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Extinction, extirpation, and exotics: effects on the correlation between traits and environment at the continental level

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Ecometrics is the study of the relationship between organismal traits and environments. This study used Monte Carlo methods to assess the effects of extinction, extirpation, and exotic species on ecometric correlations at the continental scale. These potentially confounding processes arise from anthropogenic activities, taphonomic biases in fossil assemblages, and selective mass extinctions. Random, independent local extinctions introduced a predictable downward bias in ecometric correlations, which can be corrected by rarefaction if correlations are being estimated from fossil assemblages. Random global extinctions on species have a less predictable effect on ecometric correlations and introduce pronounced effects if more than 25% of the continental fauna is affected; however, global extinctions do not bias the estimation of R^2 even though they increase its uncertainty. Selective extinction and introduction of exotic species had little impact on ecometric correlations, though caution is urged in generalizing this result.

Introduction

Some folks drive the bears out of the wilderness,
Some to see a bear would pay a fee,
Me, I just bear up to my bewildered best
And some folks even seen the bear in me.
(Steven Fromholz 1975)

An ecometric trait is a measureable morphological feature that interacts with the environment. In some cases interaction between environment and trait is strong enough that the state of the trait in a species constrains where it can live and, thus, helps to define the limits of its geographic range (Poff 1997, Eronen *et al*. 2010a, Polly *et al*. 2011). When shared by many species, ecometric traits influence the assembly of local communities through their joint influence on the geographic ranges of those species. Functional traits can therefore influence species sorting, favoring species with a particular state in optimal environments. The average values of ecometric traits in local communities are, therefore, expected to be correlated with local environment (Thompson *et al*. 2001, Eronen *et al*. 2010a, Webb *et al*. 2010). Body mass in mammals (Damuth *et al.* 1992), body size in snakes (Head *et al.* 2009), hypsodonty in ungulates (Eronen *et al.* 2010b), tooth morphology in mammals (Evans 2013), limb proportions in carnivorans (Polly 2010), stomata counts in leaves (Beerling *et al.* 2002), and leaf-shape in plants (Wolf 1990, Royer *et al.* 2005) are examples of ecometric traits where the average value in a community is strongly enough correlated with an environmental or climatic parameter the average trait value can be used to predict environment.

The study of ecometrics is useful for developing trait-based proxies for studying paleoenvironments and for understanding the relationship between biotic and climatic changes (Willis & MacDonald 2011). A transfer function is established using data from the modern world that relates mean trait value to the environmental parameter of interest. Paleoenvironmental parameters can then be estimated from the mean trait value in fossil assemblages (Kowalski & Dilcher 2003, Royer *et al.* 2005, Head *et al.* 2009, Eronen *et al.* 2010a, 2010b, 2010c).

Extinction, extirpation (local extinction), or introduction of species can introduce noise in ecometric correlations if the cause of the extirpation is unrelated to changes in environment. Ecometric correlations between traits and environments arise through a rich historical interaction in deep time between geographic sorting, adaptive trait evolution, and phylogenetic sorting involving both extinction and adaptive radiation, all of which involve fitness gradients related to trait function (Jablonski 2005, Fritz *et al.* 2013). Throughout most of geological history, extinction, extirpation, and immigration were caused primarily by climate, environment, or local community interactions. In recent history, changes in species ranges have been affected by a special kind of biotic interaction that is unrelated to fitness, namely human extirpation. Human influences have included purposeful removal, such as the extirpation of livestock-preying carnivores (Laliberte & Ripple 2004), large-scale transformation of dominant vegetation, such the clearing of forests for agriculture (Tucker & Richards 1983), and translocation of species from one ecosystem to another, such as the introduction of mongooses to control rodent pests (Lowe *et al.* 2000). The 21st century ranges of animals, especially groups such as mammalian carnivorans, may therefore not be in ecometric equilibrium and the influence of the functional relationship between ecometric traits and environments may be masked. For example, grizzly bears (*Ursus arctos*), which are now largely restricted to mountainous forested environments, ranged across most of the North American high plains prior to 1850 (Mattson and Merrill 2002, Servheen 1990); reindeer or caribou (*Rangifer tarandus*), which are now restricted to high latitudes, ranged south into New England and Wisconsin prior to the mid-1800s (Bergerud 1974); and, prior to 1830 there were sporadic reports of the jaguar (*Panthera onca*), which is now restricted to tropical and subtropical regions, as far north as Pennsylvania and the Great Lakes (Rafinesque 1832, Daggett & Henning 1974). Ecometric correlations between the environment and the average value of a trait across species in a community could easily be altered by anthropogenic extirpations and introductions, perhaps in a systematic way that obscures the underlying ecometric pattern. The effect of human impacts on ecometric patterns can be minimized by using pre-disturbance ranges of species instead of their current ranges, but in many cases human effects predate historical accounts (Laliberte & Ripple 2004, Willis & Birks 2006, Carrasco *et al.* 2009). The expected effect of anthropogenic modification of species ranges is to lessen the strength of correlation between traits and environments.

Ecometric correlations can also be lessened by non-anthropogenic extinctions that are independent of environmental changes, such as the K-Pg asteroid impact, or by non-environmental barriers that prevent species from dispersing into regions with which their traits are compatible, such as when ocean barriers separate areas of similar habitat (note that convergent evolution might reproduce ecometric patterns on either side of such barriers).

Nevertheless, the functional relationship between ecometric traits and the environment might still exert an influence in certain situations, even in the face of anthropogenic disturbance. For example, exotic species introduced into new environments are unlikely to flourish if their traits are not compatible with their the local environment. Species that are extirpated are likely to have been removed from environments

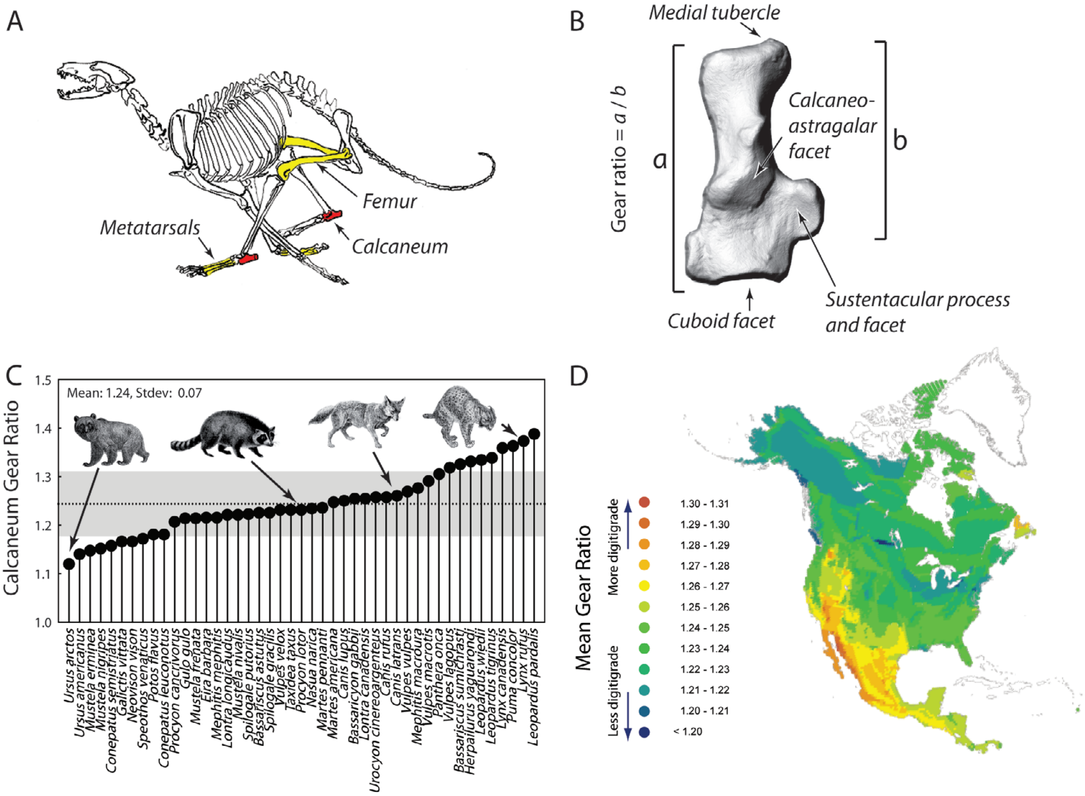

Fig. 1. The ecometrics of locomotion in North American carnivorans. (**A**) Skeleton of a dog, *Canis familiaris*, showing the location of the femur, metatarsals, and calcaneum, three structures that are indicative of limb mechanics. (**B**) Calcaneum in dorsal view, showing measurements of (**a**) the total length of the calcaneum and (**b**) the distance of the sustentacular process from its proximal end, which are used to calculate the ecometric gear ratio used in this study. (**C**) Scree plot of the calcaneum gear ratio in the 45 North American carnivorans included in this study. Mean (dashed line) and standard deviation (grey area) for the entire North American fauna are shown. **D.** Map of the mean calcaneum gear ratio in local assemblages sampled at grid points spaced at 50 km intervals.

with which their traits were compatible, thus weakening the ecometric correlation, but they are unlikely to be pushed into refuges with environments that are incompatible with their trait adaptations, therefore extirpation is unlikely to introduce false ecometric correlations. Similarly, species that expand into or retreat from agriculturally modified landscapes are likely to do so on the basis of trait-environment interactions in the altered landscapes (Poff 1997, Van Kleunen *et al*. 2010). Thus, the functional relationship between trait and environment should hold, even if ranges and environments are so altered that the trait is not at ecometric equilibrium.

In this paper, we examined the effects that random and non-random changes in species composition have on ecometric patterns using a dataset of hindlimb traits from North American carnivorans. Polly (2010) demonstrated in this group that the gear ratio of the calcaneum, a bone of the rear ankle, is correlated with locomotor posture and habit and that its ecometric average in faunas sampled at 50 km intervals was correlated macrovegetation cover and ecological province at continental scale (Fig. 1). We used an expanded version of those data set to evaluate the correlation between mean gear ratio and five environmental and climatic factors. We conducted three Monte Carlo experiments to assess the effects on ecometric correlations of random local extirpation, random global extinction, and selective extirpation of large body sized species. We also evaluated the effect of the introduction of the small Asian mongoose *Her-*

pestes javanicus (also known in the literature as *H. auropunctatus*), has on ecometric correlations at the continental scale. This exotic species was introduced into the Caribbean in the mid-19th century, where it has become naturalized (Lowe *et al*. 2000). *Herpestes javanicus* is the only carnivoran in the Caribbean islands, making it the sole contributor to the local ecometric averages there, and the islands have a different climate and vegetation than most areas of the North America, thus this species has the potential to strongly influence ecometric correlations.

We expected that anthropogenic removal of species causes greater distortion to ecometric patterns than does the introduction of exotic species because extirpation is unlikely to be related to a particular ecometric trait (thus producing local assemblages that are not at "ecometric equilibrium"), whereas successful introduction of an exotic species is likely to be related because it must have traits compatible with its new habitat in order to flourish (thus reinforcing "natural" ecometric patterns). Our assessments are relevant to interpreting ecometric patterns from modern communities that have undergone anthropogenic alteration, paleoassemblages that have been altered by mass extinction, and fossil assemblages that affected by small sample sizes or systematic taphonomic biases.

Material and methods

Ecometric traits

The trait we used is the calcaneum "gear ratio", which is a single-bone proxy for the proportion of the out-lever to the in-lever of the hind foot (Polly 2010). Specifically, the gear ratio is the proportion of the maximum length of the calcaneum (measured from the medial tubercle to cuboid facet) to the position of the sustentacular facet (measured from the medial tubercle to the distal margin of the sustentacular process, where the latter intersects the body of the calcaneum) (Fig. 1B). This ratio is correlated with the metatarsal/femur ratio, the classic measure of digitigrady and locomotor mechanics in mammals (Gregory 1912, Garland & Janis 1993). The ratio ranges from one, which occurs if the sustentacular process was positioned at the extreme distal end of the calcaneum (which is not the case in any living mammal), and increases to infinity as the sustentacular process is positioned more proximally. In practice the ratio ranges from about 1.0 to 1.5 in living carnivorans (Polly 2010). The proportions of the limb are essentially a mechanical trade-off between power and speed of extension, with fleet-footed, digitigrade cursors having proportionally short in-levers and strong-limbed fossorial and arboreal species having proportionally longer ones (Gregory 1912, Hildebrand 1985). The in-lever of the ankle is the calcaneal process, onto which the gastrocnemius and soleus muscles insert. In extension, the upper ankle joint rotates between the tibia and astragalus, the latter of which fits against the calcaneoastragalar and sustentacular facets of the calcaneum (Fig. 1B). The length of the calcaneum relative to the position of the sustentacular facet is thus proportional to the length of the extension in-lever of the foot relative to the center of rotation of the ankle. Not only is the gear ratio positively correlated with both the metatarsal/femur ratio and with degree of digitigrady, but it is measured on a single, blocky bone that is commonly preserved in the fossil record, making the ratio useful for studying ecometric patterns in the paleontological record (Polly 2010).

Specimens

Calcaneum gear ratio was measured on 1857 museum specimens belonging to 46 species of Carnivora (Table 1). All but two terrestrial North American species are included in these data, missing only *Bassaricyon lasius* (Harris's Olingo) and *Spilogale pygmaea* (Pygmy spotted skunk). These species respectively occur in only 1 and 35 of the 9699 grid points that we used to sample North America, so their absence has only a minor effect on the ecometric patterns we measure. Our data include the measurements studied by Polly (2010).

Geographic sampling

Carnivoran faunas and environmental data were

Table 1. The species included in this study. The mean of skeletal measurements (*see* Fig. 1) and the mean of the calcaneal gear ratio are reported for each; *n* = sample size, D = digitigrade, S = semidigitigrade, P = plantigrade.

Species	*n* (2013)	*n* (2010) corr.	*n* (2010) publ.	Posture	Mass (kg)	Calcaneum (mm)	Sustentacular process (mm)	Gear ratio (2013)	Gear ratio (2010)
Herpailurus yaguarondi	11	1	1	D	5	30.8	23.1	1.33	1.33
Leopardus pardalis	16	4	2	D	12	38.8	28	1.39	1.40
Leopardus tigrinus	2	2	1	D	2.5	25	18.7	1.34	1.34
Leopardus wiedii	2	2	2	D	3.4	27.5	20.8	1.33	1.33
Lynx canadensis	3	3	2	D	12	47.8	35.2	1.36	1.36
Lynx rufus	222	11	4	D	10	42	30.6	1.37	1.41
Puma concolor	14	1	2	D	60	70.8	51.9	1.36	1.41
Panthera onca	14	1	1	D	80	60.6	46.4	1.28	1.31
Herpestes javanicus	2	2	1	S	0.43	13	10.37	1.25	1.25
Canis latrans	301	2	3	D	13	41.1	32.6	1.26	1.24
Canis lupus	22	2	2	D	45	57.9	46.3	1.25	1.28
Canis rufus	2	2	2	D	24	49.7	39.5	1.26	1.26
Speothos venaticus	6	2	2	D	5.5	25.7	21.9	1.17	1.17
Urocyon cinereoargenteus	285	49	2	D	3.5	27.4	21.8	1.26	1.27
Vulpes lagopus	16	7	1	D	3.2	28.3	21.5	1.32	1.33
Vulpes macrotis	4	2	1	D	2	22.5	17.5	1.29	1.29
Vulpes velox	6	2	2	D	2.3	25.3	20.6	1.23	1.23
Vulpes vulpes	37	28	2	D	4.5	32.9	26	1.27	1.26
Ursus americanus	5	4	49	P	100	63.6	55.8	1.14	1.15
Ursus arctos	4	3	4	P	130	88.5	78.8	1.08	1.13
Eira barbara	12	2	1	P	4.5	27	22.2	1.22	1.22
Galictis vittata	7	2	1	P	2.35	17.5	15	1.17	1.11
Gulo gulo	4	4	1	S	12	41.5	34.2	1.21	1.21
Martes americana	3	1	2	P	0.78	18.4	14.7	1.25	1.25
Martes pennanti	3	1	26	P	3	22	17.8	1.24	1.22
Mustela erminea	2	2	5	S	0.2	6.1	5.3	1.15	1.15
Mustela frenata	239	26	1	S	0.1	8.1	6.7	1.21	1.20
Mustela nigripes	2	2	22	S	0.8	13	11.3	1.15	1.15
Mustela nivalis	2	2	2	S	0.1	3.6	3	1.22	1.22
Neovison vison	23	22	2	S	1.2	12.3	10.6	1.17	1.17
Taxidea taxus	8	3	1	P	8	29.3	23.8	1.23	1.25
Lontra canadensis	3	2	1	S	8.5	27.4	21.9	1.25	1.30
Lontra longicaudis	2	2	2	S	9	23	18.9	1.22	1.22
Conepatus leuconotus	7	2	2	S	2	21.6	18.4	1.18	1.18
Conepatus semistriatus	10	2	3	S	1.2	19.8	17	1.16	1.16
Mephitis macroura	2	1	1	P	1	16.9	13.2	1.28	1.28
Mephitis mephitis	5	2	11	P	1.7	20.4	16.8	1.22	1.22
Spilogale gracilis	5	5	1	P	0.5	11.7	9.5	1.23	1.23
Spilogale putorius	5	3	1	P	0.78	12.1	9.9	1.22	1.22
Bassaricyon gabbii	10	2	42	P	1.07	17.9	14.3	1.25	1.25
Bassariscus astutus	13	2	1	S	0.9	16.2	13.2	1.22	1.27
Bassariscus sumichrasti	2	2	1	S	0.53	19.5	14.7	1.33	1.33
Nasua narica	5	5	1	P	4	28.9	23.4	1.23	1.23
Potos flavus	4	3	2	P	2.2	23.3	19.8	1.18	1.18
Procyon cancrivorus	4	4	5	S	8	37.8	31.4	1.21	1.21
Procyon lotor	503	42	3	S	7	28.7	23.4	1.22	1.24

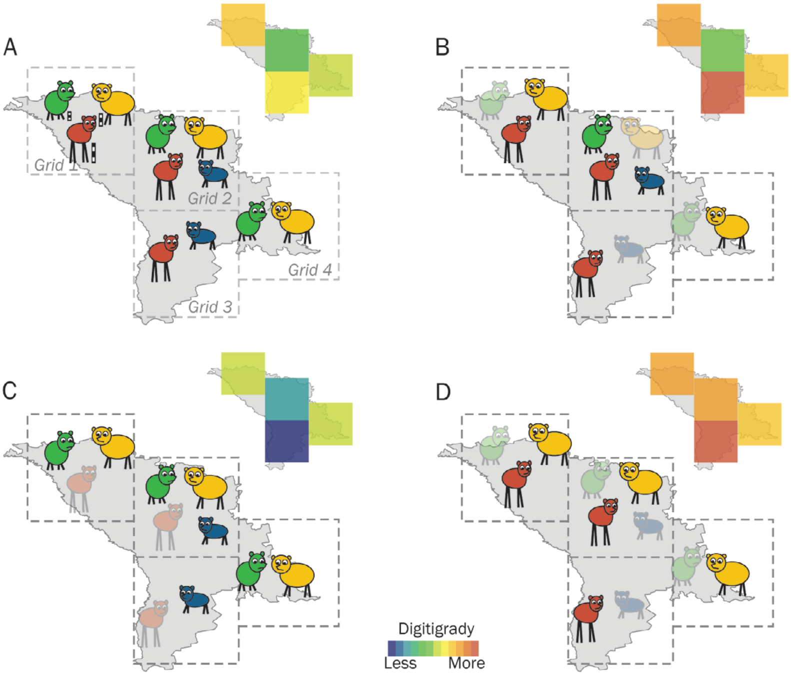

Fig. 2. The experiments performed in this paper. (**A**) Ecometric maps are created by sampling the species that occur at each 50 km grid point and averaging their calcaneum gear ratios. The ecometric map at the upper right is colored according to the mean of the species in the corresponding cell. (**B**) Experiment 1, in which species were dropped idependently at each grid point and the ecometric pattern recalculated. (**C**) Experiment 2, in which random sets of species were dropped from all grid points in which they occur and the ecometric pattern recalculated (the red species was randomly dropped in this example). (**D**) Experiment 3, in which species were dropped as in Experiment 2, but where the probability of being dropped was weighted by body mass (the smaller species were dropped in this cartoon).

sampled using a grid of points spaced evenly at 50 km intervals (Polly 2010). We used equally spaced points because the commonly used latitude and longitude grids are denser toward the poles and thus disproportionally weight high latitudes (Polly 2010, Polly & Eronen 2011). At this spatial resolution, there are 9699 grid points on the continent of North America; one or more carnivoran species occur at 8438 of them (8509 if the points where *Herpestes javanicus* occurs are included). A database of the 50 km points with their associated environmental data is available from the first author on request.

Ecometric means of local faunas

The ecometric mean of each 50 km grid point was calculated by averaging the gear ratio for all species whose geographic ranges intersect with it (Fig. 2A). Range data for North American carnivorans were taken from the *Digital Distribution Maps of the Mammals of the Western Hemisphere, 3.0* (http://www.natureserve.org/getData/mammalMaps.jsp) assembled by Bruce Patterson, Wes Sechrest, Marcelo Tognelli, Gerardo Ceballos for The Nature Conservancy Migratory Bird Program (Conservation International CABS, World Wildlife Fund US, and Environment Canada WILDSPACE) (Patterson *et al*. 2003). The digital range maps were compiled from published scientific sources, notably including Hall (1981) and Wilson and Ruff (1999), a complete list of which is packaged with the data. These geographic data include both historical ranges, as far as they are known, and areas where species have since been extirpated, making them maximal historical ranges. The ranges of some species, such as the wolf (*Canis lupus*), were probably even more extensive in pre-Columbian times than these maps indicate (Laliberte & Ripple 2004).

Environmental data

Correlation between the ecometric means and environmental factors was assessed by resampling four environmental data sets using the same 50 km grid point scheme and calculating coefficients of determination from the data points (*see* below for discussion about the effects of spatial autocorrelation).

Elevation data were resampled from the TerrainBase data set (Hastings & Dunbar 1998). TerrainBase contains elevation and ocean depth data in meters from mean sea level at 5-minute grid resolution. An elevation was assigned to each 50 km grid point from the value of the nearest neighbor point in the TerrainBase data.

Annual mean air temperature and precipitation were resampled from Willmott and Legate's (1988) database. This spatial data set was derived directly from original weather station observations (24 941 for temperature and 26 858 for precipitation) an interpolated by Willmott and Legate to a 0.5° × 0.5° grid using Shepard's distance-weighting method. We resampled their data using our 50 km grid points using the value of each of our point to its nearest-neighbor in Willmott and Legate's data.

Macrovegetation data were resampled from Matthews' *Global Distribution of Vegetation* (Matthews 1983, 1984). These data report dominant vegetation cover at one degree resolution, categorized using the UNESCO forest classification system which divides vegetation cover into 31 categories, such as tropical evergreen rainforest, cold-deciduous forest with evergreens, xeromorphic scrubland, or desert. The Matthews data classifies vegetation prior to human modification as far as possible. We assigned vegetation data to our 50 km grid points using each point's nearest-neighbor in the vegetation data set.

Ecoregion categories were resampled from Bailey (1998, 2004). These ecoregions are macroscale climatic areas defined primarily by seasonal interactions between temperature and precipitation and secondarily by dominant vegetation type. The regions are hierarchically arranged into Domains (four in North America), Divisions (28 in North America), and Provinces (59 in North America). For example, the eastern Kansas prairies belong to the humid temperate domain, the prairie division, and the forest-steppes and prairies division, whereas the east-central Texas prairies just to the south of the ones in Kansas belong to the humid temperate domain and the prairie division, but to the prairies and savannas province. Bailey's system, especially its larger hierarchical categories, is derived from Köppen (1931) and Dice (1943). We assigned an ecoregion to each of our 50 km grid points by intersecting the points with the ecoregion GIS layer available from the USDA Forest Service.

Ecometric correlations

For each of the five environmental factors, the coefficient of determination (R^2) was calculated to describe the proportion of the variance in mean calcaneum gear ratio associated with each factor. For elevation, annual precipitation, and mean annual temperature, all of which are continuous variables, R^2 was calculated simply by squaring the product-moment correlation (R). For macrovegetation and ecoregion, which are categorical variables, the variance in calcaneum gear ratio was partitioned into the sum-of-squares explained by the categories (SS_{model}) and residual sum-of-squares ($SS_{residual}$) using analysis of variance (ANOVA), from which R^2 was calculated as:

$$R^2 = SS_{model}/(SS_{model} + SS_{residual}) \tag{1}$$

Confidence intervals were calculated for R^2 using a bootstrap procedure (Manly 2007). To do this, geographic points were resampled 100 times with replacement and R^2 was recalculated. The 2.5 and 97.5 percentile values of the resulting distribution were used as to estimate 95% confidence intervals.

Spatial autocorrelation

Spatial autocorrelation is a potential source of spurious correlation between geographically distributed variables caused by the fact that points near one another tend to have similar values (Moran 1950, Cliff & Ord 1970, Clifford *et al*. 1989, Lennon 2000). We did not make any special effort to correct for autocorrelation, because it did not affect the interpretations we drew. Nevertheless, the reader should be aware that spatial autocorrelation may inflate ecometric correlation coefficients more with some environmental factors than others. For example, the ecological province variable, which is a categorical classification of geographically contiguous regions with similar climate and vegetation, has a lower spatial resolution than temperature, precipitation, elevation, or vegetation. The lower spatial resolution of the ecoregion data set will tend to inflate its correlation with the ecometric data relative to the other environmental data sets. In contrast, the temperature, precipitation, and elevation data have precisely the same spatial resolution, so any difference in correlation between them and the ecometric data is real, regardless of the effects of spatial autocorrelation. Because our focus is the effect of species sampling rather than the absolute values of the correlation coefficients and because the correlation between traits and environment is itself a spatial correlation, we did not adjust our data for these autocorrelation effects because of the risk of removing the very effect we were trying to study.

Effects of within-species sampling

In addition to exploring how the gain or loss of species affects ecometric correlations, we also assessed how within-species sampling affects the ecometric values of individual species and, consequently, the correlations between the ecometric means of local communities and environmental factors. Differences between the ecometric pattern in the original data set ($n = 276$ individuals representing 45 native terrestrial North American carnivorans and one exotic, *Herpestes javanicus*; (Polly 2010) and our expanded data ($n = 1857$ individuals representing the same 46 species) were assessed by comparing the changes in species mean and the local communities means at each of the 50 km grid points. First, the Pearson product-moment correlation (R) was calculated between the original and new mean point values. Second, anomalies between the two data sets were calculated by subtracting the new point values from the original ones and mapping the residuals. The anomaly map was visually inspected for patterns that would indicate a biased change in the geographic distribution of the mean gear ratio. Note that sample sizes were misreported in Polly (2010) because of a miss-sorted data column, as discussed below.

Randomization and rarefaction experiments

We conducted three experiments in which we simulated the effects of extinction on ecometric patterns by dropping species and recalculating the ecometric correlations. In the first experiment, we randomly dropped species at each grid point independently of which species were dropped at other points (Fig. 2B). This experiment simulated localized extinctions randomly distributed across the continent and mimicked the effects of either incomplete point sampling of modern faunas and randomly distributed taphonomic biases among fossils sites. In the second experiment, we randomly dropped species from all points at which they occur (Fig. 2C). This experiment simulated the effects of complete, but random extinction of species. In the third experiment, we dropped species from all points where they occur with a probability that was a function of their body mass (Fig. 2D). This experiment simulated the effect of selective extinction, such as occurred in the Late Pleistocene mass extinctions (Koch & Barnosky 2006) and is occurring today in a possibly localized fashion with large carnivores (Berger 1999, Laliberte & Ripple 2004), and of non-randomly distributed taphonomic biases in the fossil record (e.g., selective preservation of large or small body size taxa).

For these experiments, we used a modified form of rarefaction analysis (Sanders 1968, Simberloff 1972, Raup 1975), which is a type of statistical power analysis, to study the effect of species loss on ecometric correlation. For each experiment, we dropped species from the analysis, recalculated mean calcaneum gear ratio for each grid point, and recalculated the correlation between gear ratio and the five environmental variables. In all three experiments, we started by dropping one species and recalculating, continuing one by one until there were only three species left. In the first two experiments, the species that were dropped at each step were chosen completely randomly, whereas in the third experiment the species were chosen randomly but with the choice weighted by the natural logarithm of their body mass (as reported in Table 1) so that the likelihood of a species being dropped was proportional to ln(body mass). Specifically, the probability of selecting a species was weighted by –1 × ln(body mass) + 5, which produces a linear, positive weighting scale in which small body sizes are more likely to be included in the sample than large ones. Each step in the rarefaction was repeated 25 times to estimate the variance due to which particular species were dropped.

Results and discussion

Comparison of original and expanded data sets

Despite a nearly sevenfold increase in the number of individuals in our data set as compared with that in Polly (2010), neither the ecometric means of individual species nor the ecometric means of local faunas changed appreciably. Of the 32 species whose sample size (*n*) was larger in the 2013 data set, there was no change in the mean gear ratio of 14 and there was a maximum change of 0.06 in *Galictis vittata* (which included a change in a now-corrected mismeasurement in the original data) (Table 1). This result indicates that differences in calcaneum gear ratio between species are large enough that within-species means can be sufficiently estimated from relatively small numbers of individuals.

Note that sample sizes were misreported in Polly (2010). The sample size column of appendix 13.1 of that paper, which was added after review, was sorted alphabetically by species whereas the rest of the table was sorted by family. This mistake is evident in the discrepancy between the *n* reported in appendix 13.1 and table 13.3 of the 2010 paper. The sorting mistake had no impact on the other data or statistics reported by Polly (2010). We report the correct *n* for the 2010 data here (Table 1).

The expanded sample also had no appreciable impact on the ecometric correlations (Table 2). R^2 values were not significantly different between the data sets for any of the five environmental variables (as judged by the 95% confidence intervals). Furthermore, the correlation between data sets was very high ($R = 0.975$) when the mean values at each of the 50 km grid points were compared. The average change in mean gear ratio at corresponding grid points was 0.002, as compared with the range of 0.142 between grid points within the data set. To determine whether the changes, however small, were geographically biased anomalies were calculated by subtracting the new data set from the original. Increases in gear ratio tended to be scattered through the mountainous west and in the far north (driven by *Panthera onca*, *Canis lupus*, and *Vulpes lagopus*) and decreases tended to be in the northern Midwest and Great Plains (driven by *Vulpes vulpes* and *Lynx rufus*) (Fig. 3). However, the anomalies were small, the maximum being 0.05 and the minimum –0.01 (out of the total range of 0.142 between points). Thus, the large increase in the

Table 2. Comparison of R^2 of mean calcaneum gear ratio and five environmental variables from three data sets.

	Original data (without *H. javanicus*)		Expanded data (with *H. javanicus*)		Expanded Data (without *H. javanicus*)	
	R^2	95% CI	R^2	95% CI	R^2	95% CI
Elevation	0.07	0.06–0.07	0.06	0.056–0.073	0.07	0.056–0.080
Annual precipitation	0.01	0.01–0.02	0.03	0.022–0.036	0.02	0.016–0.033
Mean annual temperature	0.48	0.46–0.49	0.50	0.479–0.509	0.49	0.476–0.510
Vegetation	0.49	0.47–0.51	0.50	0.484–0.514	0.50	0.470–0.518
Ecological province	0.70	0.69–0.72	0.69	0.676–0.707	0.69	0.666–0.710

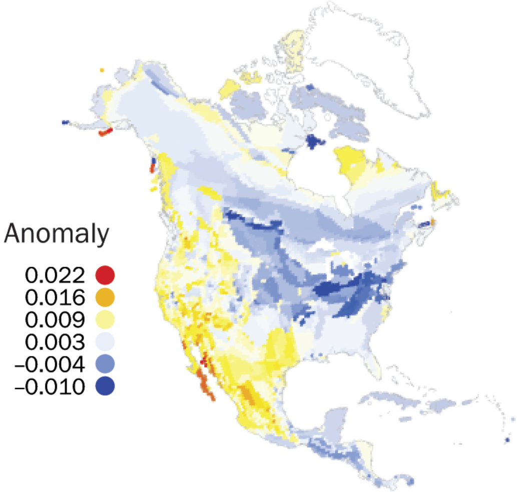

Fig. 3. Map showing anomalies in the mean gear ratio of carnivoran faunas between the 2010 data set and the current expanded one. Warm colors show where gear ratio increased, cold colors show where it decreased. The scale is comparable to that of Fig. 1D.

number of individuals used to estimate the ecometric pattern did very little to change it.

Strength of ecometric correlations

Visual inspection of the relationship between gear ratio and the five environmental variables helps understand the relative strengths of correlation and the effects of different patterns of extinction, as discussed below. The scatter plots in Fig. 4 show the striking distinction between the variables with strong and weak relationships to gear ratio: neither elevation nor annual precipitation have a relationship, but mean annual temperature, vegetation, and ecological province do, regardless of effects of spatial autocorrelation.

Experiment 1: random, independent local extinction

When the loss of species is independent at each grid point, the ecometric correlations decline steadily and predictably toward zero as more species are removed (Fig. 5A–J). In this experiment, species were selected randomly for extinction at each 50 km grid point from the list of all North American carnivorans and dropped from the calculation of the mean gear ratio at that point if they occurred there. The effect of extinction at one grid point was independent of the effects at others, modeling a situation in which the extirpation (or taphonomic recovery) of species differs locally from one point to the next. One can think of this model of extinction as randomly moving each data point in Fig. 4 independently, with the change proportional to the number of species used in the calculation. When most of the species are included in the analysis, the change at each data point is small and the basic pattern of correlation is preserved despite the noise introduced by local changes in species composition; however, when only a few species are included, the change at each data point is large and the basic correlation is lost.

Our results demonstrate that even when 50% of the species are lost in this fashion, the R^2 values for temperature, vegetation, and ecological province are substantially higher than for elevation and precipitation. This suggests that local taphonomy, local extirpation, or local errors in records of whether a species is present will not affect ecometric studies so long as the effects at each geographic point in the analysis are independent of one another. This pattern of preservation is likely to be the case in the fossil record, where each site has its own preservational idiosyncrasies (e.g., one site may be a carnivore den that selectively preserves medium size species, another may be a floodplain deposit that selectively preserves large species, and another may be an owl accumulation that selectively preserves small species); however, this pattern is unlikely in modern mammal faunas where extirpations and introductions tend to occur at regional scales.

Experiment 2: random global extinction

When the loss of species was global, the effect was quite different (Fig. 5K–T). In Experiment 2, species were randomly selected for extinction once from the North American faunal list and then excluded from the calculation of the ecometric mean at every grid point at which they occur. This experiment thus models global extinction of species.

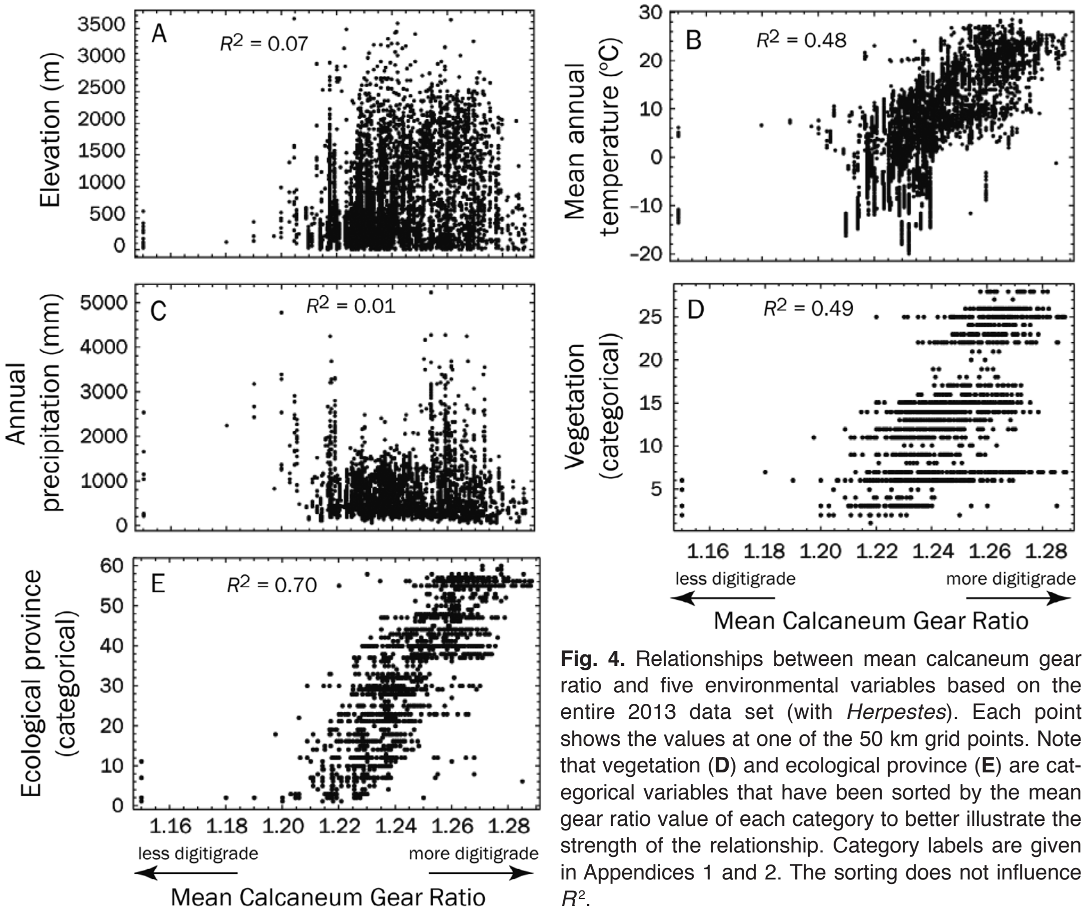

Fig. 4. Relationships between mean calcaneum gear ratio and five environmental variables based on the entire 2013 data set (with *Herpestes*). Each point shows the values at one of the 50 km grid points. Note that vegetation (**D**) and ecological province (**E**) are categorical variables that have been sorted by the mean gear ratio value of each category to better illustrate the strength of the relationship. Category labels are given in Appendices 1 and 2. The sorting does not influence R^2.

The effects of global extinction were far less predictable than local, independent extinctions. For variables whose real ecometric correlation is high (temperature, vegetation, and ecological province), the R^2 value could be higher or lower as a result of extinction, though more often lower. Nevertheless, even with only a few species remaining in the analysis, the expectation of R^2 remained high (i.e., the average R^2 when 40 species are extinct is similar to R^2 with no extinction). The reason for the unpredictable behavior is that each extinction affects a large and variable number of the data points, proportional to the size of the species' geographic range (which are listed in Appendix 3). Loss of a species with a large geographic range and with a gear ratio that is either especially low or especially high will affect the mean of many of the local assemblages. If some regions are systematically affected, for example, by the loss of an arctic species, the resulting shift could increase or decrease the ecometric correlation. For example, the jaguar, *Panthera onca*, a species with a high gear ratio, has a large distribution in the warmer southern part of the continent. Mean annual temperature is positively correlated with mean gear ratio (Fig. 4B). Loss of *P. onca* will tend to decrease the mean gear ratio at many of the geographic points where mean annual temperature is high, which will cause a decrease in the ecometric correlation. Conversely, the loss of the arctic fox, *Vulpes lagopus*, which is also comparatively digitigrade, would decrease the mean gear ratio at many of the coldest points, and thus increase in the ecometric correlation. Interestingly, the R^2 for temperature, a continuous variable, was often near 0.0 after ten or more species were extinct, whereas the R^2 for vegetation and ecological province, which are categorical variables, seldom dropped below 0.4. For variables whose real correlation is low, the

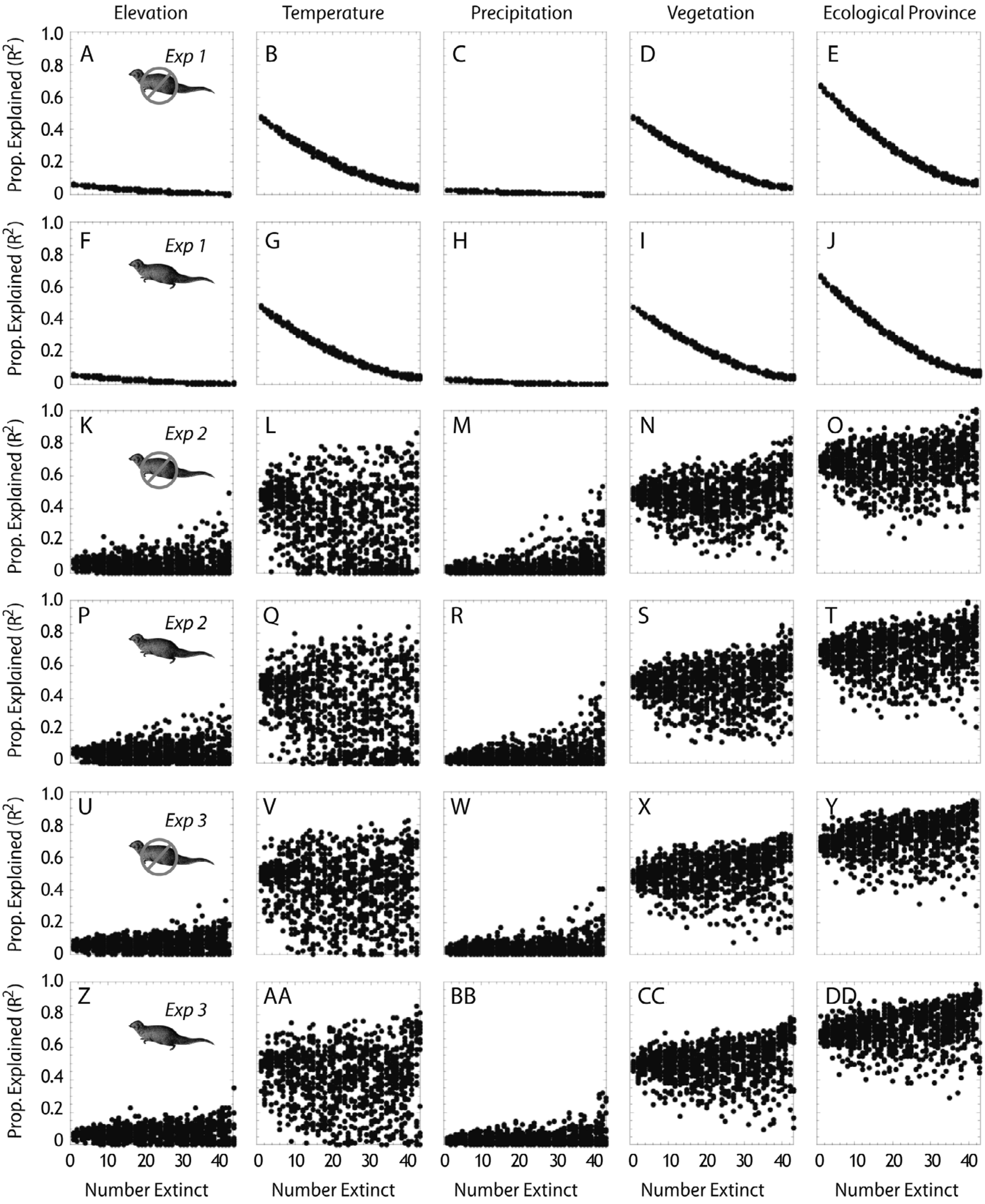

Fig. 5. Results of the three Monte Carlo experiments shown as rarefaction graphs (elevation, annual precipitation, mean annual temperature, macro-vegetation cover, and ecological region). The *x*-axis shows how many of the species were included in the calculation and the *y*-axis shows the proportion of variance of the mean gear ratio is explained by that variable (R^2). (**A**–**E**) Experiment 1 without *Herpestes javanicus* (independent extinction at each grid point). (**F**–**J**) Experiment 1 with *H. javanicus* (independent extinction at each grid point). (**K**–**O**) Experiment 2 without *H. javanicus* (random species-wide extinction). (**P**–**T**) Experiment 2 with *H. javanicus* (random species-wide extinction). (**U**–**Y**) Experiment 3 without *H. javanicus* (species-wide extinction weighted by body mass). (**Z**–**DD**) Experiment 3 with *H. javanicus* (species-wide extinction weighted by body mass).

effect of extinction often raised the R^2 value, but never much higher than 0.2.

Global extinction of species thus could have a profound effect on measuring ecometric patterns. Nevertheless, variables with a high and low ecometric R^2s will only be conflated when more than a quarter of the species are lost (i.e., 10 out of 45), and with categorical variables only after about three quarters are lost. Logically, the extirpation of species from large regions, such as has been the case with large carnivorans such as grizzlies, wolves, jaguars, and mountain lions, is likely to have a similar effect as the global extinctions modeled here. This suggests that if large regional extirpations affect more than a quarter of the fauna, ecometric patterns may be confounded.

Experiment 3: non-random global extinction

When the global loss of species was not random but related to body size, the effect on ecometric correlations was essentially the same as if the extinctions were random (Fig. 5U–DD). This result is interesting because it more realistically models real carnivoran extirpations, which have preferentially involved large predators, and the Late Pleistocene extinctions than the other experiments. The reason that body size filtering has no effect is because the correlation between gear ratio and body mass is complex. Many large carnivorans, such as canids and felids, tend to be digitigrade and have a high gear ratio, but at the same time the largest species (bears) are strongly plantigrade and have low gear ratios. Thus a bias in extinction by body size affects both extremes of the gear ratio and has very little effect on the overall pattern. If selection probability had been weighted by a factor with a stronger correlation to gear ratio, the outcome of this experiment might have been quite different.

The effect of exotic introductions

Herpestes javanicus is the only established exotic carnivoran in North America. To address whether its presence biases ecometric correlations, we conducted all our analysis with and without it. Its potential for biasing is strong because it is the only carnivoran to occur on many Caribbean islands, whose climatic and vegetation conditions are outliers for North America, and as a singleton taxon in these areas, it is the sole contributor to the ecometric mean in most of the areas where it was introduced. Nevertheless, its effect on ecometric correlations (Table 2) or the Monte Carlo experiments (Fig. 5) was minimal. For none of the five environmental variables did its inclusion cause the R^2 value to change by more than 0.01, hardly enough to have an appreciable affect and certainly not enough to make a strong correlation appear weak or vice versa.

There are three main reasons why *H. javanicus* does not have a strong impact on ecometric correlations. First, it is only one among 45 other species contributing to the ecometric patterns. The gain or loss of a single species is unlikely to change the relationship between mean locomotor morphology and environment in the North American carnivoran meta-community. Second, its geographic distribution includes only 73 of the 8509 grid points in North America (Appendix 3). Each grid point contributes equally to the correlation, and so the effect of *H. javanicus* is minimized even if its effect on the mean at those points is strong. Third, and most important for generalizing these results, the gear ratio value of *H. javanicus* (1.25) is typical of the areas where it has become naturalized: regions where mean annual temperature is warm, where vegetation consists of tropical and subtropical formations, and in tropical and subtropical maritime provinces (cf. Fig. 4). Thus, even if it formed a greater proportion of the carnivoran fauna and was distributed more widely, it would be compatible with the ecometric results derived from other species. Note that while an introduced species may not have an effect on ecometric patterns, it may well have an effect on local ecosystems.

Conclusions

We found that the effects of extinction, extirpation, and range changes have a minimal effect on ecometric correlations when they affect no more than a quarter of the species. At a continental scale, correlations between calcaneum gear ratio, an index that represents one aspect of average locomotor specialization within a local community, are either very strong (as with mean annual temperature, vegetation cover, or ecological province) or very weak (as with elevation and annual precipitation). The gain or loss of even more than a quarter of species does not alter the ecometric correlations enough to prevent weakly and strongly correlated environmental variables from being distinguished, even though extinctions alter the correlations.

The effects of independent local extinctions are different from global extinctions. Independent local extinctions always cause a decline in ecometric correlations and the amount of decline has a strong curvilinear relation to the proportion of the species that are affected. Despite the downward bias in correlation, up to three quarters of species can be dropped from the analysis with this mode of extinction without danger of misidentifying variables with high or low ecometric correlation. This result indicates that ecometric correlations can safely be estimated from fossil assemblages in most cases, because taphonomic and other preservational biases are usually independent from site to site. Even when only a small proportion of the total fauna is represented in the assemblages, our results suggest that the overall ecometric pattern will be recoverable. Indeed, the tight relationship between the number of species and the expected drop in R^2 suggests that the real correlation can be estimated from fossil data using rarefaction methods.

The effects of global extinction and large-scale extirpation have a stronger effect on ecometric correlations. The loss of species with large geographic ranges, which are typical in mammals, potentially affects geographic points across a large proportion of the continent. If that species is a significant contributor to local ecometric means and if its range is correlated with one or the other extreme of the environmental variable, its loss could drive the measured correlation up or down, depending on the circumstances. Thus, the effects of global extinctions have a less predictable effect on ecometric patterns than local extinctions. However, with global extinctions the statistical expectation of R^2 does not change as species are lost. This means that loss of species increases the uncertainty with which R^2 is known, but it does not bias it in any particular direction, unlike local extinction, which biases R^2 downward.

We found that selective extinction where the probability of losing a species is proportional to its body size has the same effect on ecometric correlations as does purely random extinction, at least in regard to calcaneum gear ratio. This result would likely be different if the ecometric trait in question had a more direct relationship to body size (metabolic rate or diet, for example).

Finally, the introduction of exotic species, at least in small numbers, has only minor effects on ecometric correlations. Impact of exotics is minimized when they form a small proportion of the total continental fauna and when they have invaded only small parts of a continent. Exotics succeed in establishing themselves only when their traits are compatible with their new environments, which means that their impact on ecometric correlations is also minimized because they are expected to be congruent with the pre-established pattern. The success of the exotics may, of course, have profound effects on local ecosystem functions even when they do not affect ecometric correlations.

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This paper is dedicated to Mikael Fortelius, friend and mentor. He, arguably more than anyone else, developed the ecometric insights that underpin the work in this paper through his work on regional patterns in hypsodonty. His tireless efforts at communicating ideas and bringing people together have made a significant impact on the fields of vertebrate paleontology and climate change biology. Ernie Lundelius inspired this paper by asking what happens when bears are driven out of the wilderness. He pointed out to us that in the 19th century bears, the most plantigrade of carnivorans, were extirpated from the Texas hill country and asked how this affected the correlation between digitigrady and environment in North America. We would like to thank Dean Adams, Jessica Blois, Allison Bormet, Jussi Eronen, Jason Head, Christine Janis, Michelle Lawing, Ernie Lundelius, Pasquale Raia, and an anonymous reviewer for discussions that improved this paper. We thank Jussi Eronen, Jukka Jernvall, Anu Kaakinen, Pirkko Ukkonen, and Suvi Viranta for organizing this volume and improving our manuscript. Allison Bormet and Michelle Lawing collected some of the data we analyzed. We thank Janet Braun (Oklahoma Museum of Natural History), Robert Fisher (Smithsonian Institution), Olavi Grönwall (Naturhistoriska riksmuseet, Sweden), Benjamin Hess (North Carolina State Museum of Natural Sciences), Randall Irmis (Utah Museum of Natural History), Ernie Lundelius (University of Texas, Austin), Lee Lyman (University of Missouri, Columbia), Lyn Murray (University of Texas, Austin), Francisco Pastor Vázquez (Universidad de Valladolid), Cindy Ramotnik (University of New Mexico, Museum of Southwestern Biology), Ron Richards (Indiana Stat Museum), Matthew Rowe (William Adams Zooarchaeology Collection, Indiana University), Laura Scheiber (William Adams Zooarchaeology Collection, Indiana University), Norm Slade (University of Kansas), William Stanley (Field Museum of Natural History), Jeff Stephenson (Denver Museum of Nature and Science), Phil Myers (Museum of Zoology, University of Michigan, Ann Arbor), and Eileen Westwig (Department of Mammalogy, American Museum of Natural History) for access to specimens and data in their care. This work was supported by a grant from the US National Science Foundation (EAR-0843935) and is a contribution to the Integrative Climate Change Biology (iCCB) program of the International Union of Biological Sciences.

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Appendix 1. Labels for vegetation types shown in Fig. 4D.

28	tropical/subtropical drought-deciduous woodland
27	tropical/subtropical evergreen needle-leaved forest
26	xeromorphic forest/woodland
25	xeromorphic shrubland/dwarf shrubland
24	tropical evergreen rainforest
23	trop/subtropical evergreen seasonal broad-leaved forest
22	drought-deciduous shrubland/thicket
21	evergreen broadleaved sclerophyllous woodland
20	tropical/subtropical drought-deciduous forest
19	evergreen broadleaved sclerophyllous forest
18	evergreen broadleaved shrubland/thick
17	tall/medium/short grassland
16	evergreen needleleaved or microphyllous shrubland/thicket
15	tall/medium/short grassland
14	meadow
13	medium grassland
12	tall/medium/short grassland
11	cold-deciduous forest
10	desert
9	cold-deciduous forest
8	tall grassland
7	evergreen needleleaved woodland
6	temperate/subpolar evergreen needle-leaved forest
5	ice
4	cold-deciduous woodland
3	arctic/alpine tundra
2	forb formations
1	cold-deciduous subalpine/subpolar shrubland/dwarf shrub

Appendix 2. Labels for ecological provinces showing in Fig. 4E.

60	Oceanic semideserts
59	Desert or semidesert–open woodland or shrub–desert or steppe
58	Shrub or woodland–steppe–meadow
57	Forest–steppe
56	Open woodlands, shrubs, and savannas
55	Deserts on sand
54	Semi-evergreen forests
53	Semidesert–shrub–open woodland–steppe or alpine meadow
52	Open woodland–deciduous forest–coniferous forest–steppe or meadow
51	Mediterranean hardleaved evergreen forests, open woodlands and shrub
50	Deciduous forests
49	Semi-evergreen and evergreen forests
48	Evergreen forest–meadow or paramos
47	Semideserts and deserts
46	Mediterranean woodland or shrub–mixed or coniferous forest–steppe or meadow
45	Evergreen forests
44	Coniferous open woodland and semideserts
43	Steppe or semidesert–mixed forest–alpine meadow or steppe
42	Semidesert–open woodland–coniferous forest–alpine meadow
41	Prairies and savannas
40	Semideserts
39	Dry steppe
38	Shortgrass steppes
37	Steppe–coniferous forest–tundra
36	Coniferous-broadleaved semi-evergreen forests
35	Lower Mississippi Riverine Forest Province
34	Redwood forests
33	Broadleaved-coniferous evergreen forests
32	Mixed forest–coniferous forest–alpine meadow
31	Steppes and shrubs
30	Steppes
29	Dry steppes
28	Deciduous or mixed forest–coniferous forest–meadow
27	Polar desert
26	Broadleaf forest–meadow
25	Forest-steppe–coniferous forest–meadow–tundra
24	Mixed forest–meadow
23	Steppe–open woodland–coniferous forest–alpine meadow
22	Mixed forests
21	Broadleaved forests, continental
20	Glacial ice
19	Mixed forest–coniferous forest–tundra, medium
18	Mixed deciduous-coniferous forests
17	Steppe–coniferous forest
16	Forest-steppes and prairies
15	Mixed forest–coniferous forest–tundra, high
14	Broadleaved forests, oceanic
13	Ice and stoney deserts
12	taiga (boreal forests)
11	Arctic tundras
10	Forest-tundras and open woodlands
9	Tundra–polar desert
8	Taiga–tundra, high
7	Tundras
6	Tundra–meadow
5	Open woodland–tundra
4	Taiga–tundra, medium
3	Forest–meadow, high
2	Forest–meadow, medium
1	Oceanic meadow–heath

Appendix 3. Geographic range size of North American carnivorans expressed in number of 50 km grid points at which they occur and in square kilometers.

Number of grid points	Area (km^2)	Taxon
6800	17 000 000	*Canis latrans*
6399	15 997 500	*Vulpes vulpes*
5282	13 205 000	*Mustela erminea*
5258	13 145 000	*Neovison vison*
4893	12 232 500	*Mephitis mephitis*
4728	11 820 000	*Lontra canadensis*
4649	11 622 500	*Procyon lotor*
4400	11 000 000	*Mustela nivalis*
4358	10 895 000	*Mustela frenata*
4023	10 057 500	*Canis lupus*
3861	9 652 500	*Lynx rufus*
3828	9 570 000	*Ursus americanus*
3397	8 492 500	*Urocyon cinereoargenteus*
3290	8 225 000	*Lynx canadensis*
3185	7 962 500	*Gulo gulo*
3044	7 610 000	*Taxidea taxus*
3033	7 582 500	*Martes americana*
2943	7 357 500	*Puma concolor*
2084	5 210 000	*Ursus arctos*
1917	4 792 500	*Vulpes lagopus*
1556	3 890 000	*Bassariscus astutus*
1531	3 827 500	*Spilogale gracilis*
1383	3 457 500	*Martes pennanti*
1175	2 937 500	*Spilogale putorius*
1001	2 502 500	*Mustela nigripes*
919	2 297 500	*Nasua narica*
889	2 222 500	*Panthera onca*
792	1 980 000	*Canis rufus*
716	1 790 000	*Mephitis macroura*
709	1 772 500	*Vulpes macrotis*
675	1 687 500	*Leopardus pardalis*
516	1 290 000	*Eira barbara*
498	1 245 000	*Lontra longicaudis*
470	1 175 000	*Leopardus wiedii*
465	1 162 500	*Herpailurus yaguarondi*
397	992 500	*Potos flavus*
296	740 000	*Galictis vittata*
266	665 000	*Vulpes velox*
245	612 500	*Bassariscus sumichrasti*
193	482 500	*Conepatus semistriatus*
89	222 500	*Conepatus leuconotus*
73	182 500	*Herpestes javanicus*
30	75 000	*Bassaricyon gabbii*
30	75 000	*Procyon cancrivorus*
2	5 000	*Speothos venaticus*
2	5 000	*Leopardus tigrinus*
8509	**21 272 500**	**North America**