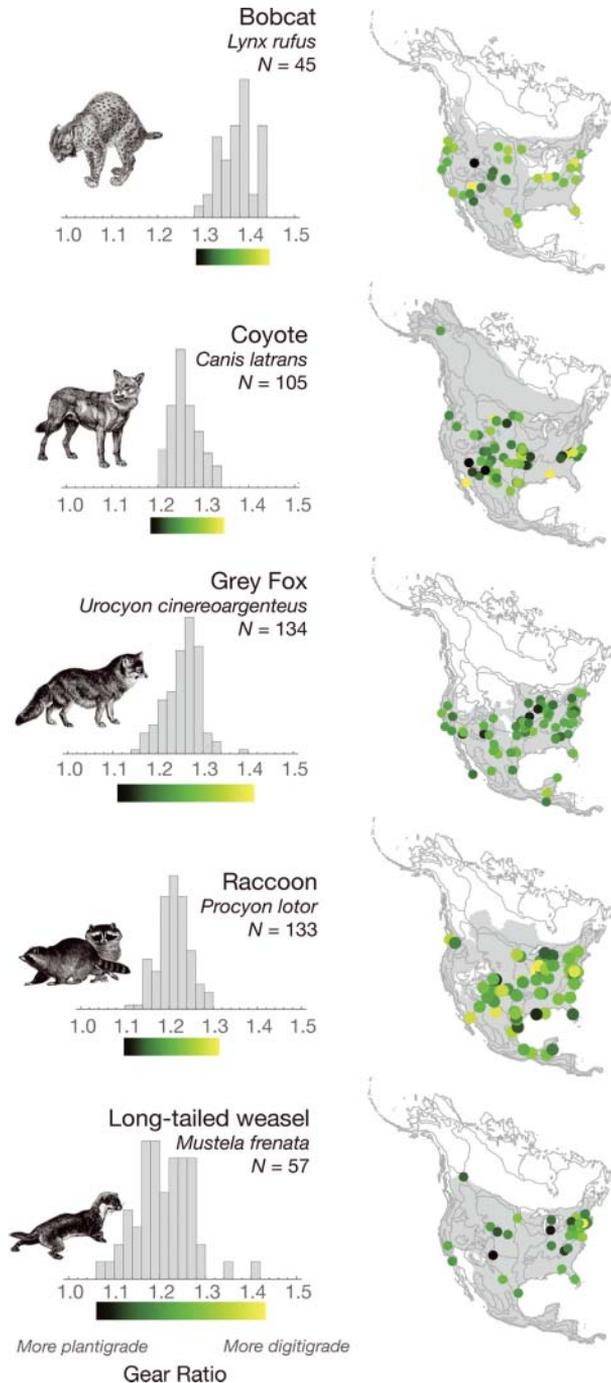


Fig. 4. Intraspecific variation in calcaneum gear ratio. Histograms show within-species variation. Maps show the range of each species in light grey, the boundaries of ecological divisions (used for binning) in dark grey, and the gear ratios of individual species colour-coded from minimum to maximum as shown by the colour bar under the corresponding histogram.

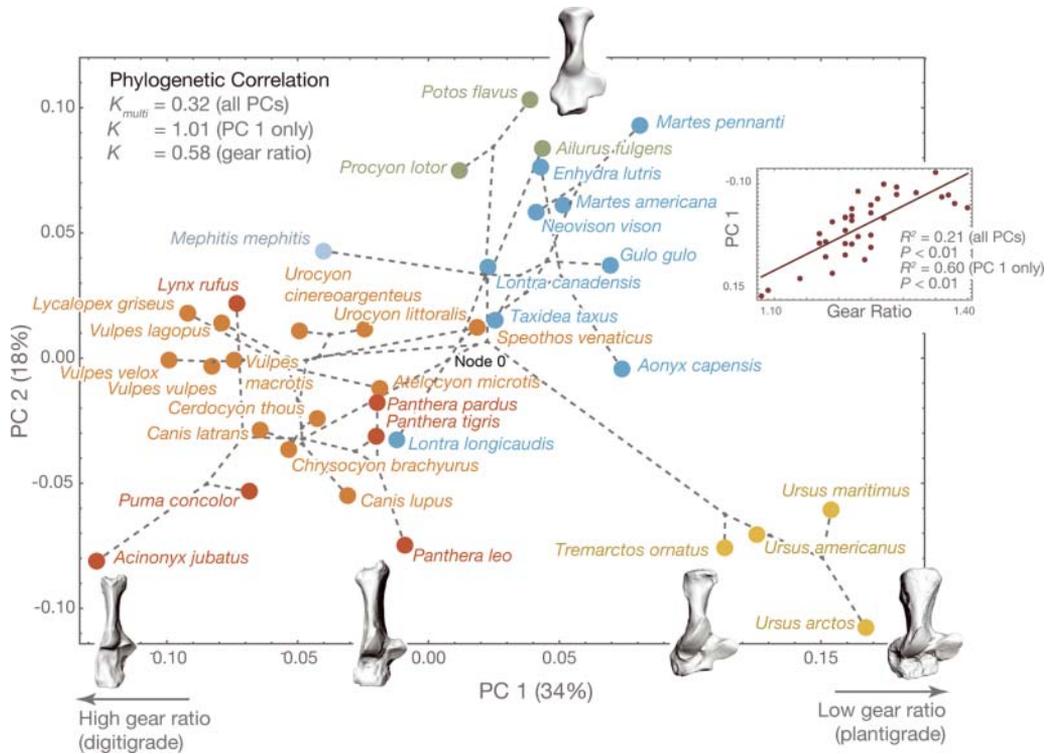


Fig. 5. The first two principal components (PC) of morphospace constructed from 3D landmarks of the carnivore calcaneum. The phylogenetic tree is shown as dotted lines (nodes of the tree are ancestral shape estimates). Family-level clades are coloured as in Fig. 3. Representative calcanea are shown to aid in interpreting the relationship between the ordination and the shape of the bone. Blomberg's K and Adams' K_{multi} report the proportion of variance that can be explained by phylogeny. Inset shows the relationship between PC1 and hind limb gear ratio.

negative end of PC1 in Fig. 5. The strong correlation of these traits with phylogeny means that hind limb locomotor function is strongly predicted by phylogenetic relationship.

Trait-based clade sorting explains hind limb means in carnivore communities

Before we looked at the overall correlation between vegetation, traits, and phylogeny in community structure, we looked individually at the geographic distribution of mean trait values and phylogenetic composition of communities.

The raw means (Fig. 6A) and the standardized effect sizes (Fig. 6B) both show that mean hind limb ratio is greatest in the southern and western part of North America and lowest in the northern parts of the continent. Regardless of other factors, it is significantly greater than expected by chance (as measured from random community assembly) in the coastal areas of Mexico, but lower only in a few places along the Great Lakes, the western Canadian lake systems, the Pacific Northwest, and western Alaska (Fig. 6C). Note that the null model of this test only evaluates whether the mean trait value in a local community is

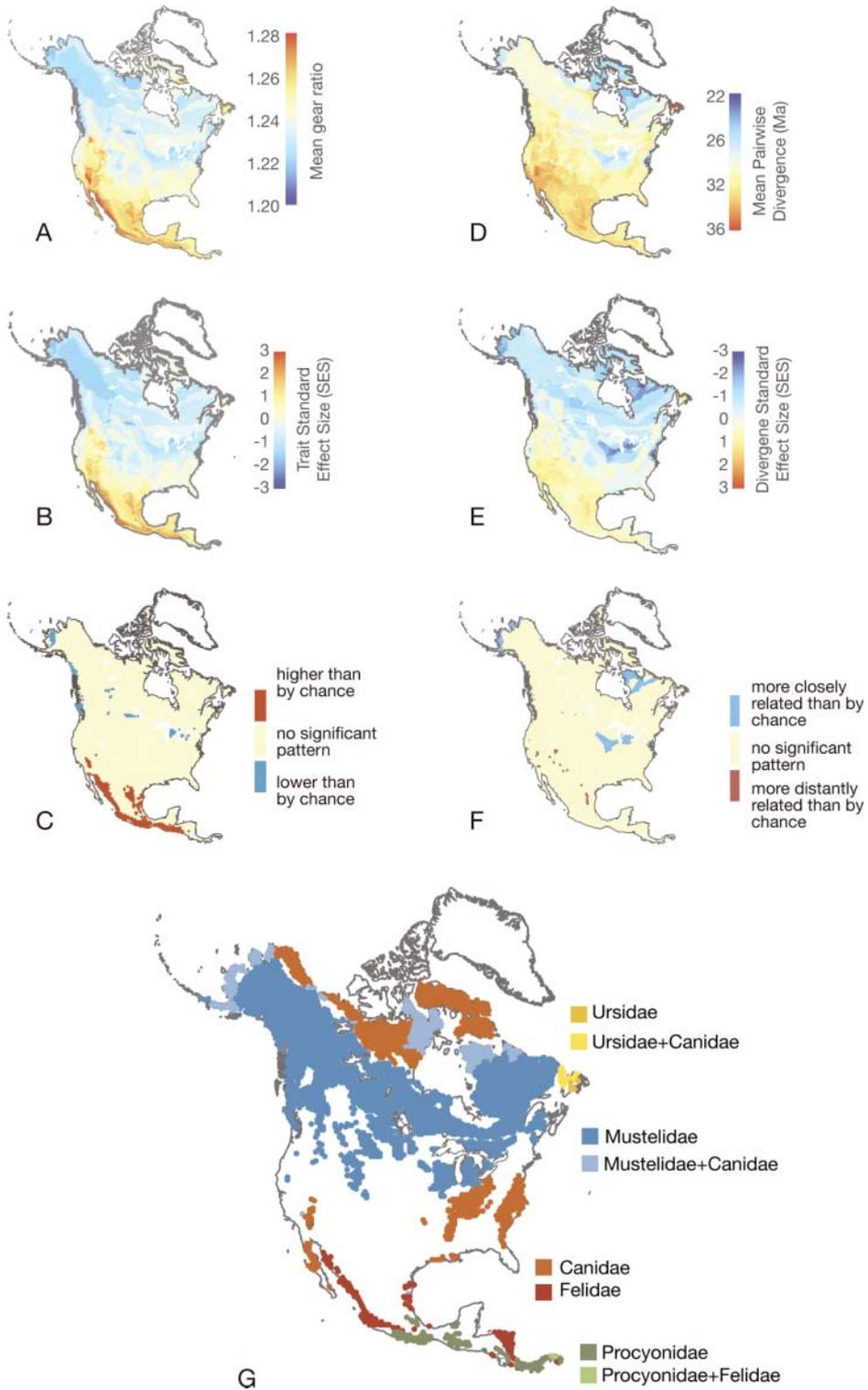
higher or lower than the mean in a randomly selected community of the same size. We showed elsewhere that there is a spatial gradient in ecometric means in hind limb ratio and that it is significantly correlated with vegetation cover ($R^2 = 0.50$) and ecological province ($R^2 = 0.70$) (Polly, 2010; Polly and Sarwar, 2014). The results shown are fully compatible with a strong gradient, which naturally results in intermediate trait values in many communities. The test here simply locates the high and low ends of the gradient.

Mean time to common ancestry has a superficially similar gradient, with southern communities composed of more distantly related species than northern ones (Fig. 6D). Mean divergence is greater than 30 million years for most of North America, the exceptions being in the far north and around the Great Lakes where mean divergence is as little as 22 million years. Standardized effect size (SES) indicates that phylogenetic distance is similar to that expected by chance in a randomly assembled community of the same size in the south, but closer than expected in the north (Fig. 6E). Community patches south of the Great Lakes, in northern Quebec, and in western Alaska are more closely related than expected by chance, whereas a few isolated patches in the desert southwest are more distantly related (Fig. 6F). Communities where phylogenetic divergence is more recent than expected by chance are those dominated either by mustelids or by both mustelids and canids, as demonstrated below. Note that mean pairwise divergence is a weak measure of the phylogenetic composition because any community that has taxa from subclades on either side of the root node will tend to have an older mean pairwise divergence. Almost all North American communities have at least one felid, so mean pairwise divergence is almost always on the older end of the spectrum.

Because mean time to common ancestry is only an indirect measure of clade sorting, we also tested whether there is a family-level bias in community composition. Our resampling test showed that one or more clades are significantly over-represented in communities over much of the continent (Fig. 6G). Mustelids form a larger proportion of communities across most of Canada than expected by chance, canids are more numerous in the high arctic tundras and in the most heavily cultivated parts of the Midwest and eastern seaboard, procyonids are over-represented in southern Central America, and felids are overly large components of communities in the coastal areas of northern Mexico. Ursids are over-represented on Newfoundland island because of significant under-representation by other clades (the carnivore fauna of Newfoundland includes only one bear species among a total of five carnivores, *Ursus americanus*, *Lynx canadensis*, *Mustela erminea*, *Martes americana*, and *Vulpes vulpes*, plus recent immigrants *Canis latrans* and *Neovison vison*).

Vegetation openness, spatial proximity, phylogeny, and hind limb ratio interact in the assembly of carnivore communities

The overall contribution of vegetation openness, spatial proximity, phylogeny, and hind limb gear ratio to the composition of North American carnivore communities was estimated with RLQ analysis. Figure 7 shows the contribution of each of these factors to the first major axis of correlation (RLQ1). The six panels show the scores on RLQ1 of hind limb gear ratio, phylogeny, the combination of gear ratio and phylogeny, vegetation openness, spatial distribution, and the combination of vegetation and space respectively. The colour coding links the data in the panels. In other words, points at the yellow end of the spectrum are found together in some carnivore communities and points at the green end are found together in others. For example, at the yellow end species with large gear ratios



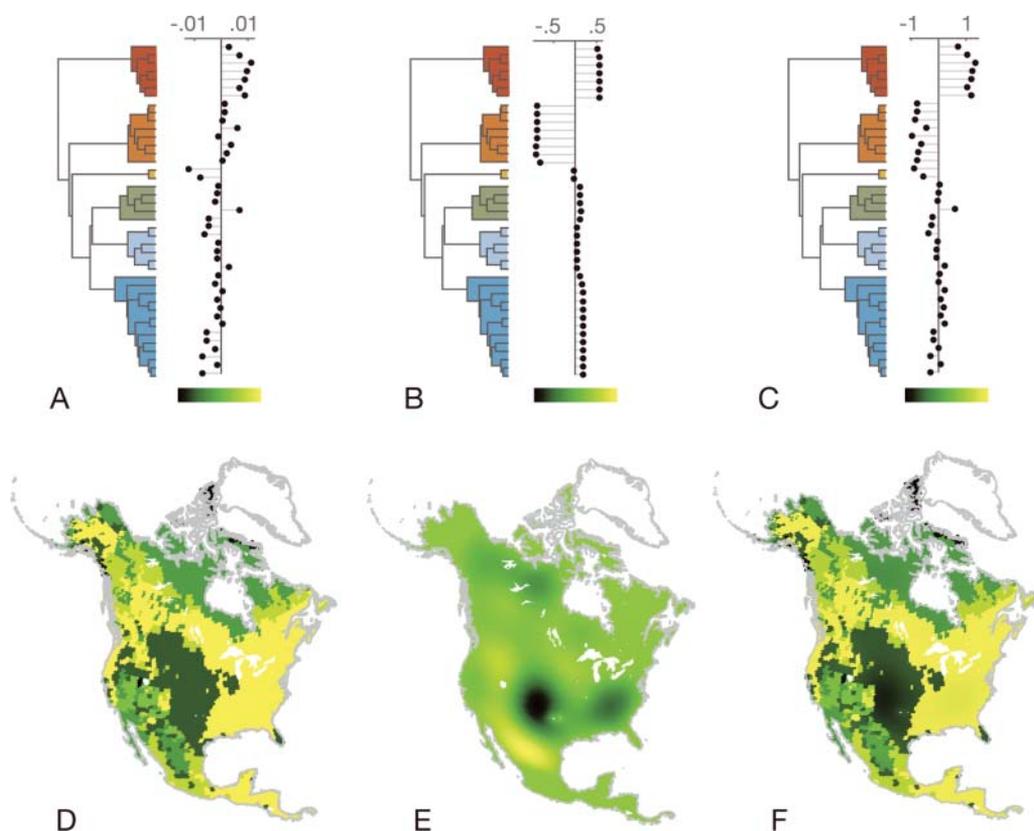


Fig. 7. Correlated patterns identified by RLQ analysis for (A) hind limb gear ratio, (B) phylogeny, (C) phylogeny and gear ratio combined, (D) vegetation openness, (E) spatial grain size, and (F) vegetation and spatial grain combined. All panels show scores on the first RLQ axis, which summarizes the greatest amount of covariation between all four data sets. A–C show RLQ1 scores for each species (plotted adjacent to the phylogeny); D–F show RLQ1 scores for each site. Scores are coloured dark green at the negative end of RLQ1 and yellow at the positive end.

(Fig. 7A) from the felid clade (Fig. 7B) tend to co-occur (Fig. 7C) in areas with low to medium vegetation openness (Fig. 7C) and occur disproportionately in areas of more open vegetation in a belt across northern Mexico and the Great Basin (Fig. 7D). In contrast, at the green end, species with low hind limb ratios, which are mostly ursids and mustelids

Fig. 6. (opposite) Community-level trait means and phylogenetic composition of North American carnivores. (A) Mean hind limb gear ratio. (B) Standardized effect size (SES) for mean hind limb gear ratio in units of standard deviation. (C) Local communities with statistically higher or lower mean values than randomly assembled communities of the same size. (D) Mean pairwise time since common ancestry in local communities. (E) SES for mean pairwise time since common ancestry in units of standard deviation. (F) Communities whose pairwise divergence time is either higher or lower than a random community of the same size. (G) Communities with more members from one or more family-level clades than expected in a randomly assembled community of the same size. Clade sorting is particularly prominent in the south, with felids and procyonids predominating, and in the north with mustelids and canids predominating.

(Fig. 7A) plus the high ratio canids (Fig. 7B) tend to co-occur (Fig. 7C) in areas with more open vegetation (Fig. 7D), disproportionately so in the Great Plains, eastern deciduous regions, and tundra (Fig. 7E). These patterns show how traits and phylogeny interact together with vegetation openness, indicating that traits and clades are sorted together, but also revealing a contrast in the sorting of felids and canids, which have similarly high gear ratios but which are sorted as clades into very different environments that have different community compositions at the family level.

Turnover in community trait distributions was substantial over the last 22,000 years

At all seven fossil sites, mean gear ratio during the last glaciation was considerably different than today (Fig. 8). Mean gear ratio changed on average by about 0.02 units, compared with a range of 0.09 units (22%) found in North American communities today. At most sites gear ratio increased since the last glaciation (i.e. the faunas became more digitigrade), but at Little Box Elder Cave it decreased by only a small amount. Trait diversity (standard deviation of the gear ratios in the community) changed on average by 0.02 units between the last glacial maximum and today, compared with an extant range of 0.06 units (33%) between communities. In most cases, trait variation decreased between the last glaciation and today, except at January Cave, a site in the Rocky Mountains of Alberta where the glacial carnivore fauna consisted almost entirely of mustelids (Burns, 1991), where it increased dramatically, and at New Trout and Brynjulfson Caves, where there was a marginal increase. These changes were driven by a combination of geographic range changes in extant species like the lion (*Panthera leo*) and fisher (*Martes pennant*), and extinction of species like the dire wolf (*Canis dirus*), saber-tooth cats (*Smilodon fatalis* and *Homotherium serum*), and short-faced bear (*Arctodus simus*).

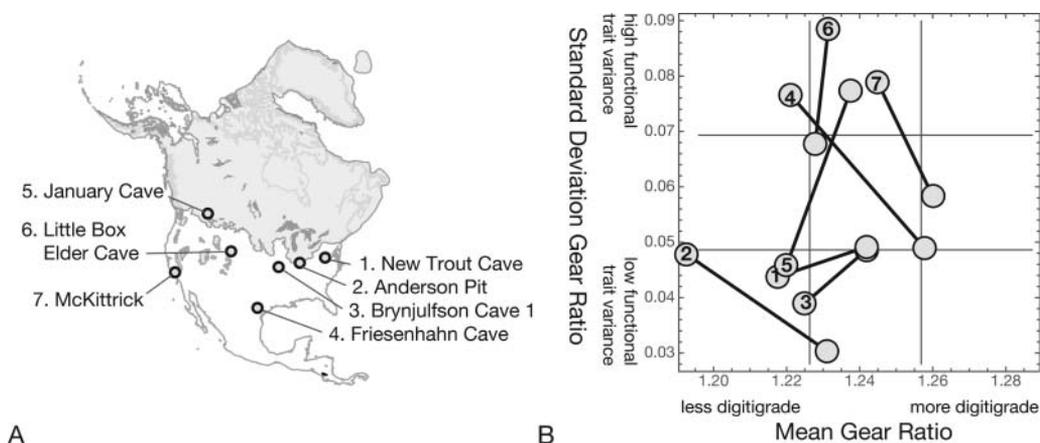


Fig. 8. Trait sorting between the last glacial maximum and the present. (A) Locations of seven fossil localities with faunas whose ages lie in the interval 40,000 to 10,000 years ago. Maximum extent of ice cover from Ehlers and Gibbard (2004). (B) Trait turnover at each of the seven locations. Numbered points give the mean and standard deviation of gear ratio in each fossil community, which are connected to points giving the modern trait values at the same geographic location. x-axis differences indicate change in the local mean trait value; y-axis differences indicate change in the variety of trait values found in the locally occurring species.

DISCUSSION

The evidence presented here indicates that ecometric patterning – geographic differences in the hind limb gear ratio in North American carnivore communities – is strongly influenced by clade-sorting processes but not by population-level adaptation within individual species. Lack of environmental gradients in trait values within species, the history of rapid turnover in traits since the last glaciation, and the deep phylogenetic structuring of hind limb functional morphology, all indicate that the ecometric pattern in hind limb ratio has not evolved *in situ*. Phylogenetic correlation in gear ratio and phylogenetic bias in carnivore community membership indicate that not only are species with similar gear ratio values more likely to be found together in a particular environment, but they are likely to be sorted as clades based on gear ratios that they share through common ancestry. As discussed in the following sections, this evidence suggests that clade sorting in the broad sense is an active process in trait-based community assembly at regional scales.

Intraspecific variation does not play a strong role in ecometric patterning

Ecometric sorting of hind limb locomotor traits does not occur by sorting of differentiated local populations. If it did, we would expect to see parallel intraspecific patterns in gear ratios within species and in the means of carnivore communities. But such correlations do not occur, or at the very least they are too weak to be detected with the sample sizes available to us. Within-species variation in hind limb ratio is present, however. Intraspecific variation (Fig. 4) is substantial, a third or more of the range observed among the means of all North American species (1.08–1.39 gear ratio units; Fig. 1C; 3011Appendix 1). However, within-species variation shows little geographic structuring (only one out of the five species have gear ratios that differ among ecological provinces) and is uncorrelated with the ecometric pattern at the community level.

The lack of intraspecific patterning might suggest that environmental gradients are either too weak to cause natural selection or that their filters are too coarse to sort local populations by the small trait differences that distinguish them. However, modelling studies have shown that weak intraspecific differentiation can occur in conjunction with strong ecometric patterning when environmental selection is strong but gene flow is high (Polly *et al.*, 2016). Indeed, gene flow is likely to be high in these five carnivore species. For example, the geographic range of the coyote (*Canis latrans*) changed dynamically over the last century, with its pre-1800 distribution confined to the Great Basin and the Mississippi extending into northern Mexico (Moore and Parker, 1992). Coyotes expanded eastward and northward beginning in the 1900s, achieving the full range shown in Fig. 4 only in the 1980s. Rapid population movements, home ranges of more than 40 km², daily movements of more than 10 km, and juvenile dispersals of 40–340 km (Andelt and Gipson, 1979; Harrison, 1992) provide ample opportunity for genetic mixing over large spatial scales. Gene flow could therefore easily prevent local differentiation in traits such as hind limb gear ratio. Despite a lack of environmental structuring of traits within the coyote's geographic range, its range boundaries are constrained by topography, vegetation, and climate, and are influenced by locomotor performance. The historic range of the coyote consisted of habitats that were largely open but which had locally available cover in the form of tall grasses, scrub, trees, or rocky areas (Moore and Parker, 1992). The opening of the eastern deciduous and boreal forests by agriculture and logging in the nineteenth and twentieth centuries created similar mixed habitats

into which the coyote expanded. Coyotes fare poorly in deep snow, which prevented northward expansion until anthropogenic clearing and packing of snow started facilitating it (Crête and Larivière, 2003). These observations suggest that environmental barriers that act on locomotion are strong at the boundaries of the coyote's distribution, but are weak within it. Even though the raccoon (*Procyon lotor*) is a much smaller animal than the coyote and consequently has smaller home ranges (about 8 km²), its dispersal distances are ordinarily up to 42 km, with instances of individuals moving more than 250 km (Priewert, 1961; Ewer, 1973).

If intraspecific variation had been correlated with community-level patterns, it would have strengthened the observed ecometric correlations between traits and environment. Previous analyses of ecometric patterns substituted species-level means for each species' trait value in local communities, which assumes that intraspecific variation is either negligible or uncorrelated with community-level ecometric patterns (Eronen *et al.*, 2010b; Polly, 2010; Lawing *et al.*, 2012; Polly and Sarwar, 2014). If the findings here can be generalized across traits, then the use of species means is justified because local trait values do not depart systematically from the species mean. Regardless, ecometric studies that use species-wide trait values can be considered conservative estimates of ecometric correlations because observed ecometric correlations could only be stronger if intraspecific variation were taken into account.

Taken together, these data suggest that the environmental gradients that filter carnivore hind limb ratios operate at the level of species or above without producing trait gradients within species. We can hypothesize that the filters establish boundaries of geographic ranges based on availability of favourable habitat types (Gaston, 2003). We can also hypothesize that the lack of trait gradients within species is due to two possible causes: (1) gene flow overcomes regional differentiation faster than environmental selection is capable of producing a gradient; or (2) selective use of a restricted range of similar habitats within the core range maintains a constant environment–fitness relationship across the entire geographic range.

What is clade sorting?

It is useful to define the terms species sorting, species selection, and clade sorting before discussing our results further. In the community ecology literature, *species sorting* refers to community assembly processes that operate by environmental filtering based on functional trait states (Poff, 1997; McGill *et al.*, 2006; Webb *et al.*, 2010). Species sorting thus produces geographic patterns in species occupancy in a heterogeneous environment and is a sorting process. In the evolutionary biology and palaeontology literature, *species selection* refers to the differential survival of clades because of clade-specific differences in rates of speciation or extinction (Stanley, 1975; Cracraft, 1982; Vrba, 1984; Jablonski, 2008a). In its strict sense, species selection refers only to cases in which clade members possess an emergent characteristic (one that collectively differs from the traits of individual species making up the clade) that directly contributes to the clade's heightened rate of extinction or speciation. In the broad sense, species selection refers to differences in speciation or extinction that are linked to traits shared by common ancestry but which affect the fitness of constituent species independently (Jablonski, 2008a). In either sense, species selection is also a sorting process because it starts with a trait that influences speciation or extinction. The evolutionary processes concern the origin of new traits rather than the fates of taxa that already possess one. Here we use the terms *species sorting* and *clade sorting* a little differently from either of the above. By *species sorting* we mean geographic sorting of species by the interaction of

environmental filters and functional traits (community assembly) independent of higher-level phylogenetic relationships. By *clade sorting* we mean trait-based environmental filtering that is biased by phylogeny because closely related species share the same or similar functional traits, thus being more frequent in an environment than expected by chance based on the trait–environment relationship alone. It is this correlated behaviour of clade members that we refer to as macroevolutionary in the title of this paper.

Clade sorting of hind limb ratio is important in carnivore community assembly

Since our previous research demonstrated that community mean values of hind limb ratio are correlated with vegetation cover (Polly, 2010; Polly and Sarwar, 2014) and because our results on within-species variation indicate that this pattern is not due to intraspecific evolutionary processes, we start with the null hypothesis that it is produced by species sorting and focus our tests on the alternative hypothesis that it occurs by clade sorting. The hypothesis of clade sorting requires the following to be true: (1) hind limb gear ratio must demonstrate differential performance along the environmental gradient to be a viable sorting factor; (2) hind limb ratio must be correlated with phylogeny and differentiated between family-level clades; (3) both hind limb ratio and family-level clades must be distributed non-randomly among communities; (4) the non-random distribution must have arisen more recently than either the traits or the clades originated; and (5) the trait and clade distributions among communities must co-vary with each other and with vegetation. We discuss each of these in turn.

Topography and vegetation affect hind limb locomotor performance

Gear ratio affects both the kinds of actions carnivores can perform and the kinds of environments in which they perform best. Calcaneum gear ratio is an integral component of hind limb extension and hence forward propulsion along with the mass of extensor muscles like the gastrocnemius, and the gear ratios of the foot, tibia, femur, and pelvis (Hildebrand, 1962; Alexander, 1968; Jenkins and Camazine, 1977; Polly, 2007). The literature on morphology and hind limb performance in mammals is extensive and will not be reviewed here; however, we point to some of the most directly relevant studies. Harris and Steudel (2002) showed that the proportional limb length and extensor muscle mass, both of which are mechanically related to extension of the calcaneum, directly affect jumping ability in cats. Their study demonstrated that within-species variation in limb mechanics affects locomotor performance, which is the prerequisite for natural selection. Interspecific differences in limb proportions are correlated with performance measured by maximum running speed, prey capture, and leaping abilities, but not with behavioural parameters such as home range size or daily movements (Garland and Janis, 1993; Harris and Steudel, 1997). Performance also varies by hind limb proportions, both within species in different environments (Klein *et al.*, 1987; Murray and Larivière, 2002) and between species in the same environment (Murray *et al.*, 1995). Hind limb proportions do not, of course, account for the entire locomotor repertoire of carnivores. Fore limb functions, for example, are critical to climbing and grasping abilities and often differentiate the abilities of taxa that have similar hind limb proportions such as felids and canids (e.g. Van Valkenburgh, 1987; Taylor, 1989; Andersson, 2004). Our focus is not on the full repertoire of locomotion, but on how the functional relationship of one specific aspect of locomotion influences geographic distributions and community assembly.

Gear ratio and calcaneum morphology have strong phylogenetic correlations

North American carnivores had a last common ancestor that lived more than 42 million years ago in the Late Eocene. Today they are divided into six distinct family-level crown clades, each of which has a comparatively recent common ancestor that lived just before or just after the Miocene climatic optimum 16 million years ago (Fig. 3). Each crown clade has a distinctive locomotor morphology (3011Appendix 1; Fig. 5), as might be expected from their deep phylogenetic splits. Felids and canids share high gear ratios, but they have evolved them independently. Ursids, which are plantigrade, have the lowest gear ratios with hardly any overlap with other families. Mephitids are all terrestrial but range from plantigrade to semi-digitigrade. Mustelids and procyonids also range from plantigrade to semi-digitigrade, and both groups include a mix of terrestrial and scansorial taxa. Mustelids are unique among North American carnivores in having natatorial (*Lontra*) and semi-fossorial specializations (*Galictis*, *Gulo*, and *Taxidea*), whereas procyonids are unique in having fully arboreal specializations (*Bassaricyon* and *Potos*). Mustelids and procyonids overlap in gear ratio, but are again distinct from the other family-level clades and have evolved hind limb specializations in parallel (Polly, 2008) (Fig. 5). Blomberg's *K* (Blomberg *et al.*, 2003), which measures the proportion of variance that can be explained by phylogenetic relationships, is 0.58, indicating that almost 60% of the variation in gear ratio values in North American carnivores is predictable by their phylogenetic relationships. Carnivores thus show strong phylogenetic differentiation in gear ratio and, by logical extension, differentiation in locomotor performance at the family level.

Mean traits, phylogeny, and family-level composition of communities are non-random

As our previous research shows, mean hind limb ratio in North American carnivore communities is non-randomly distributed with respect to vegetation cover and ecological province (Polly, 2010; Polly and Sarwar, 2014). Our results here show that not only is there a significant correlation, but that communities in some regions in Mexico have a higher mean gear ratio than would ever be expected by chance assembly and a few areas in the northern USA and Canada have a lower mean (Fig. 6A–C). These communities have more felid and mustelid members respectively than expected by chance (Fig. 6G), as clades share proportionally high and low gear ratios respectively (Figs. 1C, 5). In fact, communities across much of the continent have memberships in which one or more clades are significantly over-represented: felids and procyonids are more common as community members in the south and mustelids, canids, and ursids are more common in the north (Fig. 6G). Other research has found strong phylogenetic structuring in carnivore communities in Africa (Cardillo, 2011).

The correlation between mean traits, clade membership, and vegetation openness is confirmed by RLQ analysis, which shows that canids, ursids, and members of the musteline subclade of Mustelidae (*Galictis*, *Neovison*, and the *Mustela* species) tend to sort together in their trait–phylogeny interactions on the negative end of the RLQ1 axis (Fig. 7C) associated with the open end of the vegetation spectrum (Fig. 7D). The pattern of sorting is associated with vegetative and topographic features of the continent. Mustelids dominate in the recently glaciated terrains that are covered in boreal forest (taiga) biomes (Figs. 6, 8), felids predominate in topographically rugged, dry landscapes covered in mixed scrub vegetation, while procyonids predominate in dense tropical forests. The close links between traits and phylogeny and between phylogeny and macroenvironments indicate that the ecometric

sorting of hind limb gear ratio acts on clades that share the traits by common ancestry rather than on species that are completely independent in their sorting properties.

Interestingly, some family-level clades that have similar gear ratios are sorted into different parts of the continent.

Divergent sorting of clades with similar traits is most pronounced in canids and felids, which both have high gear ratios (Figs. 1C, 7A), are over-represented parts of communities in different regions of the continent (Fig. 6G), and are at opposite ends of RLQ1 (Fig. 7B, C). This disparity is almost certainly related to other clade-level features related to locomotion and hunting behaviour that make different uses of each group's high gear ratio. The living North American felids are all digitigrade scansors and the canids are digitigrade cursors. Despite the overlap in gear ratio in the two groups, they evolved their digitigrade stances independently from a semi-digitigrade ancestor (Polly, 2008) (Fig. 5). The two groups use the leverage provided by their high gear ratios differently: canids tend to use the lever advantage for efficient long-distance travel and pursuit, whereas felids tend to use it for springing on prey and short sprints (Janis and Wilhelm, 1993; Murray *et al.*, 1995; Bailey *et al.*, 2013).

Mustelids and procyonids are also sorted differently (Figs. 6G, 7C), despite both having medium gear ratios and typically scansorial or arboreal locomotor styles (Figs. 1C, 7A; 3011Appendix 1). Food preferences, hunting and foraging behaviours, physiology, and locomotor traits that differ between the two families probably account for the sorting of these two families into forests with different characteristics (branching patterns, frequency of fruit, extent and type of canopy) and climates (snow cover, mean annual temperature, precipitation). Nevertheless, there are similarities in the locomotor habitats into which these two families are sorted: mustelids are dominant in the boreal forests of Canada, which are historically dense with a minimum of open areas, while procyonids dominate the tropical forests of Central America, which are also historically dense with minimal open areas.

Interestingly, RLQ analysis shows that mustelids tend to sort into communities with canids while procyonids tend to sort with felids (Fig. 7C). This coordinated clade-level sorting suggests that the response of species to environmental change may not be truly independent as expected under a Gleasonian model of community reassembly and may be related to the finding of Lyons (2003, 2005) that many species responded to Quaternary environmental changes in a partially correlated way.

This mosaic pattern of taxa, traits, and environments emphasizes a fundamental ecometric principle that each trait is functionally related to a specific aspect of the environment and is only one among many characteristics that influence the distribution of a species or clade (Polly and Head, 2015). Each trait is expected to be distributed along its associated environmental gradient, but the distribution of a taxon depends on the combination of traits it possesses and on the combination of realized parameters in regional environments.

Ecometric patterning significantly post-dates the origins of family-level clades and traits

Ecometric sorting of gear ratios has occurred since the family-level clades arose. Based on extant species and phylogeny alone, the clade sorting could be interpreted as having evolved *in situ*, with the trait values of each clade having evolved as adaptations to the environments in which they currently live. In such a fossil-less scenario, one might conclude that each clade's gear ratio value allowed its rate of speciation to exceed extinction in the geographic area where it dominates today so that it radiated endemically in the areas shown in Fig. 6G. However, evidence from the geological and palaeontological records demonstrates that the

ecometric and phylogenetic patterns observed today have been radically reorganized over very short time scales compared to when the clades originated. These ecometric patterns have arisen through complex biogeographic histories of the family-level clades, for which there is strong evidence for intercontinental dispersals during their recent history as well as repeated turnovers in clade membership and community reassembly.

The biogeography of family-level clades includes a complex mixture of dispersal and endemic radiation. Even from modern geographic ranges alone, it is clear that the families did not originate in particular regions of North America. Most individual species have large geographic distributions that encompass substantial parts of North America, a few of which spread over as much as 70% of the continent. The wolf (*Canis lupus*), red fox (*Vulpes vulpes*), and brown (grizzly) bear (*Ursus arctos*) have ranges that also extend across Eurasia, and the mountain lion (*Puma concolor*), jaguar (*Panthera onca*), kinkajou (*Potos flavus*), and grey fox (*Urocyon cinereoargenteus*) extend deep into South America. The phylogeny of extinct species shows that individual North American families variously originated in North America and Eurasia and have dispersed between continents multiple times during their history. Felids originated in Eurasia and have dispersed between continents at least ten times (Johnson *et al.*, 2006; Tseng *et al.*, 2013). Lions, which are now confined to Africa and southern Asia, once ranged across most of North America and as far as northern South America (Barnett *et al.*, 2009; Stuart and Lister, 2011; Tseng *et al.*, 2013; King and Wallace, 2014). Crown canids originated in North America and have dispersed intercontinentally at least six times (Tedford *et al.*, 2009). Procyonids originated in Europe and later dispersed first to North America and then to South America as the Panamanian land bridge formed (Baskin, 1998a). The biogeography of ursids, mustelids, and mephitids is less well understood, but involves multiple intercontinental dispersals in each family (Hunt, 1998; Baskin, 1998b). The current continental pool of North American carnivores was assembled well after the families evolved their clade-specific hind limb functions.

Not only have the biogeographic distributions of the six families changed since their origin, but so too have trait and community compositions changed. As recently as 22,000 years ago, the northern part of North America was covered by glacial ice (Fig. 8). The boreal regions where mustelids and ursids now dominate local carnivore communities have been completely recolonized by both animals and plants since then. The regions south of the ice margins underwent tremendous reorganizations in community and trait compositions, with both floras and faunas changing at any given location as temperature and precipitation patterns changed (Graham *et al.*, 1996; Alroy, 1999; Jackson *et al.*, 2000; Lyons, 2005; Polly and Eronen, 2011).

Trait turnover between the last glacial maximum and today at the seven fossil sites was uniformly large regardless of their local environments (Fig. 8). At January Cave and Little Box Elder Cave, both of which were in coniferous forest biomes during the last glacial period (Anderson, 1968; Long, 1971; Burns, 1991), mean gear ratio did not change, but the amount of community-level variation did. At January Cave, variation in gear ratio is now much higher than during the last glaciation (the fauna was predominantly mustelid, but is now phylogenetically mixed with canids, felids, and ursids; 3011Appendix 2). At Little Box Elder Cave, within-community variation decreased. At New Trout Cave and Brynjulfson Cave, the within-community variation stayed about the same, but mean gear ratio increased as the faunas gained felids and lost mustelids (Parmalee and Oesch, 1972; Grady, 1986) (3011Appendix 2). Both these sites were located in non-analogue boreal forest biomes during the last glacial period (Overpeck *et al.*, 1992). At Friesenhahn Cave and McKittrick, both of which had open habitats with some deciduous or scrub forest, mean gear ratio increased and variation

within communities decreased between the glacial maximum and today, losing both saber-toothed cat and bear species due to end-Pleistocene extinctions in addition to other faunal changes (Graham, 1976; Jefferson, 1991). Presumably, the magnitudes of climatic and vegetative change following deglaciation were similar across these parts of North America, even though the kind of change differed, so that the magnitudes of gear ratio trait changes were similar even though their specific start and end points differed. The magnitude of trait changes in these faunas is in contrast to change between the last glacial maximum and today, which was minimal (Polly and Head, 2015). This observation is based on the Harrodsburg Crevice site in Indiana, where the climate and vegetation were roughly the same in the last interglacial as today (Smith and Polly, 2013). Despite the occurrence of many extinct species in the last interglacial fauna, there was almost no trait change between then and now despite the interval between the two times being almost five times as long as between the last glaciation and today. Presumably, trait turnover during the Quaternary has been cyclic, with repeated changes in environments that cycle back and forth between glacial and interglacial climates. We assume that the patterns observed today (Figs. 1, 6) are typical for interglacial periods over at least the last million years, with the caveat that several large carnivore species, including lions, saber-toothed cats, and short-faced bears, all of which have comparatively low gear ratios, were lost in the end-Pleistocene extinction. While this assumption has never been directly tested, it rests on the similarity of interglacial faunas across that time and on the observation that at least one fauna from the last interglacial had similar trait distributions as today despite extinctions (Polly and Head, 2015). Also in contrast to the uniformly large trait changes between the last glaciation and today, locomotor trait change over the last 100 years due to anthropogenic impacts on faunas varies considerably from one location to another depending on the kind of local change that has transpired (Lawing *et al.*, 2012; Polly and Head, 2015).

Changes in carnivore traits and community compositions are consistent with what we know about changes in the taxonomic structure of mammalian communities during the Quaternary. Non-analogue faunas – communities in which species lived in association that today have disjunct geographic or climatic distributions – were common around the times of the last glaciation and more recently in the Holocene (Alroy, 1999; Lyons, 2005; Polly and Eronen, 2011; Smith *et al.*, 2015; Lyons *et al.*, 2016). Extinction, independent Gleasonian range changes, and non-analogue environments have altered the composition of communities over geologically short time intervals. Changes in trait associations are part of the changes in species associations (Ackerly, 2003; Williams and Jackson, 2007; Polly and Head, 2015).

In summary, the geographic distributions of traits and clades have turned over repeatedly since their origins. The family-level crown clades all originated in the middle to early Miocene more than 10 million years ago (Fig. 3), at which point their locomotor repertoires had already been established in completely different environmental contexts than those that exist today. The high gear ratios and digitigrade locomotion in canids, for example, originated during the late Oligocene and early Miocene as open habitats were becoming more common in North America, eventually culminating in the widespread expansion of grasslands (Wang and Tedford, 2010). The crown felid radiation is similarly recent, but hind limb gear ratio has a more complicated history in the clade. Until the end-Pleistocene, the machairodontines – saber-toothed cats and their relatives – persisted as the sister-clade to crown felids. The machairodontines had quite different locomotor morphology, including a comparatively low gear ratio more like mustelids and procyonids than crown-clade felids (3011Appendix 1 and 2). The origins of locomotor modes in ursids, procyonids, mephitids,

and mustelids is less well studied palaeontologically, but the phylogenetic reconstructions in Fig. 5 suggest that their family-specific gear ratios evolved at or before the time of common ancestry of the crown species. Because the clade-specific trait values evolved many millions of years before the current geographic sorting of traits arose after the last deglaciation, we interpret the ecometric patterns seen today as having arisen from environmental sorting of clades rather than recent trait adaptations or trait-associated diversification within clades.

CONCLUSION

The hind limb traits in this study are closely linked to phylogeny with gear ratios differing strongly between families, yet they are unquestionably distributed non-randomly with respect to their functional relationships to vegetation and topography. The origin of each family-level clade's hind limb specializations occurred deep in phylogeny, either as adaptations to emerging new habitats like open grasslands or inherited from scansorial ancestors that lived in the widespread tropical forests of the early Cenozoic. Either way, their traits are now sorted into new environmental patterns that have little to do with the specific palaeoenvironmental context in which they originated. This mixture of clades and traits observed today has arisen comparatively recently in the 22,000 years since the last glacial maximum, as climatic and environmental change have reassembled communities across the entire continent. The regional reassembly processes have been influenced by functional aspects of locomotion, despite the fact that gear ratio traits are strongly linked to phylogenetic history. The lack of intraspecific correlation between gear ratio and environment helps confirm this. Dispersal and geographic range dynamics are the sorting processes that create today's ecometric patterns, not independent adaptive evolution.

Since many functional traits are correlated with phylogeny, yet are distributed predictably by environment, clade sorting is likely to be an important process for creating ecometric patterns in the modern world. Phylogenetic sorting has been found in communities of plants (Ackerly, 2003; Little *et al.*, 2010), mammalian herbivores (Fortelius *et al.*, 2002; Eronen *et al.*, 2010b), snakes (Lawing *et al.*, 2012), and bivalves (Jablonski, 2008b; Roy *et al.*, 2009). Seemingly paradoxically, clade sorting is a rare outcome in phylogenetically explicit modelling of trait–environment sorting when the simulation is conducted in a stable geographic configuration of environments (Polly *et al.*, 2016). Clade-specific traits are more likely to arise when new environments emerge (Lynch and Lande, 1993; Ackerly and Donoghue, 1995).

Our findings suggest an intriguing hypothesis: species and clade sorting may be more important than evolutionary adaptation during the Quaternary (which includes today) because its rapid, large-scale cyclic climatic changes reorganize communities and environments faster than natural selection can act. Our data show rapid turnover in the trait composition of communities since the last glacial maximum but little within-species trait differentiation with respect to environment. Furthermore, it is known that glacial–interglacial cycles had profound effects on community structure globally because of independent or semi-independent responses of species to climate cycles, often resulting in non-analogue communities (e.g. Graham *et al.*, 1996; Alroy, 1999; Jackson and Overpeck, 2000; Lyons, 2003, 2005; Polly and Eronen, 2011). Other support comes from studies showing that geographic tracking of environments by species during glacial–interglacial cycles was usually faster than their evolutionary adaptation to climatic changes, as much as two orders of magnitude faster in vertebrates (Davis and Shaw, 2001; Davis *et al.*, 2005; Parmesan, 2006; Lawing and Polly, 2011; Rödder *et al.*, 2013; Lawing *et al.*, 2016b). Evolutionary adaptations to environment may have been more common during

earlier periods of the Cenozoic when climatic and environmental change was slower and non-cyclic. The origins of many living clades of vertebrates, including the families of carnivore in this study, date back to the origin of major new environments, such as open grasslands, tundra, and alpine environments, between 5 and 20 million years ago when increasing aridity caused landscapes to open and grasslands to spread and declining temperatures caused the origin of tundra and alpine habitats (e.g. Fig. 3). Evolutionary processes of trait origins appear to be associated with these deeper environmental events. Thus large-scale changes in hind limb gear ratio over recent geological history are the product of reassembly of taxa whose traits evolved deep in the past. The effects of the rapid, repetitive climatic changes of the Quaternary thus appear to have primarily been sorting of traits and taxa rather than the origin of new clades or the adaptive evolution of their traits. This may be a general pattern, at least in terrestrial vertebrates. Klicka and Zink (1997), for example, argued that glacial–interglacial cycles have had no effect on evolution based on their observation that species divergences pre-date the onset of glacial cycles 2.5 million years ago. Lister (2004) argued that the species that make up cold-climate faunas originated at the beginning of the Quaternary, but that individual glacial cycles are shorter than the average longevity of a species and therefore have primarily affected geographic range changes, selected for phenotypic plasticity, and caused iterative pulses of genetic divergence as ranges have expanded and contracted. The evidence from carnivore hind limb gear ratio is consistent with this hypothesis, but it is contradicted by data from other clades that point to evolution as an important response to rapid climate change (e.g. Davis and Shaw, 2001; Davis *et al.*, 2005). To truly test it will require new approaches and new data.

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