



Using palaeontological data to assess mammalian community structure: Potential aid in conservation planning

M. Allison Stegner^{*}, Michael Holmes

Department of Integrative Biology, University of California, Berkeley, CA 94720, USA
 Museum of Paleontology, University of California, Berkeley, CA 94720, USA
 Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

ARTICLE INFO

Article history:

Received 1 February 2012
 Received in revised form 14 April 2012
 Accepted 17 April 2012
 Available online 3 May 2012

Keywords:

Functional groups
 Northern Great Plains
 Mammals
 NEOMAP

ABSTRACT

Taxon-free metrics of biodiversity health are crucial for present and future conservation efforts in the face of current global change. We investigated the distribution of species in combined diet and body size functional groups over the past 16 Ma in the Northern Great Plains to establish a pre-Holocene (before 11,000 ya, when humans arrived in North America) and pre-industrial baseline (11,000–500 ya) of this measure of community structure. Functional group distributions were compared on two scales to gauge the impact of time-averaging on patterns of community structure change: 1) North American Land Mammal Ages (NALMAs), and 2) individual diverse localities. Distributions were statistically compared using pairwise Fisher's exact tests with Monte Carlo P-value simulations and Holm P-value adjustment, and qualitatively assessed using correspondence analysis. When averaged over entire NALMAs, major changes in functional group distribution only take place in the Hemphillian, and at the start of the Holocene. Locality-level patterns also indicate long periods of stasis in the metric (Barstovian–Clarendonian and Hemphillian–Holocene). A threshold of global climate change is one possible explanation for the change that began in the Hemphillian, but further study is needed in that regard. Extinction of megaherbivores (>44 kg) is the primary driver of apparent differences between the Holocene and previous time periods. Although the extent of time-averaging and other taphonomic biases affect the details of observable patterns per time period, overall, proportional diversity of functional groups is a promising metric for assessing mammalian community health because it is remarkably stable through time and changes only with major external perturbations to ecosystems.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Rapid climate change today is causing local and regional habitats to shift across the landscape (Burrows et al., 2011). However, species are often prevented from tracking their preferred abiotic conditions because of the human-modified landscapes (e.g. urbanization, ranching) that surround protected lands. Consequently, managing for individual species is becoming increasingly problematic, and mandates strategies that focus on managing for ecosystem properties and functions. In light of these conservation needs, it is critical to identify metrics of community structure that can be measured and monitored through the past to establish baselines of “normal,” which can provide management benchmarks today and into the future. The fossil record is invaluable in this regard because it chronicles community structure and change over meaningful time scales and through past natural environmental changes.

Community structure has been approached quantitatively from a number of different angles: taxonomic composition (Hadly, 1996; Grayson, 1998; Grayson and Madsen, 2000; Hadly and Maurer, 2001; McGill et al., 2005; Blois et al., 2010), relative abundance (Hadly, 1996; Hadly and Maurer, 2001; Barnosky et al., 2004; Hadly et al., 2004), species richness (Grayson, 1998; Barnosky and Carrasco, 2002; Barnosky et al., 2003), evenness (Blois et al., 2010; Harnik, 2009), species–area relationships (Barnosky et al., 2005; Carrasco et al., 2009), and size and trophic structure (Badgley and Fox, 2000; Barnosky and Shabel, 2005; Rodríguez et al., 2006). Such metrics have already provided major insights. For example, “ecometrics” that relate functional traits like average community tooth height (Fortelius et al., 2002; Eronen et al., 2010b) or carnivoran locomotor morphology (Polly, 2010) to environment type (Eronen et al., 2010a; Polly et al., 2011) are useful for predicting response of communities to climate change. Another example is that Great Basin and Rocky Mountain species follow a nested subset pattern in both space and time, meaning that species' identities and relative abundances are non-random (Hadly and Maurer, 2001): this information can be used to predict which species are most likely to decline or face extirpation in a given region based on how common they are.

^{*} Corresponding author at: University of California Museum of Paleontology, 1101 Valley Life Science Building Berkeley, CA 94720–4780, USA. Tel./fax: +1 510 643 6275. E-mail address: astegner@berkeley.edu (M.A. Stegner).

The term functional group, sometimes also called “guild”, is used to describe organisms that fill the same ecological roles with respect to one or several important attributes, like diet, body size, or locomotor type. The utility of the functional group concept is largely due to the fact that these functional attributes cross taxonomic, geographic, and temporal boundaries. Functional groups are common as a means of portraying modern mammal communities (Badgley and Fox, 2000; Reed et al., 2006; Rodríguez et al., 2006; Muldoon and Goodman, 2010; Rowe et al., 2011; Terry et al., 2011), but have been used in palaeontology as well. One particularly well-studied example is the replacement of browsing with grazing ungulates as aridity increased and C4 grasslands became wide-spread during the Miocene (Janis et al., 2000; Janis et al., 2004; Wang et al., 1994). The idea of functional groups has also been relevant for the study of extinction selectivity (e.g., Quaternary megafauna: Koch and Barnosky, 2006; end-Triassic infaunal versus epifaunal bivalves: McRoberts and Newton, 1995) and for identifying palaeo habitat types (e.g., carnivore locomotor mode: Polly, 2010; leaf margin analysis: Burnham et al., 2001; Greenwood, 2005).

Diet and body size are important functional attributes of species that are independent of species identity, and are easy to define for both extinct and extant species. Gross diet categories can be determined from tooth morphology (Hillson, 2005), and linear skeletal dimension/body size relationships are well established for most major mammalian groups (Damuth and McFadden, 1990). These attributes are taxon independent, which facilitates comparisons between communities at different points in time or space that may not share the same species. Here, we use such criteria to investigate the proportion of species in body size and trophic categories in the Northern Great Plains (NGP) over the past 16 Ma. Other studies have documented relationships between environmental clines or abiotic factors and spatial differences in the distribution of species in diet and body size groups (Badgley and Fox, 2000; Terry et al., 2011); however, using combined diet and body size functional groups, as we have done in this study, is less common (but see Eisenberg, 1981; Rodríguez et al., 2006).

We established both a pre-Holocene (prior to 11,000 ya, i.e. before humans were abundant in North America) and pre-industrial baseline (between 11,000 and 500 ya, or Holocene) for comparison to the modern NGP mammalian fauna, in order to address two primary questions: 1) has mammalian community structure changed over the last 16 Ma; and 2) are differences in community structure driven by particular functional groups? We expect that climate change through time should be correlated with changes in the mammalian community structure based on spatial trends (Eisenberg, 1981; Badgley and Fox, 2000; Rodríguez et al., 2006; Terry et al., 2011). Because modern and fossil data are subject to different sampling biases, we also discuss how sampling differences affect our interpretations.

2. Study area and climate

The fossil record in the NGP is fairly complete for the period of our study, which encompasses the Barstovian NALMA through the Holocene. The geographic boundaries of the NGP follow Carrasco et al. (2009). The province has been tectonically stable through the Cenozoic, and has remained faunally distinct from other biogeographic provinces for more than 16 Ma (Prothero, 1998; Carrasco et al., 2009). It is bordered by the foothills of the Rockies on the west and the North Platte River to the south. The northern and eastern boundaries are defined by the geographic extent of the mammalian fauna characteristic of the NGP. Generally speaking, the modern NGP is an arid grassland with scattered patches of badlands and woodland. Precipitation seasonality in the NGP is high, with most rain falling between April and September, and drought during the winter months. Multi-year drought cycles are also characteristic of the Plains. Annual temperatures are seasonal, with very hot summers (commonly > 37.8 °C) and extremely cold winters (as low as –40 °C) (Barker and Whitman, 1988).

The earth experienced high overall temperatures from 18 to 14 mya, a period called the Mid-Miocene Climatic Optimum (MMCO); this was followed by a long-term cooling trend that began suddenly around 14 mya. From 8 to 6 mya, the replacement of C3 by C4 grasslands indicates not only a major floral change but also increased and widespread aridity (Axelrod, 1985; Cerling et al., 1997; Janis et al., 2000). Around 6 mya, world climate experienced a major perturbation that had widespread effects, like the Messinian Salinity Crisis; also near this time was one of the four most pronounced extinction peaks for mammals during the Cenozoic. The cooling trend continued until the mid-Pliocene, when there was another period of sustained warmth from 4.5 to 3 mya; temperatures at this time were only slightly warmer than today, but the temperature gradient from pole to equator was less extreme. Continued cooling initiated the high-amplitude glacial–interglacial cycles that characterize the Quaternary (Cronin, 2010). Much of the northern reach of the Plains (primarily Canada) was glaciated during the Pleistocene (Barker and Whitman, 1988).

3. Methods

3.1. Diet and body size distributions

Fossil data were obtained from the NEOMAP database (FAUNMAP Working Group, 1994; Carrasco et al., 2005; Graham and Lundelius, 2010) for the Barstovian through the Holocene, and modern data were extracted in ArcGIS using Digital Distribution Maps of the Mammals of the Western Hemisphere Version 3.0 (Patterson et al., 2003). We resolved species synonymies using the synonymy tables in the Paleobiology Database (Alroy, 2003), removed records for species considered *nomen dubium*, *nomen vanum*, or *nomen nudum*, and also excluded chiropterans. The geographic location of the NGP was determined according to Carrasco et al. (2009). Diet and body size were defined according to Table 1, and designations were based on information available in the Paleobiology Database, Mammalian Species Index, and other literature sources (Appendix 1). We used these body size categories for continuity with Barnosky and Shabel (2005) and Koch and Barnosky (2006). All species in a genus were assigned the same diet and body size class. We recognize that it is possible for congeneric species to have different diets and body sizes, but this is relatively uncommon in modern mammals and our categories are general enough as to render this possibility negligible in affecting our conclusions.

For differences between communities averaged over long time-spans, we binned fossil occurrence records for the Barstovian, Clarendonian, Hemphillian, and Rancholabrean NALMAs, and for the Holocene and modern. The Irvingtonian and Blancan fossil records for the NGP are too poor—both species richness and number of localities are low compared to other time periods (Table 2)—to yield meaningful information regarding community structure. Modern data are subject to very different sampling biases (discussed in Section 5) (Carrasco, 2013–this issue) and so it is included here for exploratory purposes only.

Table 1
Categories used to define diet and body size.

Functional category	Example
Herbivore	Elk— <i>Cervus canadensis</i>
Carnivore	Coyote— <i>Canis latrans</i>
Omnivore	Ringtail— <i>Bassariscus astutus</i>
Granivore	Flying Squirrel— <i>Glaucomys sabrinus</i>
Insectivore	Shrew— <i>Blarina brevicauda</i>
>44 kg “XL”	Bison— <i>Bison bison</i>
8–44 kg “L”	American beaver— <i>Castor canadensis</i>
0.5–8 kg “M”	American marten— <i>Martes americana</i>
<0.5 kg “S”	Ord’s kangaroo rat— <i>Dipodomys ordii</i>

Table 2
Number of fossil localities and species richness per NALMA for the Northern Great Plains.

Time period	Interval length	No. sites	Species richness
Holocene	0.011 Ma	100	110
Rancholabrean	0.229	57	125
Irvingtonian	3.1	15	81
Blancan	3.5	28	83
Hemphillian	4.4	66	122
Clarendonian	3.3	283	134
Barstovian	3.4	200	179

We also wanted to examine these patterns on a finer scale. However, commonly-used million year bins were insufficiently suited to this task for a number of reasons. First, million year bins may over-estimate the actual dating precision of localities in our dataset because the difference between the minimum and maximum age estimates for each locality in our dataset is greater than 1 my for the majority of records; also, the error bars around a locality's age may bridge two or more time bins. Furthermore, NALMAs represent biologically meaningful groupings that do not change markedly from beginning to end—million year bins, in contrast, are arbitrary delineations with arguable biological

basis (Barnosky et al., 2005). Finally, million year bins do not contain enough data on the geographical scale of biogeographic provinces (Barnosky et al., 2005; Carrasco et al., 2009; Carrasco, 2013—this issue). Instead, we based our finer-scale analysis on selected individual localities with a minimum of 25 species, at least 10 of which are small-bodied (see Table 3). Localities were also compared to the NALMA distributions from which they were drawn, to determine if a given locality was significantly different from the NALMA overall; i.e., is the locality typical for the time period?

We summed the number of species in each diet and body size category for each time interval, and standardized by total species richness per interval. Generic occurrences without species-level identifications (where the specimen was identified to genus but not to species) were only included for intervals where the genus was not represented by other occurrences with species-level designations (Alroy, 1996; Barnosky and Carrasco, 2002). We used pairwise Fisher's exact tests (with a Monte Carlo P-value simulation, 5000 replicates, and Holm p value adjustment for multiple comparisons) on the uncorrected distributions of functional groups (raw counts of species per group per locality or per NALMA) to compare community structure at different time intervals and among localities. Monte Carlo analysis randomly reassigns group membership of the observed data in order to test the

Table 3
Species richness by functional group, as number of species (top) and proportional richness (bottom, bold) for individual localities, the modern, Holocene, and NALMAs. XLH: >44 kg herbivores; LH: 8–44 kg herbivores; MH: 0.5–8 kg herbivores; SH: <0.5 kg herbivores; LC: >8 kg carnivores; MC: 0.5–8 kg carnivores; SC: <0.5 kg carnivores; LO: >8 kg omnivores; MO: 0.5–8 kg omnivores; SO: <0.5 kg omnivores; SG: <0.5 kg granivores; MI: 0.5–8 kg insectivores; SI: <0.5 kg insectivores.

Locality	NALMA	Age (ma)	XLH	LH	MH	SH	LC	MC	SC	LO	MO	SO	SG	MI	SI	Total richness
Modern	Modern	500 ya–present	5	2	10	26	3	8	4	1	3	2	22	2	14	102
			0.049	0.020	0.098	0.255	0.029	0.078	0.039	0.010	0.029	0.020	0.216	0.020	0.137	
Holocene	Holocene	0.011–present	13	2	15	26	9	6	5	4	2	6	14	1	7	110
			0.118	0.018	0.136	0.236	0.082	0.055	0.036	0.018	0.036	0.018	0.055	0.127	0.009	0.064
Rancholabrean	Rancholabrean	0.011–0.15	32	3	13	26	12	7	3	2	0	1	11	1	14	125
			0.256	0.024	0.104	0.208	0.096	0.056	0.024	0.016	0	0.008	0.088	0.008	0.112	
Hemphillian	Hemphillian	5.9–9	36	8	8	22	19	5	3	3	1	2	5	0	10	122
			0.295	0.066	0.066	0.189	0.156	0.041	0.025	0.025	0.008	0.016	0.033	0.000	0.082	
Clarendonian	Clarendonian	9–12.5	46	10	16	12	16	9	0	0	3	1	13	0	8	134
			0.343	0.104	0.090	0.090	0.119	0.067	0.000	0.000	0.022	0.007	0.097	0.000	0.060	
Barstovian	Barstovian	12.5–15.9	57	11	15	22	21	17	1	4	4	0	19	0	8	179
			0.318	0.061	0.084	0.123	0.117	0.095	0.006	0.022	0.022	0.000	0.106	0.000	0.045	
Schmidt	Holocene	795–830 ya	2	2	4	6	5	2	2	0	0	1	5	1	3	33
			0.061	0.061	0.121	0.182	0.152	0.061	0.061	0.000	0.000	0.030	0.152	0.030	0.091	
Beaver Creek Shelter	Holocene	2220–3890 ya	2	0	2	10	0	0	0	0	0	2	8	0	2	26
			0.077	0.000	0.077	0.385	0.000	0.000	0.000	0.000	0.000	0.077	0.308	0.000	0.077	
Jones-Miller	Rancholabrean	0.01	1	0	2	10	2	4	2	0	0	1	6	1	7	36
			0.028	0.000	0.056	0.278	0.056	0.111	0.056	0.000	0.000	0.028	0.167	0.028	0.194	
North Cove	Rancholabrean	0.01	3	0	3	10	0	2	0	0	0	1	5	0	4	28
			0.107	0.000	0.107	0.357	0.000	0.071	0.000	0.000	0.000	0.036	0.179	0.000	0.143	
Little Box Elder Cave	Rancholabrean	0.01–0.02	9	2	5	14	7	4	2	1	0	2	2	1	3	52
			0.173	0.038	0.096	0.269	0.135	0.077	0.038	0.019	0.000	0.038	0.038	0.019	0.058	
Kanopolis Local Fauna	Irvingtonian	1.8–1.5	7	1	3	4	2	0	0	0	1	0	5	1	2	26
			0.269	0.038	0.115	0.154	0.077	0.000	0.000	0.000	0.038	0.000	0.192	0.038	0.077	
Sand Draw	Blancan	4.7–1.8	5	1	3	11	5	3	1	0	0	0	3	0	3	35
			0.143	0.029	0.086	0.314	0.143	0.086	0.029	0.000	0.000	0.000	0.086	0.000	0.086	
Devil's Nest Quarry	Hemphillian	4.7–5.9	8	1	3	8	2	1	2	0	0	1	0	0	1	27
			0.296	0.037	0.111	0.296	0.074	0.037	0.074	0.000	0.000	0.037	0.000	0.000	0.037	
Bluejay Quarry	Clarendonian	9.5–11.5	9	2	4	3	1	0	0	0	0	0	5	0	3	27
			0.333	0.074	0.148	0.111	0.037	0.000	0.000	0.000	0.000	0.000	0.185	0.000	0.111	
Pratt Quarry	Clarendonian	9.5–11.5	3	1	5	7	2	0	0	0	0	1	5	0	2	26
			0.115	0.038	0.192	0.269	0.077	0.000	0.000	0.000	0.000	0.038	0.192	0.000	0.077	
Annie's Geese Cross	Barstovian	12.5–13.6	7	1	1	6	2	1	1	0	1	0	6	0	5	31
			0.226	0.032	0.032	0.194	0.065	0.032	0.032	0.000	0.032	0.000	0.194	0.000	0.161	
Myers Farm	Barstovian	12.5–13.6	8	4	1	6	2	4	0	1	0	0	2	0	5	33
			0.242	0.121	0.030	0.182	0.061	0.121	0.000	0.030	0.000	0.000	0.061	0.000	0.152	
Egelhoff Quarry	Barstovian	13.6–14	3	2	0	7	0	1	1	1	0	0	6	0	4	25
			0.12	0.08	0	0.28	0	0.04	0.04	0.04	0	0	0.24	0	0.16	
Immense Journey Quarry	Barstovian	13.6–14	7	1	2	6	0	1	0	0	0	0	6	0	5	28
			0.250	0.036	0.071	0.214	0.000	0.036	0.000	0.000	0.000	0.000	0.214	0.000	0.179	
Carrot Top Quarry	Barstovian	13.6–14	11	1	1	3	0	0	0	0	1	0	5	0	4	26
			0.423	0.038	0.038	0.115	0.000	0.000	0.000	0.000	0.000	0.038	0.000	0.192	0.000	0.154
Norden Bridge Quarry	Barstovian	13.6–14	16	4	2	10	4	6	1	0	1	0	9	0	5	58
			0.276	0.069	0.034	0.172	0.069	0.103	0.017	0.000	0.017	0.000	0.155	0.000	0.086	

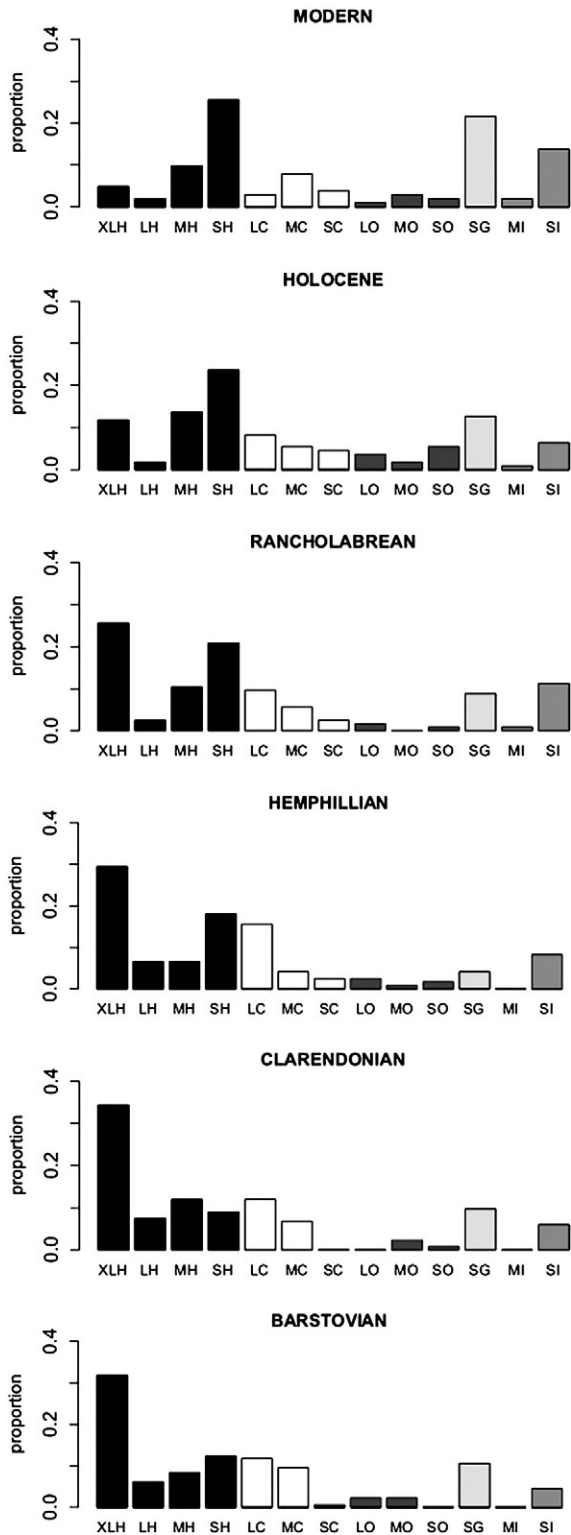


Fig. 1. Distributions show the proportion of species in each functional group for time bins in the NALMA-scale analysis. XLH: >44 kg herbivores; LH: 8–44 kg herbivores; MH: 0.5–8 kg herbivores; SH: <0.5 kg herbivores; LC: >8 kg carnivores; MC: 0.5–8 kg carnivores; SC: <0.5 kg carnivores; LO: >8 kg omnivores; MO: 0.5–8 kg omnivores; SO: <0.5 kg omnivores; SG: <0.5 kg granivores; MI: 0.5–8 kg insectivores; SI: <0.5 kg insectivores.

null hypothesis that the true difference between groups is no more different than if the data were randomly shuffled. In this way, it uses the observed data to estimate how extreme the test statistic is, and adjusts the P-value accordingly.

We also compared the corrected distributions of functional groups (proportions of species per interval) visually using correspondence analysis (CA) with Bray–Curtis distances (Figs. 2A,B and 3A,B) using the vegan package in R (Oksanen et al., 2011). Modern data were not included in the CA because differences in the modern overpower the overall scatter of points in multivariate space, obfuscating relationships among the other time periods. All analyses were performed in the R program for statistical computing (R Development Core Team, 2011).

3.2. Examining body size biases

The species richness of megaherbivores (>44 kg) is much higher than other functional groups throughout most of the last 16 Ma (between 25 and 34% of all species from the Barstovian through the Rancholabrean fall into this category) and fluctuations in their richness might mask subtle but genuine trends within other functional groups. To better understand the impact of megaherbivores we excluded them from the data and repeated all steps detailed above.

4. Results

4.1. NALMA diet and body size distributions

Diet and body size distributions for the modern, Holocene, and NALMAs are shown in Fig. 1, and results of the pairwise Fisher's tests are provided in Table 4. The mammalian communities during the Barstovian and Clarendonian, though not significantly different from one another, are different from all other time periods. These differences are characterized by a greater proportion of large carnivores, large herbivores, and megaherbivores, but fewer small herbivores, small carnivores, and small omnivores in the Clarendonian and Barstovian. The modern is different from all time periods, but only marginally different (at the $\alpha = 0.1$ level) from the Holocene. Likewise, the Holocene is significantly different from all time periods, but only marginally so from the modern and Rancholabrean. When megaherbivores are removed from the analysis (Table 5), differences between the modern, Holocene, and Rancholabrean break down, and the Holocene is no longer different from the Hemphillian.

In the CA, time periods and taxonomic groupings are ordinated simultaneously, so functional groups that are uniquely abundant are plotted in close proximity to the time period during which they are richest. Groups that have relatively the same species richness through time plot near the middle of the ordination. The displacement of functional groups from the dashed lines ($y = 0$ and $x = 0$) describes their relative loadings in the ordination—groups that are furthest from the axes are more important in differentiating time periods from one another. In the case of Fig. 2A,B, small omnivores (SO), medium insectivores (MI), and small carnivores (SC) plot near the Holocene, when their proportional species richnesses are highest. Likewise, medium omnivores (MO) and large herbivores (LH) are most rich in the Barstovian and Clarendonian. Functional groups at the center of the plot—for example, megaherbivores (XLH), medium herbivores (MH), and large carnivores (LC)—have less impact on the ordination axes that are plotted, and so they are less informative regarding the unique differences in community structure at different times.

CA of NALMAs shows three distinct groups: the Barstovian and Clarendonian, the Hemphillian and Rancholabrean, and the Holocene (Fig. 2A,B). Fig. 2A,B illustrates the “arch”, an artifact of many ordination techniques that results from the simplex geometry of CA—however, this is not a defect in the data, and we chose to interpret our CA without detrending, a common method that is only appropriate when gradients are linear (not the case in this study). If data are non-linear, detrending leads to potentially spurious interpretations (Gotelli and Ellison, 2004). In our dataset, Barstovian/Clarendonian and Holocene likely represent endpoints along a U-shaped curve—the arch is apparent when the endpoints are no more different from one

Table 4
P-values of pairwise Fisher's exact test (Monte Carlo P-value simulation with Holm P-value adjustment) on functional group distributions. Dark gray boxes indicate significance with Holm correction; light gray boxes indicate significance if P-values are uncorrected.

	Schmidt	Beaver Creek Shelter	Jones-Miller	North Cove	Little Box Elder Cave	Kanopolis Local Fauna	Sand Draw	Devil's Nest Airstrip	Bluejay Quarry	Pratt Quarry	Annie's Geese Cross	Myers Farm	Egelhoff Quarry	Immense Journey Quarry	Carrot Top Quarry	Norden Bridge Quarry	MODERN	HOLOCENE	RANCHOLABREAN	HEMPHILLIAN	CLARENDONIAN	
Beaver Creek Shelter	0.1484																					
Jones-Miller	0.7157	0.2547																				
North Cove	0.3449	0.7690	0.7822																			
Little Box Elder Cave	0.7319	0.0230	0.1224	0.2404																		
Kanopolis Local Fauna	0.5625	0.1158	0.0460	0.2168	0.3259																	
Sand Draw	0.8554	0.0770	0.4357	0.4565	0.9930	0.4019																
Devil's Nest Airstrip	0.1980	0.0056	0.0116	0.0698	0.9806	0.2503	0.6015															
Bluejay Quarry	0.1820	0.0200	0.0066	0.0770	0.1012	0.9862	0.1120	0.1120														
Pratt Quarry	0.8820	0.6261	0.2420	0.6973	0.5205	0.8320	0.6265	0.2016	0.4891													
Annie's Geese Cross	0.5315	0.1686	0.3293	0.4889	0.2795	0.9538	0.6097	0.1844	0.7171	0.5041												
Myers Farm	0.1834	0.0034	0.0482	0.1060	0.4673	0.2713	0.4801	0.2458	0.2763	0.0766	0.6047											
Egelhoff Quarry	0.3063	0.3531	0.4797	0.5657	0.0682	0.2458	0.2164	0.0230	0.1290	0.2492	0.8916	0.3707										
Immense Journey Quarry	0.1834	0.2210	0.1620	0.6771	0.1004	0.7920	0.2444	0.0664	0.7604	0.4179	0.9762	0.4227	0.7750									
Carrot Top Quarry	0.0094	0.0092	0.0030	0.0372	0.0114	0.7690	0.0216	0.0228	0.8212	0.0526	0.8660	0.2000	0.1506	0.8214								
Norden Bridge Quarry	0.1348	0.0118	0.0266	0.1260	0.1792	0.6165	0.4881	0.1480	0.5369	0.1302	0.9356	0.8618	0.3637	0.7499	0.5353							
HOLOCENE	0.9668	0.1594															0.0930					
RANCHOLABREAN			0.0250	0.2691	0.6153												0.0004	0.0678				
HEMPHILLIAN								0.7039									0.0002	0.0082	0.4991			
CLARENDONIAN									0.6855	0.0330							0.0002	0.0006	0.0156	0.0502		
BARSTOVIAN											0.1326	0.3417	0.0018	0.0866	0.1258	0.6247	0.0002	0.0010	0.0412	0.0972	0.7439	

another than from points in the middle of the U. The fact that these two groups both pull away from the others along the y axis does not in this case imply any special similarity in Holocene and Barstovian/Clarendonian community structure, but rather suggests differences in structure from the other NALMAs, which are also supported by the results of the pairwise Fisher's tests.

4.2. Individual locality diet and body size distributions

Several localities stand apart from the NALMAs during which they were deposited: Jones-Miller (Rancholabrean, eastern Colorado), Pratt Quarry (Clarendonian, northern Nebraska), Egelhoff Quarry (Late Barstovian, northern Nebraska), and Immense Journey (Late Barstovian western Nebraska). Jones-Miller, Pratt Quarry, and Immense Journey are not significant with the Holm P-value adjustment, and are no longer different when megaherbivores are removed. Egelhoff Quarry is missing representatives of several groups that do inhabit the NGP during the Barstovian: medium herbivores and omnivores, and large carnivores. While it is possible that these gaps reflect biological reality, they are more likely to be taphonomic and certainly drive the observed statistical difference.

Some sites are unique (significant without a Holm P-value adjustment) when compared to the others: Beaver Creek Shelter (Holocene, southern South Dakota), Jones-Miller, Devil's Nest Airstrip (Hemphillian, northeastern Nebraska), and Carrot Top Quarry (Barstovian, northern Nebraska) (Table 4). Both Beaver Creek and Carrot Top Quarry lack representatives of 7 and 6 functional groups respectively (Table 3), and Devil's Nest Airstrip lacks large and medium omnivores, small granivores, and medium insectivores—groups that, with the exception

of medium insectivores, are all present during the Hemphillian overall. These gaps are not characteristic of the other localities, nor of the time periods, and so are probably taphonomic signals. Differences between Jones-Miller and Carrot Top Quarry disappear when megaherbivores are removed from the analysis.

In the CA of diverse localities and time periods (Fig. 3A), Barstovian and Clarendonian sites roughly group together on the upper left hand side of the graph, with Hemphillian, Rancholabrean, and Holocene sites on the lower right. There are two exceptions: Kanopolis (Irvingtonian, central Kansas) associates with the older sites and Pratt Quarry (Clarendonian, northern Nebraska) falls with the younger sites. Separation is driven by higher proportions of small omnivores and carnivores among the younger sites, and concurrent higher proportions of medium omnivores in the older sites (see Appendix 2 for CA loadings). When megaherbivores are removed, this pattern disappears. There are few sites from the Irvingtonian and Blancan (4.7–0.15 mya), so additional sites from those time periods could potentially change the pattern in our CA.

5. Discussion

Differences in the abiotic environment from one habitat to another should lead to differences in resource availability, which in turn affect the nature of species interactions in the community. As such, we expected to see a relationship between large-scale environmental change (e.g., global temperature change) and the proportion of the community occupied by each major functional group. On the other hand, there are obvious constraints on how much this particular aspect

Table 5

Fisher's exact test P-values (Monte Carlo P-value simulation with Holm P-value adjustment) of functional group distributions, excluding megaherbivores. Dark gray boxes indicate significance with Holm correction; light gray boxes indicate significance if P-values are uncorrected.

	Schmidt	Beaver Creek Shelter	Jones-Miller	North Cove	Little Box Elder Cave	Kanopolis Local Fauna	Sand Draw	Devil's Nest Airstrip	Bluejay Quarry	Pratt Quarry	Annie's Geese Cross	Myers Farm	Egelhoff Quarry	Immense Journey Quarry	Carrot Top Quarry	Norden Bridge Quarry	MODERN	HOLOCENE	RANCHOLABREAN	HEMPHILLIAN	CLARENDONIAN	
Beaver Creek Shelter	0.0996																					
Jones-Miller	0.6469	0.2364																				
North Cove	0.2789	0.6745	0.8754																			
Little Box Elder Cave	0.8986	0.0200	0.3615	0.2142																		
Kanopolis Local Fauna	0.9524	0.2519	0.3759	0.3237	0.2749																	
Sand Draw	0.9040	0.0518	0.6753	0.3713	0.9912	0.4163																
Devil's Nest Airstrip	0.6577	0.0146	0.2090	0.1222	0.9896	0.1598	0.7491															
Bluejay Quarry	0.8266	0.1302	0.2218	0.2364	0.1238	1.0000	0.1972	0.0704														
Pratt Quarry	0.8688	0.5083	0.2891	0.5475	0.4809	0.9726	0.5159	0.3207	0.8866													
Annie's Geese Cross	0.8360	0.2657	0.9224	0.5793	0.2128	0.9238	0.5999	0.1272	0.7219	0.5551												
Myers Farm	0.4451	0.0054	0.3443	0.1390	0.4201	0.1936	0.4763	0.1734	0.2268	0.0972	0.4869											
Egelhoff Quarry	0.2661	0.2392	0.5897	0.4323	0.0464	0.3163	0.1488	0.0336	0.2863	0.1470	0.9486	0.4165										
Immense Journey Quarry	0.4217	0.4001	0.8056	0.8598	0.0710	0.7035	0.2316	0.0308	0.7195	0.5263	0.9620	0.3261	0.8936									
Carrot Top Quarry	0.4239	0.2408	0.4809	0.3965	0.0268	0.8550	0.1006	0.0168	0.8076	0.3877	0.9838	0.2472	0.8696	0.9640								
Norden Bridge Quarry	0.7085	0.0596	0.5985	0.3069	0.1948	0.5283	0.6863	0.0788	0.4489	0.2637	0.9178	0.8104	0.6195	0.6551	0.5399							
HOLOCENE	0.9814	0.1204															0.1548					
RANCHOLABREAN			0.6481	0.5621	0.7313												0.2088	0.2755				
HEMPHILLIAN								0.6283									0.0002	0.1206	0.4315			
CLARENDONIAN									0.5975	0.2791							0.0006	0.0386	0.0264	0.0460		
BARSTOVIAN											0.1646	0.3655	0.0222	0.0862	0.0702	0.5941	0.0004	0.0474	0.0444	0.0692	0.6679	

of community structure can vary, due to simple energy pyramid/trophic dynamics. Furthermore, the role of any functional group can be filled either by many species each with low abundance of individuals, or fewer species with higher abundances. In spite of this flexibility, our analysis has shown remarkable stability in the relative number of species in each functional group across millions of years.

Although studies of modern communities have found marked differences in the mammalian community structure in different environments (FAUNMAP Working Group, 1996; Badgley and Fox, 2000), in some cases the largest differences are in functional groups that cannot be practically assessed in the fossil record (e.g., aerial insectivores). In their study on Holarctic mammalian communities, Rodríguez et al. (2006) found that a single habitat type (for example, temperate steppe in North America and in Europe) could be characterized by several different functional group distributions, and that only the most extreme environments (e.g., subtropical or subarctic) had community structures that were both conserved and readily distinguished from other habitats. We have found evidence that the distribution of functional groups, when averaged over several million years, only experiences appreciable changes after long periods of stasis. The shifts to new community structure occurred during the Hemphillian, and in the Holocene. The former is broadly contemporaneous with the Messinian Salinity crisis, and the local shift from C3 to C4 vegetations, and occurs after 4 Ma of a prolonged cooling trend that followed the MMCO. The Hemphillian shift in community structure may indicate that as global cooling proceeded, it crossed a threshold which then triggered substantial biotic change; one can imagine a scenario in which global cooling led to greater habitat diversity continent-wide, and more mosaic habitats. This in turn would impact local resource availability and cause changes in body size

structure of the community. However, that idea remains to be rigorously tested. The Holocene shift correlates with rapid global warming as the last glacial period gave way to the present interglacial, and also with a rapidly growing human population, the combination of which initiated megafaunal extinctions and substantial range shifts and abundance changes in surviving species (Blois et al., 2010; Barnosky et al., 2011).

In an analysis of large (>5 kg) terrestrial North American mammals, Figueirido et al. (2012) found six distinct faunal associations throughout the Cenozoic. Relevant to our study, they detect turnover from Miocene to Pliocene fauna that was spurred by the transition from the MMCO to long-term cooling at the end of the Miocene. In their study, Miocene fauna peaked during the MMCO, around 16.5 Ma, while Pliocene fauna were most diverse around 3.5 Ma. Unfortunately, Blancan (4.9–1.8 Ma) data were too sparse to be included in our analysis and so we cannot comment with regard to Figueirido et al.'s Pliocene fauna. However, faunal changes at the Miocene/Pliocene boundary (during the Hemphillian) are in concordance with our results. Slight differences between our study and Figueirido et al. (2012) with respect to the timing of turnover and community change may be due to the fact that Figueirido et al. did not include small mammals, and they divided the NALMAs into biochron subdivisions, so our temporal scale is more coarse. Nevertheless, our general conclusions are in agreement.

Both the NALMA and individual-locality analyses show no difference through most of the last 16 Ma (when megaherbivores are included). However, a major difference between the NALMA and individual locality results is that when we remove megaherbivores, though the NALMA pattern does not change substantially, the individual locality groupings in the CA are no longer present. Furthermore, while the NALMA analysis suggests that the Holocene is markedly different from community

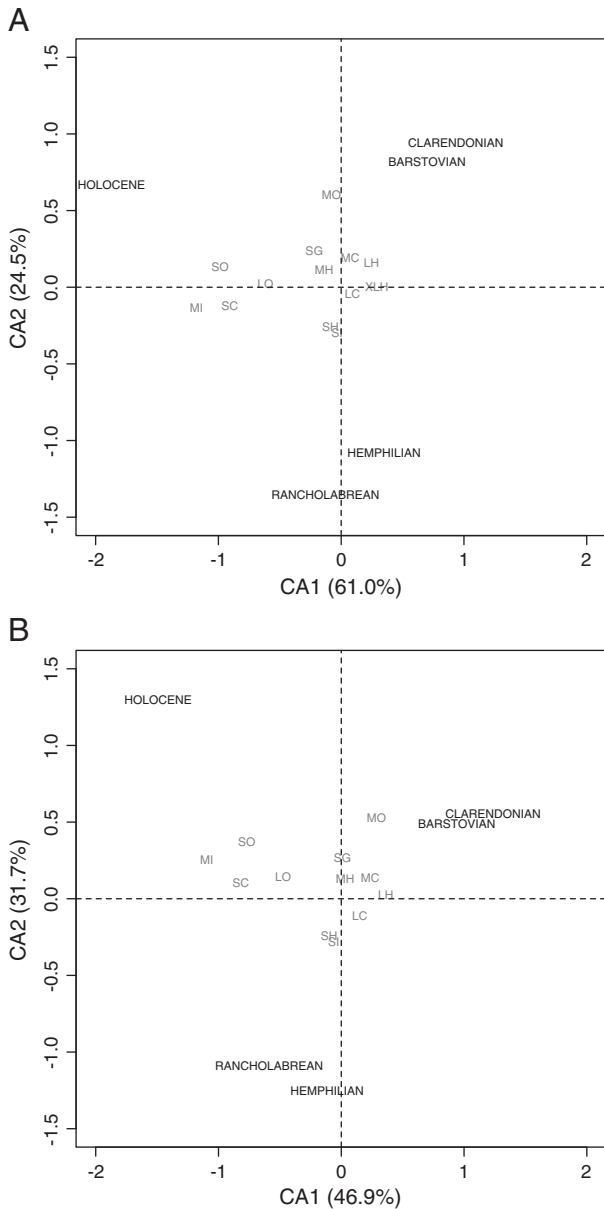


Fig. 2. A: Correspondence analysis of NALMAs and the Holocene (total inertia = 0.1376) (see Fig. 1 for abbreviations). Gray lettering indicates functional groups; black indicates time periods. B: Correspondence analysis of NALMAs and the Holocene, with megaherbivores excluded (total inertia = 0.1406). Gray lettering indicates functional groups; black indicates time periods.

structures that had been the norm since the Hemphillian, on a site-by-site level, the Holocene localities are not especially (or detectably) unique. This lack of change could be caused by two factors. First, the distribution of sites through time in our NGP study area is uneven. We are notably deficient in both Early Barstovian and Holocene diverse single localities so we may be missing real changes that took place because known individual localities at those times do not adequately sample all body sizes. Second, at the NALMA scale the composite fauna accumulates species through evolution over the course of the time period, whereas individual localities offer a snapshot of the fauna that lived during a temporal window too short for evolution to inflate species counts. By the same token, the Holocene has not yet lasted long enough to have gained species through evolution, unlike the other time periods in this study. It may be that the difference between the Holocene and other time bins would disappear in the future as new species are added.

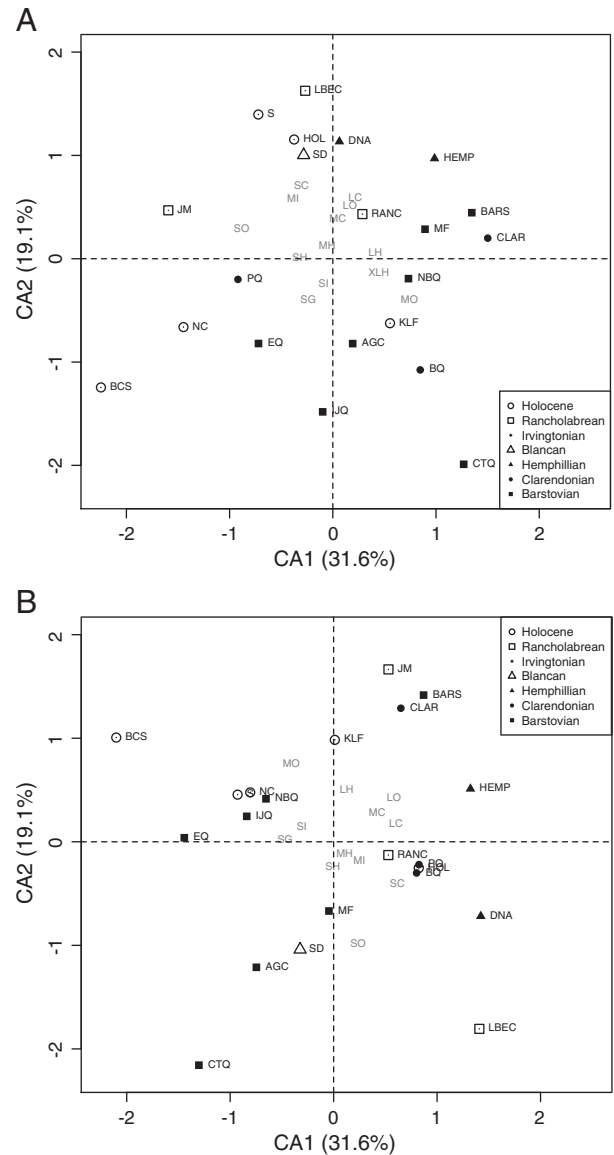


Fig. 3. A: Correspondence analysis of diverse localities, NALMAs, and the Holocene (total inertia = 0.3587). AGC: Annie's Geese Cross; BCS: Beaver Creek Shelter; BQ: Bluejay Quarry; CTQ: Carrot Top Quarry; DNA: Devil's Nest Airstrip; EQ: Egelhoff Quarry; IJQ: Immense Journey Quarry; JM: Jones-Miller; LBEC: Little Box Elder Cave; KLF: Kanopolis Local Fauna; MF: Myer's Farm; NBO: Norden Bridge Quarry; NC: North Cove; PQ: Pratt Quarry; S: Schmidt; SD: Sand Draw; MOD: modern; HOL: Holocene; RANC: Rancholabrean; HEMP: Hemphillian; BARS: Barstovian. Gray lettering indicates functional groups; black indicates time periods or sites (see Fig. 1 for functional group abbreviations). B: Correspondence analysis of diverse localities, NALMAs, and the Holocene, with megaherbivores excluded (total inertia = 0.3795). Gray lettering indicates functional groups; black indicates time periods or sites.

There are several possible explanations for the groupings we found in both NALMAs and localities; that is, similarity between Barstovian–Clarendonian, and Hemphillian–Holocene: 1) there is inertia in community structure that is independent of taxonomic composition; 2) there is a critical temperature threshold, achieved during the Hemphillian, at which point the community changes fundamentally—this is in keeping with the results of the locality-level analysis and Figueirido et al. (2012); and 3) sampling of fossils is differently biased for localities from 16 to 10 mya and from 10 mya to present. Without more localities in the Blancan and Irvingtonian of the NGP (4.7–0.15 mya) it is unclear whether the functional group distributions we see in single localities from those time periods are idiosyncratic or if they represent the true distribution at those times. Despite the slight

differences we see in analyses of NALMA-scale data and individual localities, both methods suggest an underlying model for community-level change: long periods of stasis, interrupted by rapid and apparently irreversible shifts that introduce new community structures that in turn persist for millions of years. Interestingly, this pattern conforms well to the expectations of state-shift theory, and matches observations of how biotic systems change to new states when critical environmental thresholds are crossed (Scheffer et al., 2009). However, without better sampling during the Blancan and Irvingtonian, and finer time resolution within the NALMAs, it is difficult to distinguish a stasis/rapid change model from a more continuous change model.

The Holocene marks both the end of the last glacial maximum and the first appearance of humans in North America (Grayson, 2011). These factors together likely caused the Quaternary megafaunal extinctions that took place at the Pleistocene–Holocene: in North America, 106 species of megafauna (mammals weighing > 44 kg) went extinct by the Holocene (Barnosky et al., 2011). Although this extinction was strongly biased towards large-bodied mammals, the Pleistocene–Holocene transition also impacted smaller mammals via extinction, range changes (Barnosky et al., 2011), and changes to community structure, such as reductions in species evenness (Blois et al., 2010). Our results seem at first glance to contradict those of Blois et al. (2010) and Barnosky et al. (2011). However, the loss of small mammal diversity documented by Blois et al. (2010) was largely due to local extirpations of species that are still present regionally and to changes in relative abundance—neither of these would be detectable in our analysis. Likewise, Barnosky et al. (2011) consider species weighing 2 kg or less to be small, and also did not divide small mammals by dietary group. Although some small mammal groups increase in species richness during the Holocene in our analysis (possibly a taphonomic signal), we did find that species richness of small herbivores in the Holocene was lower than in almost any other time period, so the difference between our results and those of Barnosky et al. (2011) may largely be due to differences in how species are classified and grouped. Regardless, the Holocene community is still marginally different from the Barstovian through the Clarendonian in that, both in terms of proportion and raw number of species, richness during the Holocene is higher for medium herbivores (MH), small carnivores (SC), large omnivores (LO), small omnivores (SO), and medium insectivores (MI). It is unlikely that this is the result of better sampling during the Holocene because species richness is actually lower during the Holocene and number of localities in the Holocene NPG is average.

Direct comparison of modern to fossil data is inappropriate for our analysis not only because sampling and time-averaging are so different, but also because extant mammals are often defined by characteristics that cannot preserve in the fossil record (e.g. pelage, genetic divergence, etc.; Carrasco, 2013–this issue). However, it is worth mentioning that in the modern sample, herbivores and carnivores larger than 8 kg decline in richness, while insectivores, and small herbivores and granivores are richer relative to the Holocene. If future work does not demonstrate that sampling differences are the explanation, the patterns would suggest that the modern is already perturbed from the Holocene baseline.

6. Conclusions

Distribution of functional group diversity is a suitable metric for quantifying community baselines because it is taxon-free, can be applied to past time periods, and can be measured in modern communities and monitored into the future. This makes it a useful tool for biodiversity monitoring and conservation planning. Furthermore, we have shown that patterns of functional-group diversity remain remarkably stable through long periods of time, meaning that significant changes in the metric reveal that unusual perturbations are forcing faunal change.

Both the locality and NALMA-scale analyses show major structural differences between communities from Barstovian through Clarendonian (about 7 Ma) and the Hemphillian through Holocene

(about 9 Ma). The major faunal shift took place about midway through a 14-million year cooling trend that began at the end of the MMCO, and may indicate that an environmental threshold was crossed, at which point mammalian community structure was altered. The occurrence of such large-scale climatic events as the Messinian Salinity Crisis in Europe and local shift from C3 to C4 vegetations in North America during the Hemphillian is consistent with this hypothesis.

The NALMA-scale analysis supports the idea that a significant shift in community structure occurred during the Holocene, an outcome of the sudden loss of megaherbivores through the combined pressures of human interactions and rapid climatic warming that occurred at the end of the Pleistocene. The paucity of Holocene megaherbivores is unparalleled in comparison to the last 16 Ma. At present, it is unclear whether the modern fauna is showing further departure from that “new” Holocene baseline, largely because of uncertainties in how to adequately compare the very differently-sampled modern and fossil data. However, preliminary indications suggest declines in species larger than 8 kg, and increases in insectivores, and small herbivores and granivores. While sampling of modern and Holocene species data needs to be standardized before we can make accurate comparisons, extinctions and extirpations even in historic times seem to be biased towards particular functional groups, like large carnivores and herbivores (Weber and Rabinowitz, 2002; Schipper et al., 2008).

Understanding the nature and causes of the biotic turnovers and structural changes that took place in the past takes on relevance today as we face major global change. As ecosystems on a local scale transform such that new associations of species are assembled—either in response to changing climatic patterns or human interventions—biodiversity management and conservation will increasingly need to take heed of the functional and structural indicators of community and ecosystem health, rather than managing solely for presence of certain species. Metrics such as the one we examine here should prove useful in that regard.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.04.019>.

Author contributions

Conceived research question: MAS, MH. Assembled data: MAS, MH. Designed and performed analyses: MAS. Wrote the paper: MAS. Manuscript revisions: MAS.

Acknowledgements

We are grateful to P. D. Mannion, R. Benson, and R. Butler for organizing this volume and the “Vertebrate Diversity Patterns and Sampling Biases” symposium at the 2011 Society of Vertebrate Paleontology meeting. We thank A.D. Barnosky, M.A. Carrasco, and members of the Barnosky lab for discussion and comments at various stages of this project, P.D. Polly and an anonymous reviewer for constructive comments on the manuscript, and M. Koo for help with data extraction in ArcGIS. We appreciate the people who contributed data and made data available through MIOMAP and FAUNMAP. MAS was supported by NSF grant DGE-1106400. This is University of California Museum of Paleontology contribution #2034.

References

- Alroy, J., 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127, 285–311.
- Alroy, J., 2003. North American Fossil Mammal Systematics Database The Paleobiology Database. available at <http://www.paleodb.org> 2003 accessed April 15, 2011.
- Axelrod, D.I., 1985. Rise of the grassland biome, central North America. *The Botanical Review* 51 (2), 163–201.
- Badgley, C., Fox, D.L., 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* 27 (6), 1437–1467.
- Barker, W.T., Whitman, W.C., 1988. Vegetation of the Northern Great Plains. *Rangelands* 10 (6), 266–272.

- Barnosky, A.D., Carrasco, M.A., 2002. The effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evolutionary Ecology Research* 4, 811–841.
- Barnosky, A.D., Shabel, A.B., 2005. Comparisons of mammalian species richness and community structure in historic and mid-Pleistocene times in the Colorado Rocky Mountains. *Proceedings of the California Academy of Sciences* 56 (5), 50–61.
- Barnosky, A.D., Hadly, E.A., Bell, C.J., 2003. Mammalian response to global warming on varied temporal scales. *Journal of Mammalogy* 84 (2), 354–368.
- Barnosky, A.D., Bell, C.J., Emslie, S.D., Goodwin, H.T., Mead, J.L., Repenning, C.A., Scott, E., Shabel, A.B., 2004. Exceptional record of mid-Pleistocene vertebrates helps differentiate climatic from anthropogenic ecosystem perturbations. *PNAS* 101 (25), 9297–9302.
- Barnosky, A.D., Carrasco, M.A., Davis, E.B., 2005. The impact of the species–area relationship on estimates of paleodiversity. *PLoS Biology* 3 (8), e266.
- Barnosky, A.D., Carrasco, M.A., Graham, R.W., 2011. Collateral mammal diversity loss associated with late Quaternary megafaunal extinctions and implications for the future. Comparing the Geological and Fossil Records: implications for Biodiversity Studies. Geological Society, London, Special Publications 358, 179–189.
- Blois, J.L., McGuire, J.L., Hadly, E.A., 2010. Small mammal diversity loss in response to Pleistocene climate change. *Nature* 465, 773–775.
- Burnham, R.J., Pitman, N.C.A., Johnson, K.R., Wilf, P., 2001. Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. *American Journal of Botany* 88 (6), 1096–1102.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiesslin, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J., Richardson, A.J., 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334 (6056), 652–655.
- Carrasco, M.A., 2013. The impact of taxonomic bias when comparing past and present species diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372, 130–137 (this issue).
- Carrasco, M.A., Kraatz, B.P., Davis, E.B., Barnosky, A.D., 2005. Miocene Mammal Mapping Project (MIOMAP). University of California Museum of Paleontology. <http://www.ucmp.berkeley.edu/miomap/>.
- Carrasco, M.A., Barnosky, A.D., Graham, R.W., 2009. Quantifying the extent of North American mammal extinction relative to the pre-anthropogenic baseline. *PLoS One* 4 (12), e8331.
- Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehrlinger, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389 (6647), 153–158.
- Cronin, T.M., 2010. Cenozoic climate change. In: Cronin, T.M. (Ed.), *Paleoclimates: Understanding Climate Change Past and Present*. Columbia University Press, New York, NY, pp. 81–111.
- Damuth, J., McFadden, B.J. (Eds.), 1990. *Body size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, New York, pp. 49–69.
- Eisenberg, J.F., 1981. *The Mammalian Radiations: And Analysis of Trends in Evolution, Adaptation, and Behavior*. University of Chicago Press, Chicago.
- Eronen, J.T., Polly, P.D., Fred, M., Damuth, J., Frank, D.C., Mosbrugger, V., Scheidegger, C., Stenseth, N.C., Fortelius, M., 2010a. Ecometrics: the traits that bind the past and present together. *Integrative Zoology* 5, 88–101.
- Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C., Fortelius, M., 2010b. Precipitation and large herbivorous mammals, part I: estimates from present-day communities. *Evolutionary Ecology Research* 12, 217–233.
- FAUNMAP Working Group, 1994. FAUNMAP: a database documenting late Quaternary distributions of mammal species in the United States. *Illinois State Museum Scientific Papers*, 25 (1–2), pp. 1–690.
- FAUNMAP Working Group, 1996. Spatial responses of mammals to Late Quaternary environmental fluctuations. *Science* 272, 1601–1606.
- Figueirido, B., Janis, C.M., Perez-Claros, J.A., De Renzi, M., Palmqvist, 2012. Cenozoic climate change influences mammalian evolutionary dynamics. *PNAS* 109 (3), 722–727.
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z., Zhou, L., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research* 4, 1005–1016.
- Gotelli, N.J., Ellison, A.M., 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Inc., Sunderland, MA.
- Graham, R.W., Lundelius, E.L., 2010. FAUNMAP II: new data for North America with a temporal extension for the Blancan, Irvingtonian and early Rancholabrean FAUNMAP II Database, version 1.0 <http://www.ucmp.berkeley.edu/faunmap/about/index.html>.
- Grayson, D.K., 1998. Moisture history and small mammal community richness during the latest Pleistocene and Holocene, Northern Bonneville Basin, Utah. *Quaternary Research* 49, 330–334.
- Grayson, D.K., 2011. *Glaciers, sea levels, and the peopling of the Americas. The Great Basin: A Natural Prehistory*. University of California Press, Berkeley, USA, pp. 45–63.
- Grayson, D.K., Madsen, D.B., 2000. Biogeographic implications of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. *Journal of Mammalogy* 81 (4), 1100–1105.
- Greenwood, D.R., 2005. Leaf form and the reconstruction of past climates. *New Phytologist* 166, 355–357.
- Hadly, E.A., 1996. Influence of late-Holocene climate on northern Rocky Mountain mammals. *Quaternary Research* 46 (3), 298–310.
- Hadly, E.A., Maurer, B.A., 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. *Evolutionary Ecology Research* 3 (4), 477–486.
- Hadly, E.A., Ramakrishnan, U., Chan, Y.L., van Tuinen, M., O'Keefe, K., Spaeth, P.A., Conroy, C.J., 2004. Genetic response to climatic change: insights from ancient DNA and phylogenetics. *PLoS Biology* 2 (10), e290.
- Harnik, P.G., 2009. Unveiling rare diversity by integrating museum, literature, and field data. *Paleobiology* 35 (2), 190–208.
- Hillson, S., 2005. *Teeth*, second edition. Cambridge University Press, Cambridge.
- Janis, C.M., Damuth, J., Theodor, J.M., 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *PNAS* 97 (14), 7899–7904.
- Janis, C.M., Damuth, J., Theodor, J.M., 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207, 371–398.
- Koch, P.L., Barnosky, A.D., 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics* 37, 215–250.
- McGill, B.J., Hadly, E.A., Maurer, B.A., 2005. Community inertia of Quaternary small mammal assemblages in North America. *PNAS* 102 (46), 16701–16706.
- McRoberts, C.A., Newton, C.R., 1995. Selective extinction among end-Triassic European bivalves. *Geology* 23 (2), 102–104.
- Muldoon, K.M., Goodman, S.M., 2010. Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *Journal of Biogeography* 37, 1144–1159.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. *vegan*: Community Ecology Package. R package version 2.0-2. <http://CRAN.R-project.org/package=vegan>.
- Patterson, B., Ceballos, G., Sechrest, W., Tognelli, M., Brooks, T., Luna, L., Ortega, P., Salazar, I., Young, B., 2003. Digital Distribution Maps of the Mammals of the Western Hemisphere. NatureServe.
- Polly, P.D., 2010. Tiptoeing through the trophics: geographic variation in carnivorous locomotor ecomorphology in relation to environment. In: Goswami, A., Friscia, A. (Eds.), *Carnivore Evolution: New Views on Phylogeny, Form, and Function*, pp. 374–410.
- Polly, P.D., Eronen, J.T., Fred, M., Dietl, G.P., Mosbrugger, V., Scheidegger, C., Frank, D.C., Damuth, J., Stenseth, N.C., Fortelius, M., 2011. History matters: ecometrics and integrative climate change biology. *Proceedings of the Royal Society B* 278 (1709), 1131–1140.
- Prothero, D.R., 1998. The chronological, climatic, and paleogeographic background to North American mammalian evolution. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.), *Evolution of Tertiary Mammals of North America: Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*, 1. Cambridge University Press, Cambridge, pp. 9–36.
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria 3-900051-07-0. URL <http://www.R-project.org/>.
- Reed, A.W., Kaufman, G.A., Kaufman, D.W., 2006. Species richness–productivity relationship for small mammals along a desert–grassland continuum: differential responses of functional groups. *Journal of Mammalogy* 87 (4), 777–783.
- Rodriguez, J., Hortal, J., Nieto, M., 2006. An evaluation of the influence of environment and biogeography on community structure. *Journal of Biogeography* 33, 291–303.
- Rowe, R.J., Terry, R.C., Rickart, E.A., 2011. Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92 (6), 1366–1375.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461, 53–59.
- Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher Jr., T.E., Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., da Fonseca, G.A.B., Derocher, A.E., Dublin, H.T., Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Hapold, D., Hapold, M., Hare, J., Harris, R.B., Hawkins, C.E., Hayward, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medelín, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powell, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds III, J.E., Rondinini, C., Rosell-Ambal, R.G., Rullin, M., Rylands, A.B., Savini, S., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., de Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., van Strien, N., Talukdar, B.K., Taylor, B.L., Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytsulina, K., Veiga, L.M., Vié, J.-C., Williamson, E.A., Wyatt, S.A., Xie, Y., Young, B.E., 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322, 225–230.
- Terry, R.C., Li, C.(L.), Hadly, E.A., 2011. Predicting mall-mammal response to climatic warming: autecology, geographic range, and the Holocene fossil record. *Global Change Biology* 17, 3019–3303.
- Wang, Y., Cerling, T.E., MacFadden, B.J., 1994. Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 269–279.
- Weber, W., Rabinowitz, A., 2002. A global perspective on large carnivore conservation. *Conservation Biology* 10 (4), 1046–1054.