Evolutionary Ecology Research, 2011, **13**: 833–850

Topographic and climate change differentially drive Pliocene and Pleistocene mammalian beta diversity of the Great Basin and Great Plains provinces of North America

Amy Lynn Atwater and Edward Byrd Davis

Department of Geological Sciences and the Museum of Natural and Cultural History, University of Oregon, Eugene, Oregon, USA

ABSTRACT

Hypothesis: The Great Basin of the western USA has currently elevated beta (between-site) diversity because topographic change, mediated by regional tectonic activity, has driven increased habitat packing throughout the past 17 million years.

Organisms: Non-volant (non-flying) land mammals, excluding introduced species and humans.

Times and places: Late Miocene to Recent of the Great Basin of the USA, centred on Nevada, and (as a control system) the central Great Plains of the USA, centred on Nebraska.

Analytical methods: We obtained mammalian faunal lists from the FAUNMAP II database and partitioned the data into intervals based on mammalian biochronology. We estimated beta diversity for each time-slice based on richness and evenness. We used cluster analysis of sites by taxon relative abundance to investigate unexpectedly high evenness beta diversity of the Great Plains Holocene.

Results: Beta diversity is higher in the Great Basin than the Great Plains at all intervals except the Holocene, which revealed unexpectedly high (and as yet unexplained) evenness-beta for the Great Plains. Our overall results support the hypothesis that Great Basin beta diversity has been driven primarily by tectonic change.

Keywords: alpha diversity, beta diversity, climate change, desert ecosystem, gamma diversity, Great Basin, Great Plains, paleoecology, tectonic change.

INTRODUCTION

Research has shown that desert ecosystems tend to have higher landscape-scale beta (β) diversity than non-desert ecosystems (Tueller *et al.*, 1991; Kelt *et al.*, 1996; MacNally *et al.*, 2004). Some workers have suggested that the desert ecosystems of the Great Basin have been shaped

Correspondence: E.B. Davis, Department of Geological Sciences and the Museum of Natural and Cultural History, University of Oregon, Eugene, OR 97403, USA. e-mail: edavis@uoregon.edu

primarily by late Cenozoic climate cycling, with deserts during warm intervals serving as 'diversity sinks' that are rescued by species shifting into them during cooler intervals (Brown, 1971; Cronquist, 1978; Johnson, 1978). As an alternative, Davis (2005) hypothesized that these desert assemblages have higher β diversity because of the region's topographic complexity, driven by tectonic expansion over the Neogene. These ideas about Great Basin desert ecosystems can be extended to desert ecosystems in general: Is modern desert macroecology shaped primarily by tectonic setting or by Pleistocene climate cycling? The source of desert β diversity is important to conservation biology in our current era of rapidly changing climates: if the macroecology of a region has been shaped by tectonic-scale forces, it should be more stable under climate change than a region shaped primarily by Pleistocene climate cycling. To test his hypothesis, Davis (2005) compared mammalian β diversity in the Great Basin and the Great Plains of the western United States over the last 17 million years, using data from the MIOMAP and FAUNMAP fossil databases combined with data from modern natural history collections. Unfortunately, at that time, published data had not been compiled for the mammalian faunas of the Plio-Pleistocene, leaving an almost 5 million year gap between the latest Miocene and the late Pleistocene.

Recently, the Pliocene and Pleistocene published data for North American fossil mammals have been assembled in a new database, FAUNMAP II (http://www.ucmp.berkeley.edu/faunmap/). We use this database to revisit the results of Davis (2005), filling in the gap to allow an additional test of the hypothesis of a tectonic driver of β diversity.

Beta diversity quantifies the relationship between average local diversity (α diversity) and overall diversity within a region (γ diversity) (Whittaker, 1960). As with α and γ diversity, β diversity can be expressed in terms of either richness or evenness. Richness describes the number of species in a community, while evenness describes the distribution of relative abundances of individuals within those species. Following Davis (2005), we used the work of Kiflawi and Spencer (2004) to calculate richness-based β diversity and Olszewski (2004) to determine evenness-based β diversity.

The Pleistocene and Holocene fossil record in the Great Basin indicates that the habitats varied greatly through glacial/interglacial cycles, with the basins filling to become internally drained lakes (Cole and Armentrout, 1979) during interglacial intervals; this pattern can be best observed today in the northern Great Basin. Thus, the climate cycling is referred to as pluvial/interpluvial in the Great Basin. This shallower time climate cycling has been invoked as a more important driver of β diversity than deeper time tectonic change (Brown, 1971; MacNally *et al.*, 2004); that is, the diversity of assemblages seen in the Great Basin reflects a periodic mixing of species as they moved to optimal habitats during pluvial and interpluvial times, not a general evolutionary trend towards increased habitat packing in a topographically complex landscape.

This tectonic and climatic background led Davis (2005) to two hypotheses that we also test:

1. The elevated β diversity of the Great Basin is a result of habitat packing (Kelt, 1999), with high-elevation and low-elevation faunas combining to produce more regional diversity than could be supported in an area of similar size but no relief.
2. The Great Basin has higher β diversity because of recent faunal overlap; current diversity represents an influx of taxa from neighbouring provinces, which created a supersaturated system yet to be thinned through competition (cf. Brown, 1971; Cronquist, 1978; Johnson, 1978; Davis, 2005).

Following Davis (2005), we use the central Great Plains of the USA as a control for this natural experiment in the Great Basin, comparing the results from the Great Basin to the same tests on the Great Plains. The Great Plains do not have tectonic instability like the Great Basin and also have a rich paleontological history with many published localities accessible in databases (Davis, 2005).

STUDY REGIONS

Great Basin

The Great Basin region includes part of the Basin and Range physiographic province of the western USA (Dickinson, 1979; Graham, 1999). It is bounded to the north by the Columbia Plateau, to the east by the Colorado Plateau and the Rocky Mountains, to the south by the southern Basin and Range, and to the west by the Sierra Nevada and Klamath Mountains (Graham, 1999). This area underwent extensional normal faulting and now consists of many repeated internal drainage systems and mountain ranges.

The Great Basin is the northern half of the Basin and Range geographic province, a distinct landscape rhythmically varying between narrow plains and steep mountains, which has been shaped by tectonic forces that began pulling the land apart longitudinally starting ~17 million years ago (Ma) (McQuarrie, 2004). This longitudinal tension created the basins as fault-bound grabens dropped between elevationally stable horsts. Unlike most mountainous areas, created by compressional tectonic forces that drive land upward, the Basin and Range province has been created by tensional forces, increasing the total land area at the same time as generating topographic complexity, with a decrease in average elevation creating distinctly different habitats in a relatively small area.

The environment of the Great Basin is very arid because of the rain shadow created by the Sierra Nevada to the west, which has existed since before Great Basin extension (Crowley *et al.*, 2008; Hren *et al.*, 2010). Most precipitation in the Great Basin comes in the form of snowfall in the winter months, and is unavailable to primary producers (Cronquist, 1978). The mixture of topographic relief and arid climate creates two very different classes of habitats in the Great Basin: high-elevation arid woodland and low-elevation desert scrubland, leading to a diversity of habitats for mammals.

Great Plains

The Great Plains of the central USA are made up of low-relief grasslands extending from the northern to southern border. They are bounded to the east by the Central Lowland and to the west by the Rocky Mountains (Graham, 1999). We have used a subsection of the central Great Plains of approximately the same area and latitude as the Great Basin, centred around Nebraska (Davis, 2005).

METHODS

Faunal data

The data included in this analysis are from four sources, three of which were used by Davis (2005). All datasets are available on the internet.

Modern and Miocene faunal data

Data for Recent and Miocene occurrences in the Great Basin and Great Plains were taken directly from Davis (2005). Modern data are a compilation from the collections of the University of California Museum of Vertebrate Zoology (MVZ: http://mvz.berkeley.edu/) and the Mammal Networked Information System (MaNIS: http://manisnet.org/). The MVZ data were used for Nevada, representing the Great Basin, and the MaNIS data for Nebraska, representing the central Great Plains. Miocene data were compiled from the MIOMAP database (Carrasco *et al.*, 2005). See Davis (2005) for a discussion of these three data sources.

Pliocene and Pleistocene faunal data

We have supplemented the Modern and Miocene data (Davis, 2005) with additional Pliocene and Pleistocene data (Fig. 1) from the NEOMAP implementation of the FAUNMAP II database (http://www.ucmp.berkeley.edu/neomap/). The FAUNMAP II database includes the original FAUNMAP data (Graham *et al.*, 1994) analysed by Davis (2005), but adds published mammalian occurrences back to the Miocene–Pliocene boundary, ~5 Ma (Graham and Lundelius,

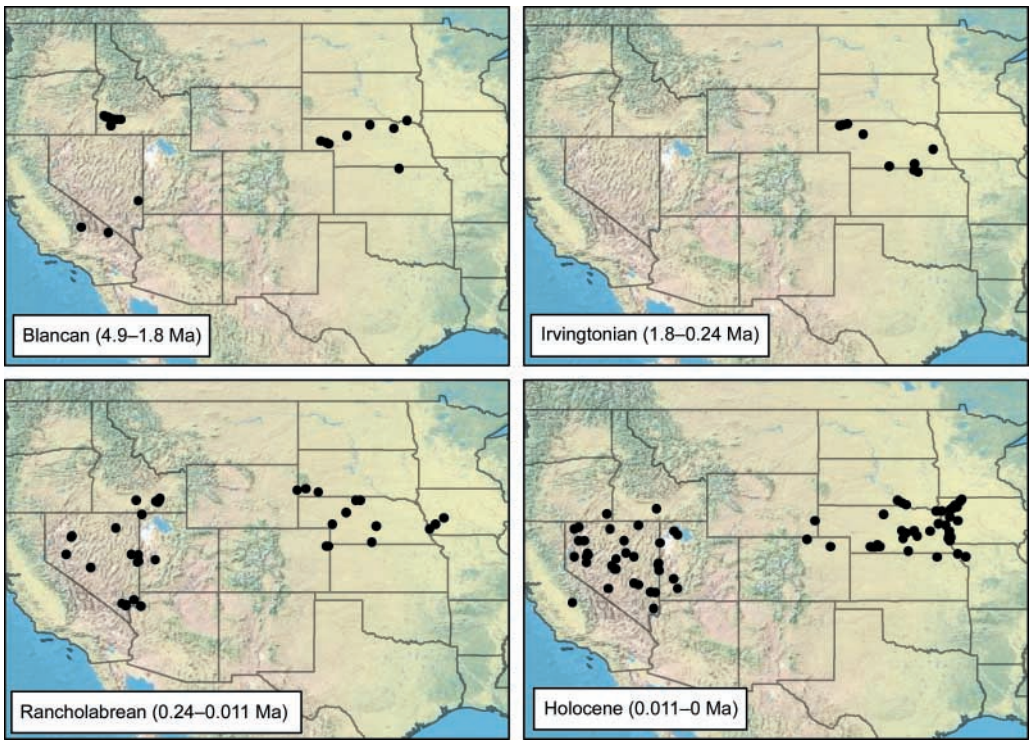

Fig. 1. Maps of localities included in our analysis. Each panel represents a North American Land Mammal Age. Dots indicate individual localities, but the dataset may include multiple distinct horizons within these localities. Sampling improves through time, but each interval samples similar geographic areas of the Great Basin and Great Plains, so dispersion of samples should not be a concern. The Irvingtonian contains only Great Plains samples with adequate richness for inclusion in our analysis.

2010). The FAUNMAP II data are compiled for the continental USA (including Alaska) and Canada. The taxonomy of fossil occurrences in FAUNMAP II has been updated to match the most recent published references, revising some of the information contained in the original FAUNMAP database. As noted by Davis (2005), Pleistocene fossil sites contain many species found in modern assemblages, but reflect approximately an order of magnitude more time averaging than modern natural history collections. In an effort to establish a finer temporal resolution, we do not lump the FAUNMAP II data from multiple levels into single localities as Davis (2005) did with the FAUNMAP data. We have grouped faunal units into the North American Land Mammal Ages after Tedford *et al.* (2004), for comparison with the MIOMAP data presented by Davis (2005).

Standardization of faunal data

The FAUNMAP II data were standardized following Davis (2005) to make them comparable with the fossil and modern data. Data for subspecies were lumped within species. Introduced species and *Homo sapiens* were removed from the FAUNMAP II dataset. Bats were removed because, as volant mammals, they are not restricted by the same geographical barriers as the other mammals, and they are typically poorly preserved in the fossil record. Following standard practice (Alroy, 1996; Barnosky and Carrasco, 2002; Davis, 2005), generic and familial indeterminate identifications were kept only for intervals that had no lower-level identifications for that taxonomic group. After taxonomic standardization, we removed all localities that contained fewer than five taxa. These poorly sampled localities could artificially lower average α diversity, leading to erroneously high β diversity values. Davis (2005) chose the five-taxon limit as a qualitatively best balance between the overall number of localities and the strong effect individual sites with low α diversity have on average α. While an assemblage with fewer than five taxa might be representative of a truly species-poor ecosystem, most paleontological samples with extremely low taxon counts reflect poor sampling.

Beta estimation of first-order jackknife

Following Davis (2005), we used jackknife β diversity (Kiflawi and Spencer, 2004) for our analysis of richness-based β diversity. This metric calculates the ratio of the richness of organisms summed over the study area, the γ diversity, to the average richness at a single locality within the study area, the average α diversity ($\overline{\alpha}$), minus one. Jackknife β diversity uses the first-order jackknife estimate of species richness, $\hat{\gamma}$ (Heltshe and Forrester, 1983), to account for the effects of differing sample sizes between regions and to produce a variance for the β diversity estimate. The formula for the variance of $\hat{\gamma}$ was published incorrectly by both Davis (2005) and Kiflawi and Spencer (2004). Davis (2005) used the correct formulas in his calculations, and the other formulas published in Davis (2005) are correct. The incorrect formula was:

$$\mathrm{var}(\hat{\gamma}) = \frac{K-1}{K}\sum_{s=1}^{\gamma\,\mathrm{obs}}\left(s^2 f_s - \frac{u^2}{K}\right)$$

The parentheses should include the summation, as in Heltshe and Forrester (1983):

$$\mathrm{var}(\hat{\gamma}) = \frac{K-1}{K}\left(\sum_{s=1}^{\gamma\,\mathrm{obs}} s^2 f_s - \frac{u^2}{K}\right)$$

where $\hat{\gamma}$ is the first-order jackknife estimate of regional richness, K is the total number of collections (sites, localities, etc.), u is the number of singletons (species found at only one site), and f_s is the number of sites containing s of the singletons. That is, the variance in $\hat{\gamma}$ depends strongly on the distribution of singletons in sites. If there are many singletons, but spread among many sites, then sampling is relatively good and variance will be low; however, if there are many singletons and they are concentrated in one or two sites, variance will be high: high per-site singleton count squared, times the number of sites. This reflects the reality of sampling at the regional scale: if the sampling is of uniform quality across the landscape, then we expect rare taxa to be present at multiple sites as singletons, producing lower variance of $\hat{\gamma}$. If sampling is poor at the majority of the sites, then we expect to see only singletons at the fewer, well-sampled sites, producing higher variance of $\hat{\gamma}$.

Beta estimation of rarity gain

To complement the richness-based jackknife β diversity, we used the additive formulation of β diversity of Olszewski (2004), which is based on relative abundance distributions. The relative abundance of species becomes lower as scale changes from locality to region, which led Patil and Taillie (1982) to name this evenness-metric of β diversity 'rarity gain'. Rarity gain indicates the gain in relative abundance of rare taxa when summed in the entire region, compared with averages from individual localities (Olszewski, 2004). This means rarity gain β diversity would be higher in a study area where a taxon is common in one locality yet rare in another, even though a single group of taxa is present in all of the localities sampled, producing a low richness-based β diversity. Consequently, rarity gain is more sensitive to changes in faunas, picking up on changes in relative abundance before taxa become extirpated or extinct. Olszewski's (2004) formulation of rarity gain relies on Hurlbert's (1971) reformulation of Simpson's (1949) evenness metric. Simpson's (1949) evenness measures the probability that any two individuals taken from a sample will be from different species, while Hurlbert's (1971) reformulation takes the inverse and normalizes for sample size. A variance calculation is also available for rarity gain, allowing assessment of the significance of differences between regions and intervals. We used the same calculations as Davis (2005).

Terminology

To facilitate interdisciplinary understanding, here we define the paleoecological terms we use in our study. First, this research spans the geologic epochs of the Miocene (23 to 5.3 Ma), Pliocene (5.3 to 2.6 Ma), Pleistocene (2.6 Ma to 11.7 ka), and Holocene (11.7 ka to today). (Ma = mega-annum, or millions of years ago, and ka = kilo-annum, or thousands of years ago.)

The North American Land Mammal Ages we use are a geologic time scale based upon the evolution and extinction of the North American mammal fauna extending from 66.5 Ma to today (Woodburne, 2004). Our time scale spans three of these ages, the Blancan (4.9 to 1.8 Ma), Irvingtonian (1.8 Ma to 240 ka), and Rancholabrean (240 to 11 ka). Because many sites are only dated by comparison with the distinct mammal faunas of each land mammal age, we must time-average our data by binning them into these land mammal ages. Time averaging is the combination of fossil organisms from different times into one analysis unit; it can be created artificially, as we have done here, or it can be a consequence of the natural process of fossil accumulation. For example, each of our fossil sites probably

represents some degree of natural time averaging, but that effect is usually small compared with the binning into land mammal ages.

Taphonomy is the study of the path fossils take from the death of an organism to discovery and study by scientists. The taphonomic pathway of a site includes all of the physical, chemical, and biological alterations of the fossils on their way to discovery. Often the phrase 'taphonomic pathway' is shortened to 'taphonomy'. Consequently, a scientist may practise the discipline of taphonomy while investigating the taphonomy of a particular site.

Cluster analysis

As revealed in the Results and explored in the Discussion, rarity gain values for the Great Plains Holocene were significantly higher than expected. To further investigate this result, we performed a cluster analysis of Holocene localities by relative abundance of species, using the same relative abundance data we had used to calculate rarity gain. We hypothesized that the elevated rarity gain was caused by time averaging across a major faunal transition, either the glacial–interglacial transition or the transition across the megafaunal extinction. Localities were clustered using a standard Ward's distance hierarchical clustering algorithm in JMP v.8.0.2 (SAS Institute, 2009). This method is logical for grouping locality data, as it seeks to minimize the variance in clusters with the addition of new values. That way, it produces natural groups that have the smallest possible variance. Other clustering methods were investigated but did not affect the results, and so are not reported.

RESULTS

Sampling

The percent singletons, taxa found in only one locality, gives a simple index of sampling quality. Sampling steadily improves through the study interval, stretching from 40–50% singletons at the beginning of the Pliocene to ~20% for Holocene faunas (Table 1). For comparison, the singleton rates for the Recent from Davis (2005) were 13.3% for the Great Basin and 11.1% for the Great Plains. These Recent numbers reflect intensive natural history collecting, and can consequently be used as a basis of comparison for the fossil intervals.

To test for a sampling effect on our β diversity estimates, we performed multiple linear regressions, testing the combined effects of number of localities and length of bin on rarity gain and jackknife β. There was no strong relationship between β diversity estimate and number of localities/length of bin, supporting the assumption that overall sampling bias did not drive our results. The relationship between number of localities/bin length and jackknife β was not significant ($P = 0.84$ and $R^2 = 0.043$). Similarly, the relationship of rarity gain to number of localities/bin length was not significant ($P = 0.51$ and $R^2 = 0.16$).

First-order jackknife

None of the intervals show a significant difference between Great Plains and Great Basin jackknife β, so no single interval clearly shows that β is greater in one region or the other

Table 1. Summary sampling data and β diversity estimates

	Locations (*n*)	Species (*n*)	Singletons (*n*)	% Singletons	JKβ	JK var	RGβ	RG var
Great Basin	17	70	32	45.7	8.895	0.048	0.109	0.0005
Blancan	40	115	33	28.7	11.83	0.029	0.119	0.0002
Rancholabrean	166	93	19	20.4	9.147	0.004	0.111	0.00003
Holocene								
Great Plains								
Blancan	14	86	36	41.9	6.025	0.046	0.059	0.0002
Irvingtonian	9	68	34	50.0	5.270	0.066	0.061	0.0002
Rancholabrean	28	108	42	38.9	9.019	0.026	0.091	0.0002
Holocene	63	72	14	19.4	5.937	0.009	0.140	0.0001

Note: Jackknife β is based on richness, while rarity gain is based on evenness. JK = jackknife; RG = rarity gain.

(Fig. 2, Table 1). Confidence limits for each β value are large compared with the differences between regions; this is a consequence of the large numbers of singletons in the data. The results show the same pattern throughout: β diversity is greater in the Great Basin than in the Great Plains in all of our complete time intervals. This pattern of diversity (four consecutive intervals with the Great Basin highest: +, +, +, +), when combined with the data from Davis (2005) to create an overall pattern (three intervals of Great Plains highest, followed by seven of the Great Basin highest: −, −, −, +, +, +, +, +, +, +) is significant ($P = 0.05$) in a one-tailed runs test, suggesting that the greater diversity in the Great Basin seen in all of the time intervals is not random. Beta values are consistently higher, but not significantly so, in each Pliocene and Pleistocene interval than the late Miocene values from Davis (2005) (Fig. 2). Values peak in the Rancholabrean and decline into the Recent.

Rarity gain

Great Basin rarity gain remains constant from the Blancan to the Holocene with no value significantly different from any other (Fig. 3). From the late Early Hemphillian to the Blancan there is a significant drop in rarity gain, and rarity gain increases significantly from the Holocene to Recent. The Great Plains remains constant with no significant differences between intervals except for the unexpected, significantly higher Holocene value (Fig. 3). The differences between the Great Basin and Great Plains are significant in the three intervals for which data are available for both study regions: the Blancan, Rancholabrean, and Holocene. Great Basin β diversity is higher than that in the Great Plains in the Blancan and the Rancholabrean, but, unexpectedly, Great Plains β diversity is significantly higher than that in the Great Basin in the Holocene. This result does not follow the same trend seen in the richness analysis, where the Great Basin had consistently higher β diversity. For the Irvingtonian, there are not enough Great Basin sites for a valid comparison with the Great Plains.

Davis (2005) compiled β diversity estimates for the Recent Great Basin and Great Plains faunas from natural history museum collections amassed within the last ~100 years. There is

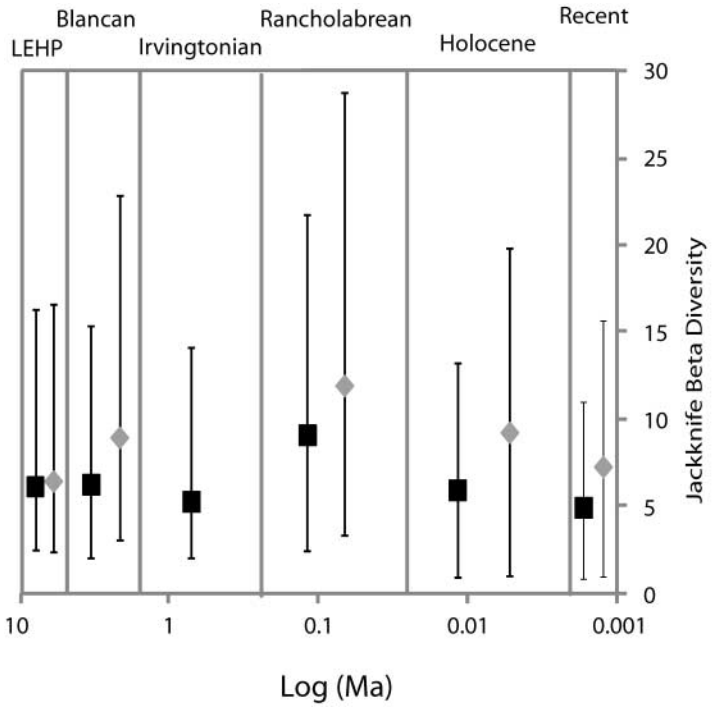

Fig. 2. Plot of jackknife β diversity through time in the Plio-Pleistocene. Time is plotted in Log (Ma) for simplicity of viewing. The Great Basin values are diamonds and Great Plains values are squares. The plot shows six intervals: Late Early Hemphillian (LEHP, 6.6–5.7 Ma), Blancan (4.9–1.9 Ma), Irvingtonian (1.9–0.15 Ma), Rancholabrean (0.15–0.013 Ma), Holocene (0.013 Ma–present), and Recent (<100 years old). The Late Early Hemphillian and Recent values are from Davis (2005) and are included for complete context. Bars are not standard error: they represent 95% confidence intervals and can be used to directly judge significance. While confidence limits are too large to infer clear results for any single interval, Great Basin values are consistently higher than Great Plains values, lending support to the hypothesis of elevated Great Basin β diversity.

a significant difference between the Holocene interval and the Recent for both the Great Basin and the Great Plains, but they show opposing trends, with the Great Basin increasing to the Recent and the Great Plains decreasing.

Cluster analysis

The cluster analysis of Great Plains Holocene localities by relative abundances shows a continuum of localities with no distinctive clusters or obvious breaks (Fig. 4). These Holocene faunas are distributed evenly through relative abundance space, showing no sign of distinct glacial and interglacial faunas or of distinct pre- and post-megafaunal extinction faunas (Fig. 4). The cluster analysis does not support a hypothesis of time averaging distinct faunas to create the elevated rarity gain of the Great Plains Holocene.

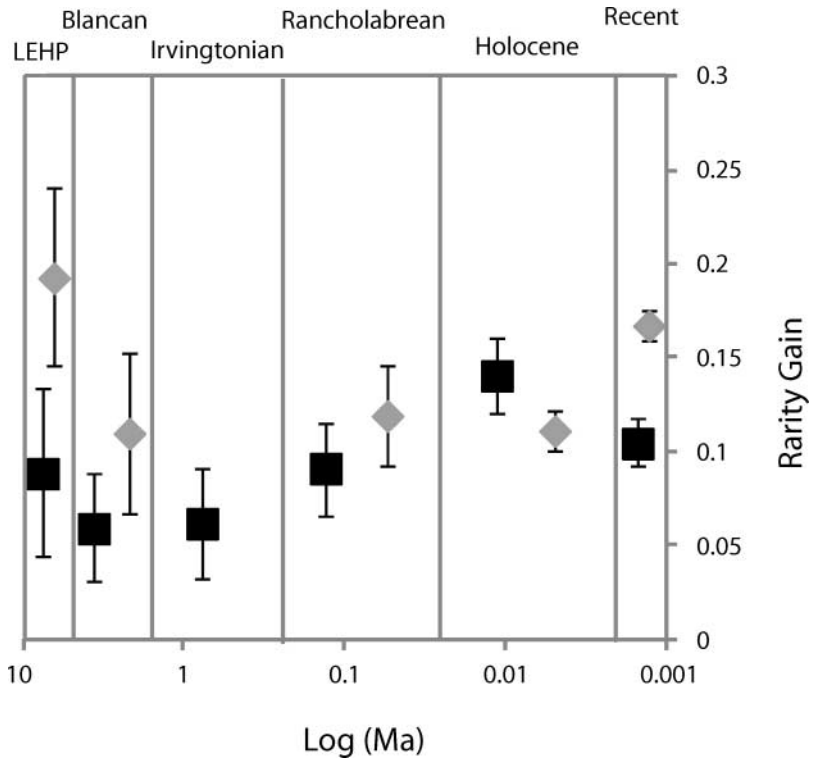

Fig. 3. Plot of rarity gain through time in the Plio-Pleistocene; details as in Fig. 2. Confidence limits are small enough for rarity gain to see significant differences between regions for each interval. Great Basin values are significantly greater in all but the Holocene, where the Great Plains value is unexpectedly high. See Discussion and Conclusions for details on this Holocene diversity spike.

DISCUSSION

Overall, our results support the hypothesis of Davis (2005), that tectonic change in the Great Basin structured Recent mammalian β diversity. We reach this conclusion because of the relative stasis of Great Basin β diversity throughout our study interval, suggesting that the modern macroecological structure was established more than 5 Ma, when the current level of topographic complexity was reached. There is a suggestion that climate may have played an additive role in structuring Recent Great Basin β diversity because rarity gain for the Great Basin increased significantly from the Holocene to the Recent. The role of climate must be acknowledged; Great Basin β diversity is not structured by only one process, but by the interplay between long-term tectonic processes and shorter-term climatic processes. Our results suggest that future climate change, away from pluvial–interpluvial cycling, will probably depress the β diversity of the Great Basin, but the topographic structure of the region will continue to support elevated β diversity compared with surrounding provinces.

One persistent problem with paleontological database analyses, as undertaken here, stems from using published data instead of museum collections data as the sole source (Davis and Pyenson, 2007). Data compiled from published papers can be problematic because the authors of the myriad studies included in the database usually did not have paleomacroecology,

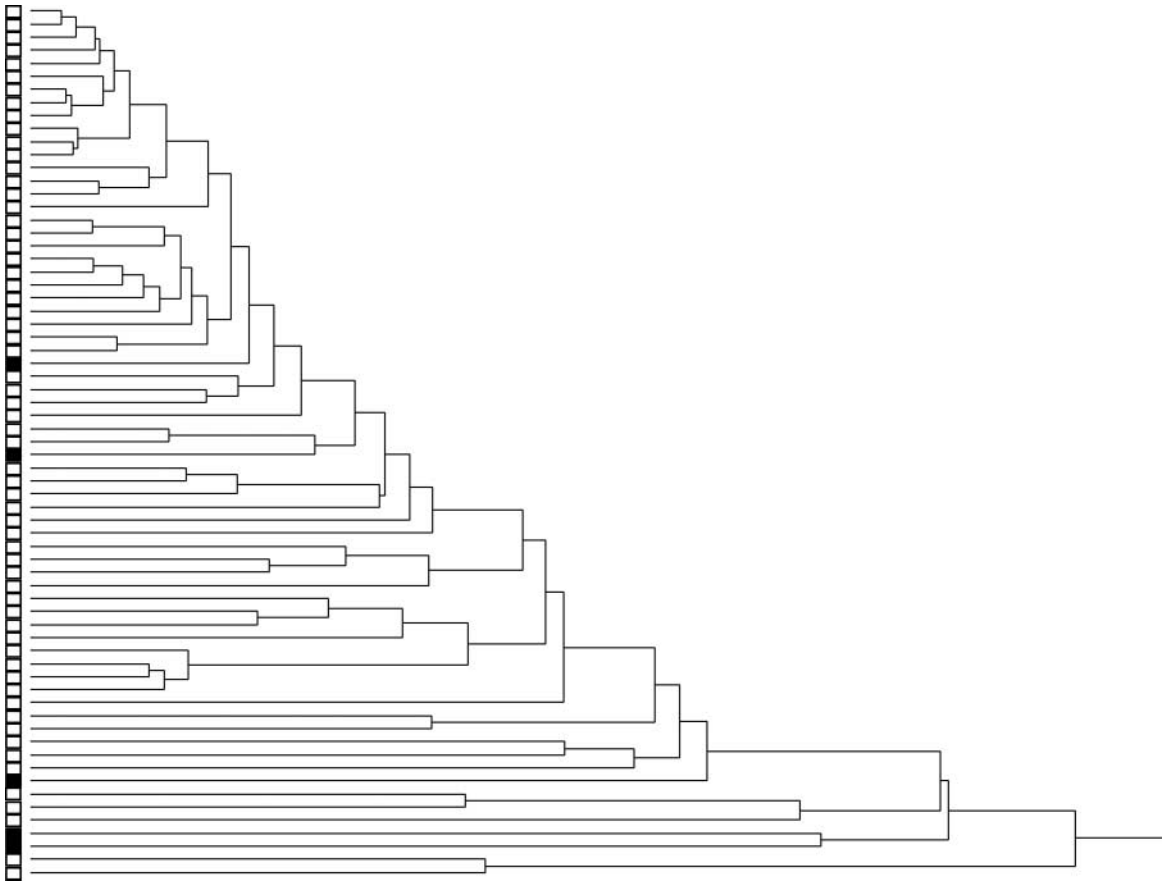

Fig. 4. Dendrogram of Great Plains Holocene localities, scaled by distance. Localities have been marked dark/open by the presence/absence of megafauna. The pectinate shape of this dendrogram suggests no strong clustering for two distinct faunas, as would be expected if a pre- and post-glacial or pre- and post-megafaunal-extinction signal were driving the Holocene Great Plains rarity gain.

the study of deep-time changes in landscape-scale ecology, as their focus. Consequently, they may have focused primarily on one taxon to the exclusion of others, or they may have simply published vouchers for each taxon, creating an inaccurate picture of the richness and/or evenness of a site (Davis and Pyenson, 2007). This problem is tractable, and surveys of Great Basin Miocene sites have indicated no systematic bias in occurrences and no consistent positive or negative bias in relative abundances (Davis and Pyenson, 2007; Gusey and Davis, 2010). On the other hand, there are clear problems with the identification of fossil specimens in the Holocene and Pleistocene, arising from a similarity-based approach to fossil identification (Bell *et al.*, 2010). At best, traditional identification adds noise to the data at the macroecological scale, but at worst it might dampen or erase any signal of distinction from modern faunas. Apomorphy-based identifications should eventually alleviate this problem (Bell *et al.*, 2010), but concerns over changing climate prevent us from postponing our large-scale investigations until that time. The unexpectedly high Holocene rarity gain for the Great Plains (Fig. 3) could be caused by a taxonomic bias in publications; several sites from that interval had extraordinarily high abundances for one or two species. However, we investigated that possibility and found little support for the publication bias hypothesis (see section on Holocene rarity gain spike for details).

The Great Basin β values are not static through the study: they decrease at the Plio-Pleistocene boundary, from the late Early Hemphillian to the Blancan, show no significant change through two interval transitions, and increase significantly from the Holocene to the Recent. This pattern of change indicates something biologically important is happening in the Great Basin during this time, and it cannot be caused by changes to the topography, which became relatively static soon after the beginning of the Pliocene (McQuarrie, 2004). The pattern does not appear to be the result of a sampling bias because there is no relationship between number of sites and rarity gain. The pattern of change in Great Basin rarity gain is likely biological and scale-dependent, a consequence of the much shorter Recent interval catching a single, equilibrated interpluvial fauna. Another possibility is that the upswing in Recent rarity gain is a consequence of human-mediated changes in ecosystem function. Human activity could have forced species to retract into more discrete microhabitats, reducing faunal overlap between localities, leading to an increase in β diversity.

The Rancholabrean and Holocene bring a new bias into play, compared with the Miocene and Recent data of Davis (2005). These are the first intervals where a systematic bias towards archaeological sites in the publication data could have affected the relative abundances of species. The Rancholabrean brings the First Americans, and the publication emphasis shifts from faunal-based paleontological studies to cultural-context-based archaeological studies, which often document many specimens of resource taxa and one or no specimens of non-cultural-resource species. This bias led to larger standard errors on our estimated γ evenness. In addition, the microhabitats sampled may have been artificially selected by human occupants, creating an inaccurate picture of β diversity. To account for the apparent bias in abundances at some sites, we re-ran our analyses of the Rancholabrean and Holocene, truncating relative abundances at two standard deviations above the mean abundance for the interval. Trimming the data in this way allowed us to test the sensitivity of our results to the abundance outliers. Hurlbert's (1971) evenness metric is sensitive to the relative abundance of the most common taxa, so it would be reasonable to expect these extremely high abundances to have an effect on the derived rarity gain for the interval. The paleontological assemblages in our data do not have such extreme abundances, so trimming

the data allowed us to test the hypothesis that abundance outliers were the source of changes in rarity gain. The resulting datasets produced qualitatively identical results with lower variances, suggesting that the emphasis on archaeological sites has had no systematic effect on the rarity gain. We have not reported the results of this exploratory analysis, instead keeping our focus on the least-altered dataset. We have not been able to address the potential for biases in the habitats sampled by archaeological sites that might be created by habitation selection by ancient humans (distinct from potential bias in modern human site exploration), but a bias of that type would tend to depress, not elevate, β diversity.

Singletons

The high percentage of singletons in our dataset was initially a concern, because the percent of singletons gives a simple index of sampling quality. Some of our samples are up to 50% singletons, so we found it necessary to understand how those rare taxa affect our overall results. The jackknife analysis uses the singleton rate to calculate both $\hat{\gamma}$ and its variance, so the prevalence of singletons is accounted for in the uncertainty of that parameter estimate. Rarity gain does not have the same direct connection to singleton rate; consequently, we removed all singletons from our samples and reran the rarity gain analysis for both the Great Basin and the Great Plains. Removing the singletons produced no significant difference in rarity gain values, suggesting the high singleton rate in our data does not control our rarity gain results. The singleton-trimmed dataset was not statistically different from the full dataset, so we have presented only the results for the full dataset because it has a much larger sample size, providing the best statistical power.

Holocene rarity gain spike

The most striking result of our analysis came from our 'control' region, the Great Plains, which shows significantly higher rarity gain during the Holocene than the Great Basin. This result was unexpected because the Great Plains have been tectonically quiescent throughout the study interval and have experienced the same climate transitions as the Great Basin. It is possible that this elevated rarity gain is a consequence of biased sampling, but our investigation into the literature that supports the FAUNMAP II database, combined with our cluster analysis of the faunas from the interval, suggests this rarity gain has biological meaning.

We initially hypothesized that the climate cycling of the last 2 million years is the cause of this high rarity gain. The majority of our sites for the Great Plains are from the modern state of Nebraska, which is located at the transition from the central to northern Great Plains. This location caused the region to experience dynamic transitions from glacial to interglacial periods in the Pleistocene, ranging from partially ice-covered arctic desert to temperate grassland (Prentice *et al.*, 1991). It is important when comparing the Rancholabrean, Holocene, and Recent values for the Great Plains to account for the different amounts of time averaging within sites. The Rancholabrean, stretching over 200,000 years (Bell *et al.*, 2004), saw a complete glacial–interglacial cycle. It is deeper in time than the other two intervals, meaning that generally each of its sites can average more time. The Holocene, stretching back only 11,700 calendar years ago, sees only the last part of the transition from glacial to interglacial and has very little time averaging. The Recent, of course, records only the beginning of anthropogenic climate change and has no more than century-scale time

averaging in its sites. The relative precision of Holocene sites breaks up the data, producing faunas from very specific time slices of the transition to interglacial. Rancholabrean sites average faunal change through more time, creating a more uniform sampling across the landscape that reflects the average condition through the much longer interval; consequently, the time-averaged Rancholabrean values capture the same signal as the instant snapshot of the Recent. It has been demonstrated in other contexts that the time averaging of fossil sites does a better job of capturing local diversity than natural history collection (Hadly, 1999; Barnosky *et al.*, 2003); here, we are suggesting that the different levels of time averaging in the Rancholabrean and Holocene have captured faunal information differently. The longer-term averaging of the Rancholabrean captures the regional macroecological trend, but the shorter-term averaging of the Holocene causes the signal of the climate transition to confound the regional macroecological signal.

We clustered the sites by relative abundance to investigate this hypothesis. We reasoned that the hypothesis of time averaging would produce distinctive clusters of glacial and interglacial sites, which were dominated by different species. In the end, however, the results rejected this hypothesis, indicating no distinct clusters (Fig. 4). While this continuum of faunas could be interpreted as capturing a gradual transition from glacial to interglacial, it does not fit our initial prediction for the time-averaging hypothesis. Glacial–interglacial transitions are generally regarded as climatically abrupt (Crowley and North, 1988); however, mammal faunas take ~5000 years to accommodate the transition (FAUNMAP Working Group, 1996; Terry *et al.*, 2011), so it is possible that our results reflect a smooth transition of faunas from the glacial to the interglacial. If the transition to an interglacial ecology were the primary driver of Holocene rarity gain, we would expect the Holocene to have a value closer to the Rancholabrean, which also time averages glacial and interglacial faunas. It is possible that the high rarity gain of the Great Plains Holocene represents a real and unprecedented macroecological signal in the region at that time.

In that vein, we explored the effect of the megafaunal extinction as a potential explanation for the higher rarity gain in the Holocene Great Plains. Approximately 11.5 to 10 ka, 15 genera of megafauna went extinct in North America (Barnosky *et al.*, 2004); it seemed that including sites from both before and after the megafaunal extinction might artificially elevate the β diversity. This could be because (1) the abundances of megafauna simply had a strong effect on the rarity gain calculation, or (2) after the extinction, faunas reorganized and had a strongly different abundance distribution. To test this hypothesis, we removed all localities with megafauna present and re-ran our rarity gain numbers. Even when localities containing megafauna were removed, the Great Plains rarity gain was still significantly higher than that of the Great Basin for the Holocene, rejecting the hypothesis that the megafaunal extinction was responsible for the spike. In addition, we would have expected the cluster analysis to show strong separate clustering of megafaunal and non-megafaunal sites, which it did not (Fig. 4). Thus the Holocene rarity gain spike cannot be explained by the megafaunal extinction.

In the end, the high rarity gain in the Great Plains Holocene is unexpected, currently unexplained, and deserves further investigation. To explore the pattern further, we plan to compile FAUNMAP II data from the surrounding Great Plains regions and investigate whether they show similarly high Holocene values relative to the Recent. If climate cycling is creating this pattern, we would expect to see it strongest in the region that experienced the most dramatic changes in climate and environment between full glacials and interglacials, the central and northern Great Plains. By including areas north and south of our current

study region, we will be able to determine whether high Holocene diversity levels are common throughout the area or are restricted to regions that experienced strong climate transitions. We also plan to investigate the effect of variability in taphonomy in relation to geographic area sampled and faunal sample size (Milideo *et al.*, 2011), and to explore possible connections to collateral diversity loss in Holocene small mammal faunas (Barnosky *et al.*, 2011).

Comparison with Davis (2005)

Davis (2005) did not have data from the Plio-Pleistocene; consequently, he lumped all of the FAUNMAP data into a single time slice. Our study was able to use FAUNMAP II to fill in those gaps. Here, we compare our Rancholabrean and Holocene results to his equivalent Pleistocene time slice. Our Great Basin jackknife β diversity values are both higher than those found in the Pleistocene interval of Davis (2005), but our Great Plains values are not. His value was 8.6 for the Great Basin, lower than both of our Great Basin values (Table 1). For the Great Plains, Davis (2005) calculated 6.4; our Rancholabrean value was higher, but our Holocene value was not (Table 1). The higher richness values of Rancholabrean and Holocene β diversity seen in the Great Basin compared with Davis (2005) could be a consequence of the finer resolution in the present study: by lumping multiple levels within a site, Davis (2005) artificially increased $\overline{\alpha}$, leading to a systematically lower β. The Great Plains Holocene data suggest this lumping did not consistently alter $\overline{\alpha}$. Another case can be made for biological process. FAUNMAP only included data back to the radiocarbon limit, ~40 ka (Graham *et al.*, 1994); adding the remainder of the Rancholabrean in FAUNMAP II gives us data on mammal faunas back to ~150 ka, so the higher β values incorporate much more time than was available to Davis (2005).

Our rarity gain results also do not show a consistent pattern, but most of our values are lower than the lumped Pleistocene value of Davis (2005). Both Great Basin values are below 0.168 (Table 1), the value Davis (2005) derived from FAUNMAP, but the Great Plains values are split, with the Rancholabrean below Davis's (2005) value of 0.119. These results are exactly the opposite of those for the jackknife β, making clear the disconnection between patterns of relative abundances and occurrences in these data.

CONCLUSIONS

We examined published mammal paleofaunal information for the Great Basin, compiled into the FAUNMAP II database (Graham *et al.*, 1994), to test the hypothesis that tectonic change over the Neogene drove the currently elevated β diversity of the region. We compared the Great Basin to a comparable region of the Great Plains, to provide a control region free from tectonic effects. Our results confirmed the hypothesis of a tectonic driver of β diversity in the Great Basin, but revealed an unexpected pattern of β diversity in the Great Plains.

Incomplete sampling rendered our richness-based results equivocal, with no intervals showing significant differences between the test and control regions. The Great Basin had consistently higher β diversity in the richness analysis, producing a pattern significantly more regular than expected by a random distribution of relative values. This pattern lends weight to the tectonic hypothesis, but the large variance in individual estimates leaves the richness-based test equivocal at best.

Evenness-based β diversity (rarity gain) showed a strong significance in each interval, but the relative position of the Great Basin and Great Plains was not consistent. The Great

Basin had higher rarity gain in all intervals except the Holocene. The consistency in evenness-based β diversity of the Great Basin is the evidence upon which we base our conclusion that tectonic change drove the evolution of the modern macroecology of the Great Basin.

The unexpectedly high Holocene rarity gain for the Great Plains requires additional explanation. Because the region was topographically quiescent, we cannot invoke the same driver as for the Great Basin. We have considered three main hypotheses to explain this spike: sampling bias, transition to interglacial climates, and megafaunal extinction. So far, we have been able to tentatively reject sampling bias, indicating this spike has biological meaning, but we have not been able to conclusively test our other hypotheses. We plan to broaden our analysis of the Great Plains Holocene in the hopes that we can establish the spatial dimensions of this trend and isolate the physical or biological factors that might be driving it.

To further explore the hypotheses explaining greater β diversity in desert ecosystems, we plan to examine deserts on other continents that (1) do not have the same history of topographic evolution and (2) have similarly well-sampled Plio-Pleistocene fossil records. Candidate areas at this time include the desert ecosystems of the Arabian Peninsula and Australia.

Mammalian macroecology in the western USA shows strong evidence of both tectonic and climatic drivers. In the current context of inexorably changing climates, it will become necessary to understand the three-way interplay among evolution of the landscape, the climate, and the organisms living at their interface (Barnosky, 2009). In some regions, such as the Great Basin, landscape evolution is the strongest driver, while in others climate dominates ecology at the landscape scale (Guralnick, 2006; Szabo *et al.*, 2009). Understanding the differences in macroecological rules between regions is essential to informing landscape-scale conservation policy.

ACKNOWLEDGEMENTS

We thank R. Graham, E. Lundelius, and A. Barnosky for making the FAUNMAP II data available to us. We thank M. Carrasco and J. McGuire for work on standardizing FAUNMAP II data and making them available on the web. We owe thanks to the members of the Hopkins Lab, who provided critical feedback on early drafts of this paper: S. Hopkins, J. Orcutt, W. McLaughlin, K. Stilson, and B. McHorse. We thank the two anonymous reviewers whose critical commentary improved the final form of this paper.

REFERENCES

Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **127**: 285–311.

Barnosky, A.D. 2009. *Heatstroke: Nature in an Age of Global Warming*. Washington, DC: Island Press.

Barnosky, A.D. and Carrasco, M.A. 2002. Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.*, **4**: 811–841.

Barnosky, A.D., Hadly, E.A. and Bell, C.J. 2003. Mammalian response to global warming on varied temporal scales. *J. Mammal.*, **84**: 354–368.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. and Shabel, A.B. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science*, **306**: 70–75.

Barnosky, A.D., Carrasco, M.A. and Graham, R.W. 2011. Collateral mammal diversity loss associated with late Quaternary megafaunal extinctions and implications for the future. In *Comparing the Geological and Fossil Records: Implications for Biodiversity Studies* (A.J. McGowan and A.B. Smith, eds.), pp. 179–189. Special Publication #358 of the Geological Society of London. London: The Geological Society.

Bell, C.J., Lundelius, E.L., Jr., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R., Jr. *et al.* 2004. The Blancan, Irvingtonian, and Rancholabrean mammal ages. In *Late Cretaceous and Cenozoic Mammals of North America* (M.O. Woodburne, ed.), pp. 232–314. New York: Columbia University Press.

Bell, C.J., Gauthier, J.A. and Bever, G.S. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary herpetofaunal stability hypothesis. *Quaternary Int.*, **217**: 30–36.

Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.*, **105**: 467–478.

Carrasco, M.A., Kraatz, B.P., Davis, E.B. and Barnosky, A.D. 2005. Miocene Mammal Mapping Project (MIOMAP). Available at: http://www.ucmp.berkeley.edu/miomap/.

Cole, M.R. and Armentrout, J.M. 1979. Neogene paleogeography of the western United States. In *Cenozoic Paleogeography of the Western United States* (J.M. Armentrout, M.R. Cole and H. TerBest, eds.), pp. 297–323. Los Angeles, CA: Pacific Section SEPM.

Cronquist, A. 1978. The biota of the Intermountain Region in geohistorical context. *Great Basin Nat. Mem.*, **2**: 3–15.

Crowley, B.E., Koch, P.L. and Davis, E.B. 2008. Stable isotope constraints on the elevation history of the Sierra Nevada Mountains, California. *GSA Bull.*, **120**: 588–598.

Crowley, T.J. and North, G.R. 1988. Abrupt climate change and extinction events in Earth history. *Science*, **240**: 996–1002.

Davis, E.B. 2005. Mammalian beta diversity in the Great Basin, western USA: paleontological data suggest deep origin of modern macroecological structure. *Global Ecol. Biogeogr.*, **14**: 479–490.

Davis, E.B. and Pyenson, N.D. 2007. Diversity biases in terrestrial mammalian assemblages and quantifying the difference between museum collections and published accounts: a case study from the Miocene of Nevada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **250**: 139–149.

Dickinson, W.R. 1979. Cenozoic plate tectonic setting of the Cordilleran region in the United States. In *Cenozoic Paleogeography of the Western United States* (J.M. Armentrout, M.R. Cole and H. TerBest, eds.), pp. 1–13. Los Angeles, CA: Pacific Section SEPM.

FAUNMAP Working Group. 1996. Spatial responses of mammals to late Quaternary environmental fluctuations. *Science*, **272**: 1601–1606.

Graham, A. 1999. *Late Cretaceous and Cenozoic History of North American Vegetation North of Mexico*. New York: Oxford University Press.

Graham, R.W. and Lundelius, E.L., Jr. 2010. FAUNMAP II: new data for North America with a temporal extension for the Blancan, Irvingtonian, and early Rancholabrean. FAUNMAP Database, Version 1.0. Available at: http://www.ucmp.berkeley.edu/faunmap/index.html.

Graham, R.W., Lundelius, E.L., Jr., Graham, M.A., Stearley, R.F., Schroeder, E.K., Anderson, E. *et al.* 1994. *FAUNMAP: A Database Documenting Late Quaternary Distributions of Mammal Species in the United States*. Illinois State Museum Scientific Papers #25(1–2). Springfield, IL: Illinois State Museum.

Guralnick, R. 2006. The legacy of past climate and landscape change on species' current experienced climate and elevation ranges across latitude: a multispecies study utilizing mammals in western North America. *Global Ecol. Biogeogr.*, **15**: 505–518.

Gusey, A. and Davis, E.B. 2010. Diversity biases of the published record of fossils at nine Miocene mammalian faunas of Nevada and Oregon. Paper presented to the Society of Vertebrate Paleontology Annual Meeting, Pittsburgh, PA.

Hadly, E.A. 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **149**: 389–409.

Heltshe, J.F. and Forrester, N.E. 1983. Estimating species richness using the jackknife procedure. *Biometrics*, **39**: 1–11.

Hren, M.T., Pagani, M., Erwin, D.M. and Brandon, M. 2010. Biomarker reconstruction of the early Eocene paleotopography and paleoclimate of the northern Sierra Nevada. *Geology*, **38**: 7–10.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**: 577–586.

Johnson, N.K. 1978. Patterns of avian geography and speciation in the Intermountain Region. *Great Basin Nat. Mem.*, **2**: 137–159.

Kelt, D.A. 1999. On the relative importance of history and ecology in structuring communities of desert small animals. *Ecography*, **22**: 123–137.

Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W. *et al.* 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology*, **77**: 746–761.

Kiflawi, M. and Spencer, M. 2004. Confidence intervals and hypothesis testing for beta diversity. *Ecology*, **85**: 2895–2900.

MacNally, R., Fleishman, E., Bulluck, L.P. and Betrus, C.J. 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *J. Biogeogr.*, **31**: 917–929.

McQuarrie, N. 2004. Reconstructing the Basin and Range province: the evolution of an extensional orogen in time and space. *GSA Abstracts with Programs*, **36**: 24.

Milideo, L., Falk, C., Semken, H. and Graham, R. 2012. *Multivariate analysis of a Late Holocene faunal transect across the forest-prairie ecotone*. Paper presented to the Society for American Archaeology Annual Meeting, Memphis, TN.

Olszewski, T.D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos*, **104**: 377–387.

Patil, G.P. and Taillie, C. 1982. Diversity as a concept and its measurement. *J. Am. Stat. Assoc.*, **77**: 548–561.

Prentice, I.C., Bartlein, P.J. and Webb, T.W., III. 1991. Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology*, **72**: 2038–2056.

SAS Institute. 2009. *JMP*, version 8.0.2. Cary, NC: SAS, Inc.

Simpson, E.H. 1949. Measurement of diversity. *Nature*, **163**: 688.

Szabo, N.D., Algar, A.C. and Kerr, J.T. 2009. Reconciling topographic and climatic effects on widespread and range-restricted species richness. *Global Ecol. Biogeogr.*, **18**: 735–744.

Tedford, R.H., Albright, L.B., III, Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., Jr., Storer, J.E. *et al.* 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene Epochs). In *Late Cretaceous and Cenozoic Mammals of North America* (M.O. Woodburne, ed.), pp. 169–231. New York: Columbia University Press.

Terry, R.C., Li, C.L. and Hadly, E.A. 2011. Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record. *Global Change Biol.*, **17**: 3019–3034.

Tueller, P.T., Tausch, R.J. and Bostick, V. 1991. Species and plant community distribution in a Mojave–Great Basin desert transition. *Vegetatio*, **92**: 133–150.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.*, **30**: 279–338.

Woodburne, M.O., ed. 2004. *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. New York: Columbia University Press.