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RESEARCH PAPER

Mammalian beta diversity in the Great Basin, western USA: palaeontological data suggest deep origin of modern macroecological structure

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ABSTRACT

Aim Recent work indicates that desert assemblages have elevated beta (β) diversity (between-locality turnover of species composition). This study compares β diversities between the Great Basin and the Great Plains of the western USA over the last 17 Myr. Today, the Great Basin is a topographically diverse desert scrubland to woodland and the Great Plains are low-relief temperate grassland, but 17 Ma they were more similar in topography, climate and land cover. A georeferenced database of mammal occurrences, complied from several sources, is used to test two hypotheses for the elevation of Great Basin β diversity: (1) that tectonic change of the topography has driven increased habitat packing in high- and low-elevation habitats, and (2) that climatic cycling in the Pleistocene has driven faunas from neighbouring provinces to overlap in the region.

Location The Great Basin of the USA, centred on Nevada, and the central Great Plains of the USA, centred on Nebraska.

Methods Mammalian faunal lists compiled from published records and the records of many museums, available online, were partitioned into time-slices ranging from the recent to 17 Myr old. Beta diversity was calculated for each time-slice in two ways: multiplicative β diversity using first-order jackknife richness, and additive beta diversity using Simpson's evenness.

Results Beta diversity is elevated in Nevada relative to Nebraska today. Beta diversity has been higher in the Great Basin since the Pleistocene and possibly since the late Early Hemphillian (*c.* 7 Ma). Beta diversity in the Late Barstovian (*c.* 13.5 Ma) of the Great Plains was higher even than β diversity in the Great Basin of today.

Main conclusions The elevated β diversity in the Hemphillian supports the tectonic change hypothesis. The patterns of β diversity in the Recent, Pleistocene and Hemphillian all suggest that local-scale processes are important. The β diversity of the Late Barstovian Great Plains supports other studies indicating increased primary productivity or species packing.

Keywords

Alpha diversity, beta diversity, climate change, desert ecosystem, gamma diversity, Great Basin, Great Plains, palaeoecology, tectonic change.

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INTRODUCTION

Recent work comparing the small mammal faunas of deserts throughout Earth has revealed uniformly high β diversity (between-locality turnover) in these arid-adapted communities, including the Great Basin of western USA (Kelt *et al.*, 1996). There is also evidence that the β diversity of vegetation (Tueller *et al.*, 1991) and birds and butterflies (Mac Nally *et al.*, 2004) are elevated in the Great Basin relative to non-desert parts of the continent. In addition to being a desert, the Great Basin has a distinctive tectonic history (Stewart, 1971; Cole & Armentrout, 1979; Dickinson, 1979; McQuarrie, 2004) that could also account for its elevated β diversity. By comparing the fossil record of mammal communities in the Great Basin to the more

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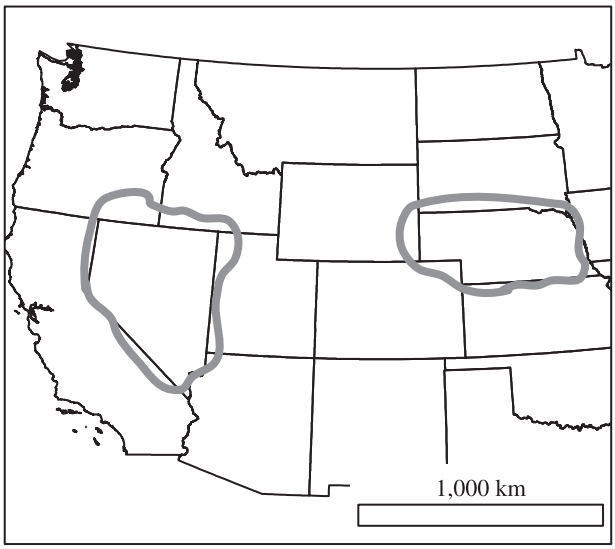

Figure 1 Map of the western USA, indicating the study areas in grey. The area to the west, centred on Nevada, is the Great Basin. The area to the east, centred on Nebraska, is the central Great Plains. All maps are Alber's equal-area conic projection, USGS version for the contiguous USA.

stable Great Plains through the last 17 Myr (million years), and cross-referencing the palaeobotanical record of environmental change, I test the hypothesis that modern Great Basin β diversity is generated by the environmental heterogeneity of its desert environment.

Beta describes the diversity among ecological assemblages (Whittaker, 1960). As with most ecological metrics, there are several ways to measure β diversity (Whittaker, 1972; Magurran, 1988; Kiflawi & Spencer, 2004). Here, I follow the work of Kiflawi and Spencer (2004), working with richness-based β diversity, and Olszewski (2004), working with evenness-based β diversity.

The Great Basin of western USA is a cold desert of systematically varying mountainous and flat terrain (Fig. 1). The terrain has been shaped by tectonic forces operating over the last 17 Myr, which slowly pulled the Great Basin apart longitudinally and created a series of basins and mountain ranges (Stewart, 1971; Cole & Armentrout, 1979; Dickinson, 1979; McQuarrie, 2004). The Sierra Nevada, to the west of the Great Basin, creates the rain shadow that dries the climate. Although the southern part of the Great Basin experiences limited monsoonal summer moisture, most of the limited precipitation in the Great Basin falls as snow during the winter (Cronquist, 1978). This intersection of climate and terrain creates a series of high elevation 'islands' of arid woodland habitat, separated by 'seas' of low elevation desert scrubland (Brown, 1971; Johnson, 1975; Brown, 1978).

This topography, dominated by barriers to dispersal, creates an expectation of elevated β diversity, through either evolutionary change or densely packed habitats (Brown, 1971; Mac Nally *et al.*, 2004). The isolation of the basins and ranges could foster evolutionary change, as seen in butterflies (Austin & Murphy, 1987); however, mammal and bird lineages show little or no evolutionary structuring within the Great Basin (Rogers, 1991a,b; Johnson & Marten, 1992). Only *Thomomys townsendii*, polyphyletically descended from *Thomomys bottae*, shows this structuring (Patton & Smith, 1994). The Great Basin, instead, is apparently an area of faunal overlap (Johnson, 1978).

Macroecological research has shown that the high elevation floras and faunas of the Great Basin behave as island assemblages (Johnson, 1975; Behle, 1978; Brown, 1978; Wells, 1983). Non-volant mammals, poor dispersers across lowland deserts, exhibit nested faunas (Brown, 1971; Hadley & Maurer, 2001). While early research suggested that the faunas are nested because they are dominated by extinction (Brown, 1971, 1978; Grayson, 1987; Patterson, 1987; Cutler, 1991), recent research indicates that the faunas are dynamic, with mechanisms other than extinction at work (Grayson & Livingston, 1993; Kodric-Brown & Brown, 1993; Skaggs & Boecklen, 1996; Lawlor, 1998; Grayson & Madsen, 2000; Hadley & Maurer, 2001). Brown (1971) suggested that the nested island faunas were created by Holocene warming forcing formerly widely distributed faunas upward onto the high-elevation islands.

These biological and tectonic factors lead to two major hypotheses concerning the origin of elevated β diversity within the Great Basin in comparison to the Great Plains. (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 it is a region of recent faunal overlap; current diversity represents an influx of taxa from neighbouring provinces, which have created a supersaturated system yet to be thinned through competition (cf. Brown, 1971; Cronquist, 1978; Johnson, 1978).

If (1) were true, β diversity would be expected to track the evolution of topographic relief in the Great Basin, with diversity levels reaching modern values at or before 5 Ma (million years ago), when the Great Basin reached its modern relief. If (2) were true, greater β diversity would not be seen until the development of climate cycling in the Pleistocene, as faunas began to be 'stirred' by the relatively rapid climate changes (Cronquist, 1978). Using the mammalian fossil record of the Great Basin, it is possible to test these hypotheses, by establishing whether Miocene faunas exhibit elevated β diversity.

To provide a 'control' on the natural experiment of tectonism in the Great Basin, the Great Basin results are compared with the same analyses on the central Great Plains. This area, containing the state of Nebraska and parts of surrounding states (Fig. 1), is tectonically stable and palaeontologically rich. Nebraska has had relatively low relief for the 17 Myr critical to this study (Swinehart *et al.*, 1985).

The local fossil records in the Great Basin and the Great Plains record a mosaic of information, influenced by both the macroecology of the palaeofaunas and the sampling filters of taphonomy. Taphonomy is the sum of all sampling effects (scavenging, hydraulic sorting, mechanical weathering, chemical change) on a fossil sample between the times of organisms' deaths and when they are discovered. To get a good signal for β diversity, it is necessary to get a cross-taphonomic signal. Isolating taphonomic

regimes can tell a lot about the evolution of α diversity, as in Bambach's (1977) study that demonstrated different α diversity patterns in high-stress, variable nearshore and open marine invertebrate communities through time. In this case, however, I want to summarize what is happening across multiple habitats, each often represented by a different taphonomic regime. Carefully considering the taphonomy for critical well-sampled intervals in the past 17 Myr allows me to detect the influences of sampling, verifying that the β diversity signal reflects biological reality.

While the Great Basin underwent tectonic expansion, the Earth experienced global cooling. This cooling was the result of a complex interaction between ocean circulation and the alteration of atmospheric CO_2 levels, driven by tectonic change in the southern hemisphere and the Himalayas (Raymo & Ruddiman, 1992; Flower & Kennett, 1993, 1994; Raymo, 1994). Movement of continents away from Antarctica allowed formation of the circumpolar current and the first continental glaciers in east Antarctica (Kennett, 1995). At the same time, uplift of the Tibetan Plateau intensified global chemical weathering, drawing down atmospheric CO_2 and intensifying global cooling (Raymo & Ruddiman, 1992). Climate changes in a mosaic fashion across the terrestrial surface; global warming might be expressed locally as cooling or a change in precipitation (National Assessment Synthesis Team, 2001). Consequently, it is necessary for palaeoecologists to consider both changes in global mean climate and in local climate, where available (Barnosky, 2001; Barnosky & Carrasco, 2002).

STUDY REGIONS

Great Basin

The Great Basin includes the northern and central portions of the Basin and Range physiographic province of western USA (Dickinson, 1979; Graham, 1999). The Great Basin is bounded on the east by the Rocky Mountains and the Colorado Plateau, on the west by the Sierra Nevada and the Klamath Mountains, on the north by the Columbia Plateau and on the south by the southern Basin and Range (Graham, 1999). The Basin and Range consists of a series of repeated internal drainages and mountain ranges, formed by extensional normal faulting (Stewart, 1971). The area included in this study extends from latitude 44° N to 36° N and longitude 120° W to 113° W (Fig. 1). The study area is confined to the US state of Nevada (286,297 km^2) for the Pleistocene and the Recent collections, in order to keep sample sizes tractable (Fig. 2a,c).

Great Plains

The Great Plains (or High Plains) province of the central USA consists of low-relief grasslands that extend from the northern to the southern border, bounded on the east by the Central Lowland and on the west by the Rocky Mountains (Graham, 1999). The area included in this study is in the central part of the Great Plains, extending from about latitude 44° N to 39° N and longitude 105° W to 95° W (Fig. 1). This area was included because of its similar latitude to Nevada and its high concentration of Miocene fossil sites. The study area for the Pleistocene and the Recent collections is confined to the US state of Nebraska (200,343 km^2), again, to keep sample sizes tractable (Fig. 2b,d).

METHODS

Faunal data

The data included in this analysis are from four sources, all of which are available on the Internet.

Modern faunal data

Modern faunal data for Nevada come from the collections of the University of California Museum of Vertebrate Zoology (MVZ) (http://elib.cs.berkeley.edu/mvz/). These data are individual specimen records, each with information about its geographical provenance. To make them comparable to the fossil data, which include a certain amount of spatial averaging, I grouped the specimens into localities based on basins and ranges (Fig. 2a). There is a small amount of geographical error in the information with these specimens, because it was often originally recorded as a written description of provenance, and many were collected before topographic maps became widely available. Despite this small error and my grouping by landforms, these data are more precise than the fossil data; we know the times of death to the day, which we will never know for fossils.

The MVZ data for Nebraska does not have adequate geographical coverage; the specimens are mostly from the northern part of the state. I supplemented them with data from the Mammal Networked Information System (MaNIS: http://elib.cs.berkeley.edu/manis/). MaNIS is a distributed database network that concurrently searches 12 natural history museum collections. The MaNIS data included in this study are compiled from the collections of the University of Kansas Biodiversity Research Center, the University of Michigan Museum of Zoology, the Field Museum of Natural History, the Michigan State University Museum, the University of Washington Burke Museum, the California Academy of Sciences, the Los Angeles County Museum of Natural History, the Utah Museum of Natural History and the Museum of Natural Science at Louisiana State University, in order of decreasing number of records.

MaNIS data are not provided with geographical data as precise as those of the MVZ collections, so, I grouped all of the Nebraska data by county (Fig. 2b). With the exception of Cherry County, the counties of Nebraska are relatively uniform in size and most follow the US Geological Survey township grid. Thus, the counties provide landscape-scale quadrats. Additionally, the sample sizes per county are comparable to the sample sizes from my localities in Nevada, and the few places in Nebraska where landforms subdivide the landscape, e.g. along the Niobrara River, the county boundaries reflect that subdivision. Not all counties are sampled by MaNIS, but the geographical distribution of sampling is effectively random.

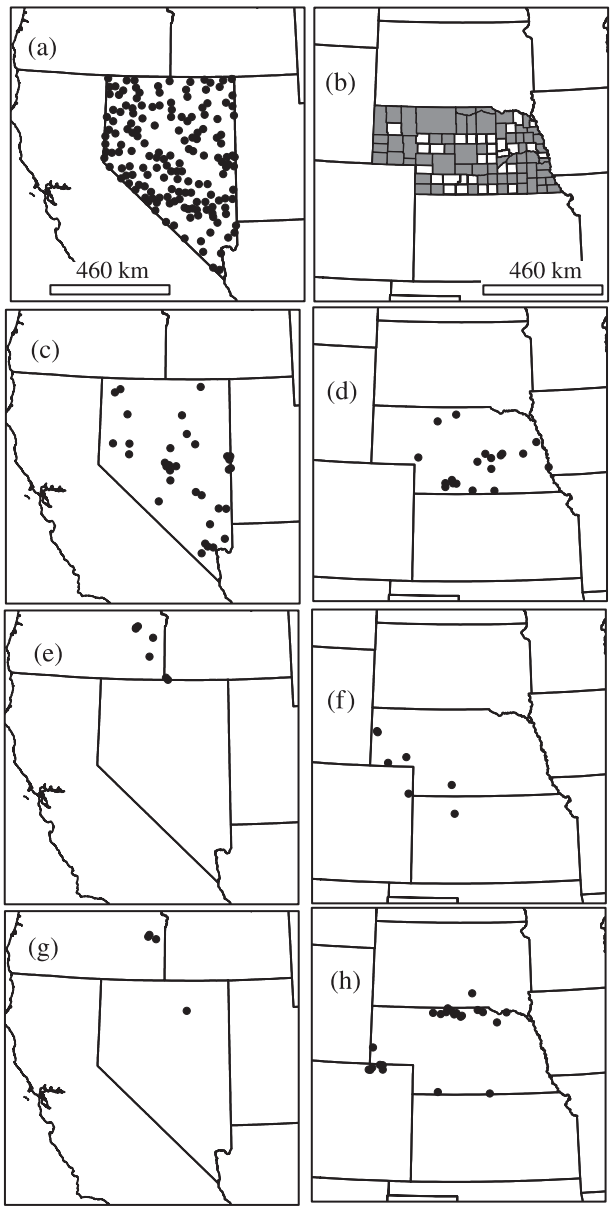

Figure 2 Localities included from: (a) Recent of Nevada, (b) Recent of Nebraska (included counties in grey), (c) Pleistocene of Nevada, (d) Pleistocene of Nebraska, (e) late Early Hemphillian of Great Basin, (f) late Early Hemphillian of central Great Plains, (g) Late Barstovian of Great Basin, and (h) Late Barstovian of central Great Plains. See Fig. 3 for age of Miocene intervals. Each point represents one physical locality included in the study.

Pleistocene faunal data

I used data from the FAUNMAP database (FAUNMAP working group, 1994: http://www.museum.state.il.us/research/faunmap/) for the Pleistocene and Holocene (Fig. 2c,d). The FAUNMAP database includes published mammalian occurrences up to the limit of radiocarbon dating, *c.* 40,000 years ago. FAUNMAP data include geographical provenance, stratigraphy, sedimentology and geochronologic age of each fossil locality. Faunal occurrence data contain, when possible, numbers of identified specimens (NISP) and minimum numbers of individuals (MNI). NISP is a count of all specimens referred to a taxon within published papers. MNI is calculated as the largest number of elements from one side, e.g. 24 left astragali (ankle-bones) and 19 right astragali give an NISP of 43 and an MNI of 24. Generic and specific taxonomy of faunal occurrences has been updated following the most recent published references. Because of their age, the FAUNMAP data contain many of the same taxa as those found today, but the localities contain more time averaging (thousands of years as opposed to < 100 years for the modern collections). Although detailed temporal data are available from FAUNMAP, in order to make the Pleistocene data comparable to the more thoroughly time-averaged Miocene data, all of the FAUNMAP data were analysed as a single time-slice. I lumped all occurrences from localities broken into stratigraphic levels, even those where the levels were known to represent different subdivisions of the Holocene.

Miocene faunal data

I used data from the MIOMAP database (Carrasco *et al.*, 2005) for the Miocene (Fig. 2e–h). These data are compiled from the primary literature following the FAUNMAP model (FAUNMAP working group, 1994; Barnosky, 2001; Barnosky & Carrasco, 2002), and recorded in a database linked to a geographical information system (GIS) at UC Berkeley. These data are grouped into time-slices of varying length, based on the recent biochronology of Tedford *et al.* (2004). Taxonomy was standardized in accordance with the MIOMAP protocols (Carrasco *et al.*, 2005), which in essence follow Janis *et al.* (1998) for carnivores and ungulates, Korth (1994) for rodents and the family level taxonomy of McKenna and Bell (1997). Most data in the database are from the published literature; publications that do not record complete locality or faunal occurrence data result in incomplete database entries. Although the lengths of the Miocene time-slices are uneven, they have been constructed because they represent times of relative faunal stability (Tedford *et al.*, 2004). These time-slices may be more useful for palaeoecological studies than slices of uniform length, as they create biologically equivalent units of comparison, instead of chronologically equivalent units (Escarguel & Bucher, 2004).

Standardization of faunal data

Subspecific identifications were removed, and data for subspecies were summed within species. Introduced species (exotics and domestics) and humans were omitted from the study. Bats were removed from faunal lists, because bats are (1) not restricted by the same geographical barriers as non-volant mammals, and (2) are often very poorly preserved in the fossil record. In this way, modern faunas were made more comparable to fossil faunas. As a standard practice (Alroy, 1996; Barnosky & Carrasco, 2002), generic indeterminate identifications were only kept for intervals that had no specific identifications for that genus. Similarly, familial indeterminate identifications were only

kept if there were no generic identifications within that family. For example, if a time-slice contained specimens identified only as 'Camelidae', they would be discarded if other specimens were identified as '*Megacamelus*.' Similarly, specimens identified only as '*Megacamelus*' would be discarded if there were specimens identified as '*Megacamelus merriami*.' After indeterminate taxa were removed, only localities with at least five taxa were kept in the analysis, as poorly sampled localities can artificially lower α, increasing β.

Beta estimation

Beta diversity metrics used here compare diversity summed over the study area (γ) to the average diversity at a single locality within the study area (α). Diversity is composed of richness (number of species) and evenness (relative numbers of individuals in each species) (Magurran, 1988). In order to account for both aspects of diversity, I use two different methods of estimating β diversity. The first is the multiplicative formulation of β diversity from Kiflawi and Spencer (2004), which relies on the first-order jackknife estimate of species richness (Heltshe & Forrester, 1983). The second is the additive formulation of β diversity from Olszewski (2004), which relies on Hurlbert's (1971) reformulation of Simpson's (1949) evenness metric. These recent workers emphasize calculating the variance of β diversity and testing hypotheses about β diversity (see Davis, 2005 for a more in-depth review).

The method of Kiflawi and Spencer (2004) uses the first-order jackknife richness estimator (Heltshe & Forrester, 1983) to account for the effects of differing sample sizes between regions and to produce a variance for β diversity. In this formulation, β is:

$$\beta = \frac{\gamma}{\bar{\alpha}} - 1.$$

Values of this jackknife β count the number of complete turnovers in α diversity needed to reach γ diversity. The first-order jackknife richness estimator is calculated as:

$$\hat{\gamma} = \gamma_{\text{obs}} + u\left(\frac{K-1}{K}\right),$$

where $\hat{\gamma}$ is the estimated total richness, γ_{obs} is the observed γ richness, u is the number of singletons (species found in only one site), and K is the total number of collections (sites, localities, assemblages, faunas, etc.). The first-order jackknife has a known analytical solution for its variance:

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

where f_s is the number of sites that contain s of the singletons (Heltshe & Forrester, 1983). This metric is based entirely on species richness and includes no information about relative abundance at localities. Consequently, it can be used with presence/absence data if relative abundances are not available.

In contrast, Simpson's (1949) evenness includes information about the relative abundance of species (Hurlbert, 1971; Olszewski, 2004). It measures the probability that any two individuals taken from a sample will be from different species, and is calculated as:

$$\Delta_2 = 1 - \sum_{i=1}^{S}\left(\frac{n_i}{N}\right)^2,$$

where N is the total number of individuals in the sample, n_i is the number of individuals in the i^{th} species and S is the total number of species in the assemblage (α for a single locality, γ for the sum of individuals over all localities). Δ_1, Hurlbert's (1971) measure of interspecific encounter, is the unbiased version of this diversity metric (Simpson, 1949):

$$\Delta_1 = 1 - \sum_{i=1}^{S}\left(\frac{n_i}{N}\right)\left(\frac{n_i - 1}{N-1}\right) = \frac{N}{N-1}\Delta_2$$

and has a known variance of:

$$\text{Var}(\Delta_1) = \frac{4(N-2)\sum\left(\frac{n_i}{N}\right)^3 + 2\sum\left(\frac{n_i}{N}\right)^2 - 2(2N-3)\left(\sum\left(\frac{n_i}{N}\right)^2\right)^2}{N(N-1)}.$$

Because it is not a strictly concave measurement of evenness, Δ_1 cannot be used to directly calculate β (Lande, 1996; Olszewski, 2004). That is, the values of Δ_1 at the landscape scale may be less than the average local value, producing a negative β, so Δ_2 must be used. Olszewski's (2004) method uses the additive formulation of β to produce Δ_β, a measure of β diversity in terms of Simpson's evenness:

$$\Delta_\beta = \Delta_{2,\gamma} - \overline{\Delta_{2,\alpha}} = \frac{N-1}{N}\Delta_{1,\gamma} - \overline{\Delta_{1,\alpha}} + \frac{\sum_1^K \Delta_{1,\alpha}}{N},$$

where, once again, N is the total number of specimens or individuals and K is the total number of sites (Olszewski, 2004). By propagating the variance through this equation, I can estimate the variance of Δ_β as:

$$\text{Var}(\Delta_\beta) = \left(\frac{N-1}{N}\right)^2 \text{Var}(\Delta_{1,\gamma}) + \left(\frac{N+K}{NK}\right)^2\left(\sum_1^K \text{Var}(\Delta_{1,\alpha})\right)$$

with equal weight given to all sites in $\overline{\Delta_{1,\alpha}}$. Δ_β reflects changes in both richness and evenness across the landscape (Patil & Taillie, 1982); that is, Δ_β will be higher in a study area where a taxon is common in one locality and rare in another, even if a single group of taxa is found in all localities (richness γ = richness α). Patil and Taillie (1982) call this metric 'rarity gain', as it indicates the gain in relative abundance of rare taxa when summed across a region, as opposed to averaged from individual localities (Olszewski, 2004). By comparing both richness and evenness, it is possible to discern more subtle patterns of diversity across the landscape.

Scales of comparison

Alpha diversities from the sorts of deposits typical of the Miocene records of the Great Basin and the Great Plains represent spatial averaging on the order of 10^2–10^3 km^2 and temporal averaging on the order of 10^2–10^4 years (Behrensmeyer *et al.*, 1992). The temporal bins through the Miocene calculate γ diversity for areas on the order of 10^4–10^5 km^2, but the geographical areas sampled in each interval are comparable between the Great Basin and Great Plains (Davis, 2005). Pleistocene terrestrial faunas sample α diversity from similar geographical areas to the Miocene, on the order of 10^2 km^2 (Porder *et al.*, 2003), but from much smaller temporal intervals (hence my artificial averaging of FAUNMAP data). The Pleistocene γ diversity is calculated within states of Nevada and Nebraska, with areas on the order of 10^5 km^2. The Recent data for Nevada have been organized to create localities comparable to those of the fossil record, with α diversity sampled over areas on the order of 10^3 km^2. The Recent data for Nebraska were organized by county, also producing α diversity estimates from areas on the order of 10^3 km^2. The Recent γ diversity is calculated within states of Nevada and Nebraska, with areas on the order of 10^5 km^2.

Data analysis

All data were analysed using spreadsheets constructed in Microsoft Excel 2002 and the statistical package JMPIN 5.1 (SAS Institute). To account for the multiple comparisons, I used a Bonferroni correction for the jackknife and rarity gain analyses. Because I have eight time-slices, my critical *P* value is 0.00625. I also used a runs test (Zar, 1999) to diagnose whether the observed pattern of relative beta diversity between Nevada and Nebraska is significantly different from random.

RESULTS

The major patterns of the results (Figs 3 & 4) are the same: diversity is higher in the Great Plains than in the Great Basin during the Late Hemingfordian, Barstovian and Clarendonian. There is a switch in the Early Hemphillian, with the Great Basin higher than the Great Plains. Finally, in the Pleistocene and the Holocene, the diversity continues to be higher in Nevada, representing the Great Basin, than in Nebraska, representing the Great Plains. This pattern of relative diversity (GP, GP, GP, GB, GB, GB, GB) is significant ($P = 0.05$) in a one-tailed runs test, indicating that the switch in sign of the difference between Nevada and Nebraska is not random.

First-order jackknife

The standard errors of the jackknife estimates of β are so large for the Miocene intervals that only the Late Barstovian, with a relatively large effect size (a difference of 7.92, three and a half times the effect size in the Recent), shows a significant difference ($P = 0.001$) (Fig. 3). The differences between the Great Basin and the Great Plains are not great through the Miocene, but there is a shift in the early Early Hemphillian, from greater β diversity in the Great Plains to the Great Basin. The Great Basin continues to have higher β diversity in the Pleistocene and the Recent, with a higher absolute difference than in the Miocene. The difference is not significant for the Pleistocene, but the Great Basin of the Recent is significantly more diverse than the Great Plains ($P = 0.002$, but see Discussion).

Rarity gain

There are significant differences between Great Plains and Great Basin Δ_β for the Late Barstovian ($P < 0.0001$), the late Early Hemphillian ($P = 0.002$), the Pleistocene ($P < 0.0001$) and the Recent ($P < 0.0001$) (Fig. 4). The Early Barstovian ($P = 0.01$) and the early Early Hemphillian ($P = 0.04$) meet a standard significance criterion, but do not meet the stricter Bonferroni criterion. All of the significant differences match the trends seen in jackknife β diversity, with the Great Plains higher in the Barstovian and the Great Basin higher from the Early Hemphillian to the Recent. The differences in the Pleistocene and the Recent, while significant, are not as large as those in the late Early Hemphillian (Fig. 4).

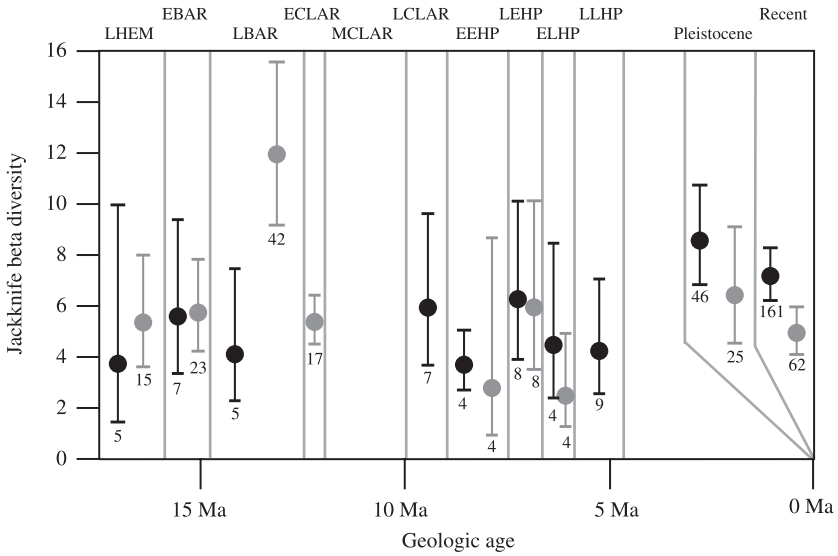

Figure 3 Plot of jackknife β diversity against time. Time flows from left to right. Great Basin in black, Great Plains in grey. Pleistocene and Recent are expanded for ease of comparison. Names of North American land mammal ages across top: LHEM, Late Hemingfordian (17.5–15.9 Ma); EBAR, Early Barstovian (15.9–14.8 Ma); LBAR, Late Barstovian (14.8–12.5 Ma); ECLAR, Early Clarendonian (12.5–12 Ma); MCLAR, Middle Clarendonian (12–10 Ma); LCLAR, Late Clarendonian (10–9 Ma); EEHP, early Early Hemphillian (9–7.5 Ma); LEHP, late Early Hemphillian (7.5–6.7 Ma); ELHP, early Late Hemphillian (6.7–5.9 Ma); LLHP, late Late Hemphillian (5.9–4.7 Ma). Error bars represent 95% confidence intervals. Numbers below each point indicate the number of localities included in that estimate.

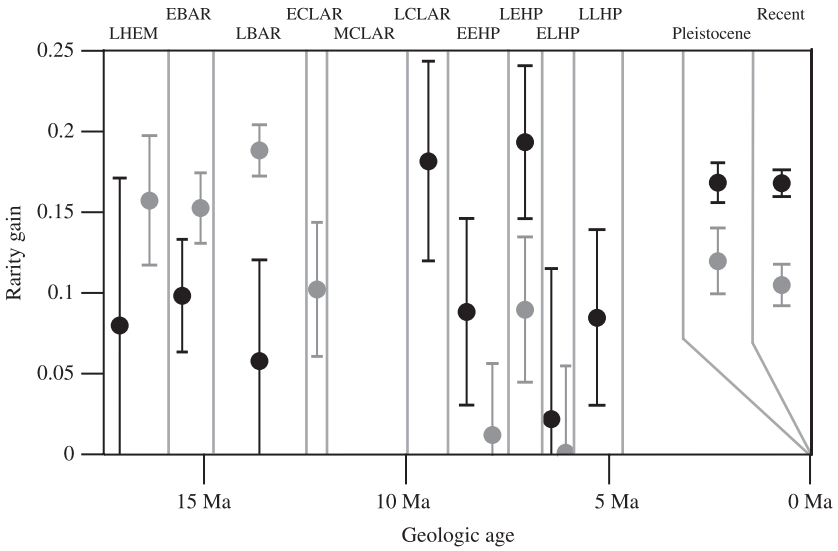

Figure 4 Plot of rarity gain (Δ_β) against time. Higher values indicate more variability in the relative abundance of species across the landscape; that is, there are changes in dominant species between sites. Lower values indicate species tend to have the same relative abundance across all sites. Time and abbreviations as in Fig. 3. Great Basin in black, Great Plains in grey. Error bars represent 95% confidence intervals.

DISCUSSION

The pattern of β diversity through the last 17 Myr is consistent between the two methods, and the significant runs test lends support to the general conclusion that β diversity was higher in the Great Plains until sometime before the Early Hemphillian, about 7 Ma, when the Great Basin began to have higher β diversity. Unfortunately, there are not enough sites in both the Great Plains and the Great Basin of the Clarendonian, the time period from 12.5 to 9 Ma, to be sure exactly when Great Basin β diversity might have become elevated.

The interesting differences in the results lie in the statistical powers of the methods. The jackknife method is not sensitive to the differences between the Great Plains and the Great Basin through most intervals, but the evenness-based metric picks up significant differences in many intervals. The differences may also reflect the relative susceptibility of the two metrics to differences in sample sizes.

First-order jackknife

The large standard errors for all of the fossil intervals (Fig. 3) are driven by two major factors: the large number of singletons, often concentrated in only one or two localities, and the small number of localities in each time-slice. These two factors are symptomatic of the undersampling common in the fossil record. A locality with a large number of singletons indicates that a segment of the regional diversity has only been sampled once, which may indicate that additional diversity remains unsampled. The small numbers of localities speak for themselves. In the end, the great uncertainty in this measurement of diversity leads me to be cautious about drawing conclusions from it alone.

Simpson's evenness

These results (Fig. 4) are slightly more difficult to interpret than the richness-based β diversity, as they indicate changes in the relative evenness of assemblages as the frame of reference changes from localities to provinces. Species that are rare at one locality will be more common at another, so summing all of the individuals in a province will result in a more even distribution than averaging the evenness from all sites within the province. Δ_β measures how much more even the province scale is than the locality scale. A higher Δ_β indicates a province with localities with very different dominance structures, but they may all include the same taxa (as discussed in Methods). So, the trend in Δ_β indicates a relative increase in the number of different evenness regimes within the Great Basin, starting in the Early Hemphillian.

Taphonomic and sampling problems

General comparability issues

The two biggest problems in comparing the Great Plains and the Great Basin are (1) the nature of floral change through the Miocene and (2) the greater emphasis on collection and publication in the Great Plains. The different vegetational histories in the Great Plains and the Great Basin must have had an important effect on their macroecologies through time. The change to grass-dominated ecosystems is the major story of ecological change in the Miocene of the Great Plains (Graham, 1999; Strömberg & Feranec, 2004). Recent evidence places the transition to grass dominance in the central Great Plains at the beginning of the Miocene, about 22 Ma (Strömberg, 2004), well before the drop in β diversity in the Great Plains between the Barstovian and the Clarendonian. The Great Basin, however, has long been dominated by the rain shadow of the Sierra Nevada, with a vegetative history of slow assemblage of arid suitable taxa over the last 20 Myr (Graham, 1999). Future, more detailed, work directed at the Pliocene and the Pleistocene should aim to tease apart the relative impacts of changing topography and flora in the Great Basin.

The Great Plains has both more abundant and more accessible fossil sites. Consequently, the sample sizes are much larger in the Great Plains than in the Great Basin for almost all sampled intervals (Fig. 3). This sample size disparity has not biased the

results directly, but the combination of larger samples in one province and smaller samples in the other could be contributing to some of the observed differences in β diversity through time. Jackknife β diversity is more susceptible to sample size differences than rarity gain (Davis, 2005). Most of the critical time-slices through the Late Miocene have the same small number of sites in both the Great Plains and the Great Basin (Fig. 3). Also, the Great Plains has many more sites than the Great Basin in the Early Barstovian, but jackknife β diversity is very similar between the two regions (Fig. 3).

Completeness of sampling could also have an effect. Less complete sampling, as in the Great Basin, would depress Δ_β, because assemblages would seem overly even. Initial published samples of fossil assemblages often capture a similar number of individuals within each species as they provide vouchers for the entire fauna. If faunas are analysed for palaeoecological reasons, or thoroughly published as parts of palaeontological remediation work, their published evenness better reflects underlying collections (Davis & Pyenson, 2003; Davis, 2005). Many of the earlier faunas in the Great Basin were published in greater detail than those from later periods. Consequently, the bias in Δ_β is in the opposite direction from the observed trend. The biggest problem for both β metrics is not a systematic bias from differences in sampling regimes, but simply the small sample sizes inherent in the fossil record.

Because β diversity is sensitive to geographical area sampled, differences in geographical dispersion of samples may also affect comparisons of β diversity (Mac Nally *et al.*, 2004). Most intervals have comparably dispersed sites in the two provinces. I have included brief discussions of the sampling within the four intervals critical to this analysis: the Late Barstovian, late Early Hemphillian, Pleistocene, and Recent. Davis (2005) includes an in-depth analysis of all intervals.

Late Barstovian

The Great Basin is represented by five localities (Fig. 2g), and the Great Plains is represented by 42 localities (Fig. 2h). At this time, the depositional settings of both areas are dominated by river and stream conditions, but the Great Plains sample derives from a larger variety of depositional systems (Galbreath, 1953; Regnier, 1960; Skinner & Taylor, 1967; Shotwell, 1968; Skinner & Johnson, 1984; Voorhies, 1990).

Both analyses indicate that the Great Plains has significantly higher β diversity than the Great Basin in this interval (Figs 3 & 4). Janis *et al.* (2000, 2002, 2004) have argued that greater α diversity of mammalian browsers in the Great Plains during this interval is a result of biological processes responding to higher primary productivity. It is possible that whatever process is structuring α diversity in this interval is also affecting β diversity, leading to both higher richness at single sites and greater patchiness of distributions across the landscape.

Late Early Hemphillian

The Great Basin and the Great Plains are both represented by eight localities (Fig. 2e,f). The spatial coverage of the Great Plains is similar to, but slightly greater than, that of the Great Basin. The Great Basin sites in this interval include river and lake environments as well as a diversity of preservational regimes (Shotwell, 1963, 1970; Becker & McDonald, 1998). The Great Plains deposits are predominantly from low-energy depositional environments, with the possible exception of some sites from the Ash Hollow Formation (Cook, 1922; Skinner *et al.*, 1977; Zakrzewski, 1988).

This interval provides the best Miocene comparison in terms of sample size and geographical coverage. The jackknife β values for the two provinces are not significantly different (Fig. 3). The difference in Δ_β, on the other hand, is comparable to the one found in the Recent (Fig. 4). This result indicates that while the actual species turnover (measured by jackknife β) is the same in the two provinces, the changes in relative abundance across the provinces had taken on the same shape as seen in modern samples. Unfortunately, the sample sizes are too low in the other parts of the Late Miocene to be sure exactly when this pattern was established or whether it is continuous with that of the Pleistocene and the Recent (Fig. 3).

Pleistocene (FAUNMAP)

The samples from the FAUNMAP database provide the best sampling from the fossil periods included in this study. The Great Basin sample (restricted to Nevada) includes 46 localities (Fig. 2c), and the Great Plains sample (restricted to Nebraska) includes 25 localities (Fig. 2d). The jackknife analysis shows no significant difference between the two areas, despite an effect size comparable to the modern difference (Fig. 3). Conversely, the Δ_β results are almost identical to those of the Recent (Fig. 4).

Recent

The Great Basin (restricted to Nevada) is represented by 161 localities (Fig. 2a), averaging 85.8 individuals per locality. The Great Plains (restricted to Nebraska) is represented by 62 counties (Fig. 2b), averaging 126.2 individuals per county. The differences in individuals per site reflect differences in spatial averaging, as Nebraska's counties are slightly larger than the Nevada localities. This difference in spatial averaging might slightly depress the β values for Nebraska.

Beta diversity can be higher in larger study areas, particularly if they have similar levels of primary productivity (Mac Nally *et al.*, 2004). Setting aside differences in productivity, the larger area of Nevada may have affected the comparison. Nevada is larger than Nebraska by 86,000 km^2. I reanalysed Nevada, removing the southernmost counties, Lincoln, Clark and Nye, whose total area is slightly larger than the difference between the states. The resulting Nevada jackknife β diversity is 6.25447 (var (β) = 0.0084), which is above the upper 95% confidence limit of Nebraska, but not significantly higher ($P = 0.07$). The rarity gain result is 0.1583 ± 0.0051 (value ± std.err.), significantly higher than that for Nebraska ($P < 0.0001$). After accounting for the different areas and spatial averaging of the regions, the results from the modern match those from the Pleistocene and

the late Early Hemphillian, with Nevada higher than Nebraska, but only significantly so when evenness is taken into account.

CONCLUSIONS

Sampling problems are a major influence on palaeodiversity studies, and this study is no exception. Even so, it is possible to draw four important conclusions. First, β diversity today is higher in the Great Basin than in the central Great Plains. This fits with both theory (which predicts higher β diversity in a region with high topographic heterogeneity, where faunas can fit into high- and low-elevation habitats) and observations (Kelt *et al.*, 1996; Mac Nally *et al.*, 2004). Evenness-based β diversity is more sensitive to this difference, suggesting that the pattern is created by ecological processes affecting dominance at the local scale. Kelt (1999) suggested that the desert faunas of western USA are shaped by processes influencing structure and dynamics at the local scale, which could create the pattern observed here.

Second, β diversity has been higher in the Great Basin for at least the last 40,000 years. Again, this difference is clearest in the evenness metric, reflecting changing dominance at the local scale. The changes in ecology across the landscape are not happening as switches, on and off, but as gradations from one dominance structure to another.

Third, there is evidence that elevated β diversity in the Great Basin dates back to the late Early Hemphillian (7.5–6.7 Ma). This result, significant in the evenness analysis but not in the jackknife analysis, and corroborated by the runs test, supports hypothesis (1), that β diversity in the Great Basin rose as a result of tectonic changes in the topography. Although the lack of concordance between the jackknife and evenness analyses may simply reflect the small sample sizes for the interval, it more likely reflects the ecological processes structuring the Great Basin assemblages. The Pleistocene and the Recent intervals show a similar discordance between jackknife and evenness results, which I suggest reflects the local-scale processes driving the landscape-scale patterns. The presence of this pattern 7 Ma suggests that those same processes have been operating since the Miocene. That is, the tectonic changes in the Great Basin did not drive a simple division into high- and low-elevation faunas, but fostered a more subtle reorganization at the local scale.

Finally, the Great Plains of the Late Barstovian had much higher β diversity than the Great Basin of today. This elevated Late Barstovian β diversity is not driven by low α diversity; the Late Barstovian α is 17.0 ± 1.96 (± std. err.) species per locality, significantly higher than the Recent α of 11.8 ± 0.83 spp./loc. These results fit with the work of Janis *et al.* (2000, 2002, 2004), who explained a Late Barstovian peak in ungulate α in terms of elevated primary productivity, possibly caused by elevated levels of CO_2. The elevated β diversity reflects both higher α and γ, which means both more species at each locality and more species overall. That is, not only are species either packed tighter or accessing more resources at the local scale, but they are also turning over more rapidly at the landscape scale. Thus, the Late Barstovian β diversity peak might reflect either (1) time-averaging in the sample (rejected by Janis *et al.*, 2004), or (2) undiscovered habitat patchiness. Because Janis *et al.* (2004) reported that the pattern of elevated ungulate α is a global phenomenon, grasslands on other continents at this time might also have elevated β diversity. Further investigation is warranted.

To sum up, I have investigated the deep time roots of β diversity in the Great Basin of the USA using collections data available online. Beta diversity in the Great Basin has been elevated since at least 7 Ma, indicating that tectonic forces have shaped the macroecology of the region. Beta diversity was anomalously high in the central Great Plains of the USA about 13 Ma, adding another layer of complexity to the diversity problem addressed by Janis *et al.* (2000, 2002, 2004).

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BIOSKETCH

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