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Possible regional tectonic controls on mammalian evolution in western North America

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ABSTRACT

Previous work has suggested that tectonically active regions act as speciation pumps for mammals and plant species, but little is known about how fast or widespread tectonism must be in order to directly influence evolution. Here, we use oxygen and hydrogen isotopic data from Miocene sedimentary deposits to characterize the topographic evolution of the southern Columbia Plateau/Snake River Plain and northern Rocky Mountain regions during the Yellowstone hotspot passage, with the ultimate goal of understanding whether topographic changes caused by the hotspot influenced mammalian evolution within those regions. We conducted oxygen isotope analyses of 130 samples of lacustrine, and paleosol carbonate from Miocene stratigraphic sections that span much of the northern Rocky Mountain region, and combined these data with previously published isotopic records. Collectively these isotopic data show that caldera formation associated with the Yellowstone hotspot has modified regional topography and rearranged drainages along the track of the hotspot, and that the hotspot has left a topographic depression in its wake.

We explore the extent to which these topographic changes influenced or are decoupled from diversity changes exhibited by the local mammal faunas and conclude that the passage of the hotspot and consequent surface uplift created rainshadows in the lee of high-elevation calderas and/or generated large volumes of volcanic materials, influencing soils and vegetation. Collectively, that may explain a possible rise in mammal diversity in the CP/SRP region at ~14 Ma, coincident with a drop in diversity in the NRM. It is still unclear, however, how different taphonomic pathways and sample-standardization problems are influencing apparent diversity peaks at this temporal and geographic resolution.

1. Introduction

Theories of mammalian evolution offer a diverse range of hypotheses regarding the primary drivers of evolutionary change, with much debate about the relative importance of biotic interactions versus perturbations to the physical environment as motors of speciation (e.g., Van Valen, 1973; Bell, 1982; Vrba, 1992; Janis and Wilhelm, 1993; Barry et al., 1995; Webb and Opdyke, 1995; Dybdahl and Lively, 1998; Martin and Fairbanks, 1999; Barnosky, 2001; Benton, 2009; Badgley, 2010; Finarelli and Badgley, 2010). Biotic interactions involve ever-escalating selective pressures rooted in competition and predation. Physical–environmental changes include processes such as climate change and episodes of tectonic activity. Changing climate ultimately rearranges climate zones that species are adapted to, or creates new combinations of climate parameters without altering topography (Parry et al., 2007; Williams et al., 2007; Barnosky, 2009). Tectonic activity dramatically alters the topography and as a consequence usually also alters regional climates and sometimes global climate (Ruddiman and Kutzbach, 1990; Kutzbach et al., 1993). Because of the steep temperature gradients across mountainous topography regional surface uplift directly correlates with changes in mean annual temperature and frequently mean annual precipitation.

Both climate change by itself and tectonic events theoretically could influence evolutionary rates because both have the potential to increase selection pressures while isolating populations and otherwise altering species' geographic ranges (Badgley, 2010; Finarelli and Badgley, 2010). For mammals, climate changes influence distributions through direct physiological impacts in some cases (for example, restriction of pikas to high mountain-tops because they cannot tolerate high diurnal temperatures; Smith and Weston, 1990; Beever et al., 2010), but more commonly through more complex ecological pathways such as altering critical vegetational aspects of habitat (e.g., Carroll and Genoways, 1980; Rosenzweig, 1995; Graham, 1999; Lomolino et al., 2010).

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Tectonism, in addition to inevitably producing climatic impacts on biota in the region (Barnosky, 2001; Badgley et al., 2008; Badgley, 2010; Finarelli and Badgley, 2010), also may introduce new topographic barriers that can physically fragment and dramatically re-arrange species ranges and introduce tectonically-controlled niches.

Recent studies that use the rich fossil record of western North American mammals to untangle the relationship between speciation rates, climate change, and tectonism reveal little if any correlation between speciation rates and climate changes alone (Alroy et al., 2000; Barnosky and Carrasco, 2002; Barnosky et al., 2005), though other studies have suggested some role for climate based on more limited subsets of taxa and alternative temporal and geographic constraints (Janis et al., 2000; Barnosky, 2001; Badgley et al., 2008; Benton, 2009). The case for major tectonic events as a motor of speciation, on the other hand, has been gaining ground in recent years (Barnosky and Carrasco, 2002; Kohn and Fremd, 2008; Kaplan, 2009; Badgley, 2010; Finarelli and Badgley, 2010), primarily based on a major faunal turnover and speciation pulse that occurred in the western United States between ~18 and ~16 Ma (Stucky, 1990; Alroy, 2000; Alroy et al., 2000; Barnosky and Carrasco, 2002; Kohn and Fremd, 2008). The timing is coincident with the breakup of the northern Rocky Mountains into accentuated basins and ranges, warping of the landscape and volcanism in the Columbia Plateau, and development of the Basin-and-Range province. Kohn and Fremd (2008) argued that tectonism in fact acts to influence biodiversity on regional to global scales, citing the increase in the percent area undergoing extension at around 17.5 Ma in the western United States as a regional driver of species diversity. As a potential example of a global driver, they pointed to a late Miocene decrease in western North American mammal diversity, which they suggested was triggered by uplift of the Tibetan Plateau to an elevation that initiated global cooling through teleconnections that affected North American climate dynamics. Badgley (2010) expanded on this idea by suggesting that tectonic activity would be expected to accelerate speciation by creating climatic and topographic heterogeneity, which would in turn affect connectivity and resource availability.

Here we explore a potential third geographic scale at which tectonism might influence mammalian evolution: the dramatic landscape changes that resulted as the Yellowstone hotspot traversed the western United States from Oregon to Wyoming. This event, commencing around 16 Ma in southwestern Oregon and still ongoing in today's Yellowstone National Park, was spatially and temporally superimposed on the subcontinental-scale tectonic activity that created the Basin and Range and segmented the northern Rocky Mountain and Great Basin regions beginning ~17.5 Ma. As the hotspot location began to migrate, western American mammal species had already attained their mid-Miocene peak diversity. Subsequently, species experienced the dramatic impact of volcanism and rapid tectonic uplift associated with activity of the hotspot, followed by regional subsidence, and development of the Snake River Plain.

To assess the effects of these tectonic events on Miocene mammal faunas, we first determine the extent of topographic change that accompanied hotspot migration; then we examine the temporal patterns of mammalian diversity in the provinces of interest. If passage of the hotspot did influence mammalian evolution, we would expect changes in mammalian diversity to coincide with topographic changes induced by hotspot migration. Finally, we discuss potential mechanisms that might relate the reconstructed tectonic events to the observed diversity patterns, and how taphonomic considerations may influence such interpretations.

2. Geologic and biogeographic setting

The landscape of the northwestern quarter of the United States underwent dramatic changes during the Miocene. Beginning ~17 Ma, a broad region that includes much of what is now Nevada, as well as parts of Idaho, Oregon, Utah, and California began undergoing crustal extension that doubled its width, and created a series of north–south trending valleys and ranges (Fig. 1).

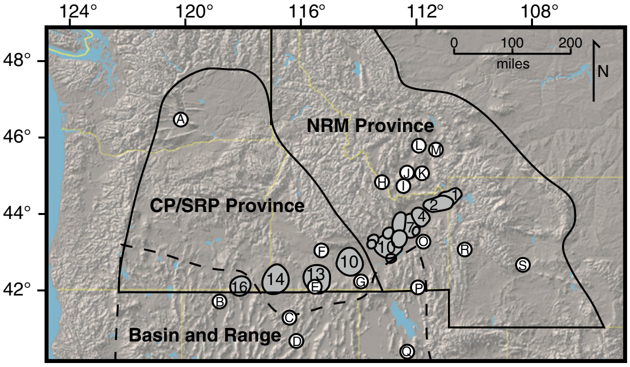

Fig. 1. Shaded relief map of the study area, with stable isotope sample localities shown with white circles. A) Eastern Washington (Takeuchi and Larson, 2005), B) Virgin Valley (Horton et al., 2004), C) Willow Creek (Horton et al., 2004), D) Carlon-Pinyon (Horton et al., 2004), E) Twin Falls (Mulch et al., 2008), F) Hagerman Fossil Beds (this study), G) Trapper Creek (Horton et al., 2004; Mulch et al., 2008), H) Railroad Canyon (Kent-Corson et al., 2006), I) Sage Creek Basin (Kent-Corson et al., 2006, this study), J) Ruby Basin (Kent-Corson et al., 2006; this study), K) Gravelly Range (this study), L) Jefferson Basin (this study), M) Madison Basin (this study), O) Idaho Falls (Mulch et al., 2008), P) Bannock Basin (this study), Q) Rush Valley (Horton et al., 2004), R) Hoback Basin (this study), S) South Wind River Basin (this study), T) North Wind River Basin (this study). Selected eruptive centers of the Yellowstone hotspot are shown by gray circles, with ages of eruption rounded to the closest Ma (from Anders and Hemming, 2004). The Basin and Range Province is outlined by dashed lines. The Columbian Plateau/Northern Snake River Plain (CP/SRP) and Northern Rocky Mountain (NRM) physiographic provinces are outlined after Hagmeier (1966).

Volcanism associated with the Yellowstone Hotspot began around 16 Ma in northern Nevada, and since then migrated to its present location in northwestern Wyoming (Pierce and Morgan, 1992). As the hot spot progressed along this path, it changed drainage patterns (Link et al., 2005; Beranek et al., 2006), and left in its wake the Snake River Plain.

To the west, a body of thermochronologic (Reiners et al., 2002), sedimentologic (Tabor et al., 1984; Gresens, 1987; Vance et al., 1987), structural (Hammond, 1979; Swanson, 1997), and isotopic (Takeuchi and Larson, 2005) evidence shows a pulse of exhumation and uplift in the central and northern Cascade Range beginning ~12 Ma, although the presence of a rainshadow over the Oregon Cascades since the Eocene (Sheldon and Retallack, 2004) indicates that the range has existed in some form since that time.

Within this changing landscape, mammals evolved, immigrated, emigrated, and went extinct, resulting in 15 biochronologic intervals defined on mammalian species composition between ~30 and 5 million years ago (Tedford et al., 2004; Table 1). That evolution was at least in

Table 1
Temporal bins into which data were sorted.

NALMA subdivision	Age boundaries	Interval length
Late Late Hemphillian	5.9–4.7 Ma	1.2
Early Late Hemphillian	6.7–5.9 Ma	0.8
Late Early Hemphillian	7.5–6.7 Ma	0.8
Early Early Hemphillian	9–7.5 Ma	1.5
Late Clarendonian	10–9 Ma	1
Middle Clarendonian	12–10 Ma	2
Early Clarendonian	12.5–12 Ma	0.5
Late Barstovian	14.8–12.5 Ma	2.3
Early Barstovian	15.9–14.8 Ma	1.1
Late Hemingfordian	17.5–15.9 Ma	1.6
Early Hemingfordian	18.8–17.5 Ma	1.3
Late Late Arikareean	19.5–18.8 Ma	0.7
Early Late Arikareean	23.8–19.5 Ma	4.3
Late Early Arikareean	27.9–23.8	4.1
Early Early Arikareean	30–27.9 Ma	2.1

part controlled by physiography is demonstrated by the recognition of distinct biogeographic provinces for mammals of the western USA today (Hagmeier and Stults, 1964; Hagmeier, 1966), which are broadly recognizable back through at least late Oligocene time (Tedford et al., 1987; Storer, 1989; Faunmap Working Group, 1996; Barnosky and Carrasco, 2002). Two biogeographic provinces comprise the region on which this study is focused: 1) the Columbian Mammal Province that covers the Columbia Plateau/Northern Snake River Plain (CP/SRP) physiographic provinces of modern Washington, Oregon, and Idaho, and 2) the Coloradan Mammal Province, broadly coincident with Northern Rocky Mountain physiographic province (NRM) of modern Montana, Idaho, and Wyoming (Fig. 1). To emphasize the physiographic connections, we refer to these coherent biogeographic regions as the CP/SRP and NRM, respectively, in this paper. The faunal and climatic connections between such biogeographic zones likely contribute to events of faunal turnover as well as periods of endemism and more localized diversification (Werdelin and Fortelius, 1997; Fortelius and Hokkanen, 2001).

Although records of mammalian diversity show fluctuation through much of the Cenozoic and vary depending on the statistical methods employed (Stucky, 1990; Alroy, 2000; Alroy et al., 2000; Barnosky and Carrasco, 2002; Barnosky et al., 2005; Kohn and Fremd, 2008), many studies find evidence that Cenozoic mammalian diversity peaked in the middle Miocene (Stucky, 1990; Alroy, 2000; Alroy et al., 2000; Barnosky and Carrasco, 2002; Kohn and Fremd, 2008), just prior to the initiation of the Yellowstone hotspot. This led to early speculation that the diversification event was driven by the Mid-Miocene Climatic Optimum (MMCO) (Barnosky, 2001). Studies that distinguish between biogeographic zones, however, have found that the largest peak in mammalian diversity occurred in the NRM ~15–16 Ma (Barnosky and Carrasco, 2002), and have attributed this peak to increased endemism in this mountainous region. Even though the northern Rocky Mountain peak diversity occurred during the MMCO, Barnosky and Carrasco (2002) favored the conclusion that tectonism drove the diversification because the adjoining, less tectonically-affected provinces exhibited no diversity peak during the MMCO, nor did any of the provinces exhibit a diversity peak during the even more pronounced Late Oligocene Warming event some 24–27 Ma.

Kohn and Fremd (2008) used a subset of the same data analyzed by Barnosky and Carrasco, concentrating only on large mammals (ungulates and carnivores). They geographically binned their data as Central Great Plains, Southern Great Plains, combined Colorado Plateau and Rocky Mountains, combined Columbia Plateau and Snake River Plain, and Mojave regions. The vast majority of data came from the Central Great Plains, and all of those regions except the CP/SRP exhibited an abrupt increase in large mammal diversity beginning 17.5 Ma, followed by a precipitous drop beginning around 11 Ma if sampling-uncorrected data is used (their Fig. 2A and B). However, by correcting for some of the known sampling biases using rarefaction they demonstrated that their observed diversity increases were driven almost entirely by ungulates from the Great Plains (their Fig. 2C), consistent with observations by Janis et al. (2000) and those of Barnosky and Carrasco (2002) who detected no diversity increase in the Columbia Plateau region (called the "Northwest" by Barnosky and Carrasco).

The only other, sampling-bias corrected analysis on a province-by-province basis was by Barnosky et al. (2005), in which not only raw diversity counts were adjusted by rarefaction to account for differing sample sizes, but also diversity counts were corrected for geographic sampling area, utilizing a species–area relationship. That study demonstrated that the geographic sampling area significantly influences apparent diversity counts. Thus in our methods explained below we attempt to account for the geographic-area sampling bias as well as sample-size biases.

3. Field studies and analytical methods

Oxygen isotope records of terrestrial sedimentary deposits can be valuable tools in understanding changes in continental-scale topography because they can record paleoelevation (e.g., Garzione et al., 2000; Rowley and Currie, 2006; DeCelles et al., 2007; Mix et al., 2011), drainage reorganization (e.g., Carroll et al., 2008; Davis et al., 2008, 2009; Doebbert et al., 2009; Kent-Corson et al., 2010), basin isolation (e.g., DeCelles et al., 2007; Davis et al., 2008, 2009; Kent-Corson et al., 2009) as well as direct interactions of topography and climate (e.g. Ballato et al., 2010; Mulch et al., 2010; Chamberlain et al., 2012). In this study we present oxygen isotope data from relevant Miocene sedimentary basins in western North America. The basins are particularly suited to understanding the tectonic influence on mammalian evolution because in most cases age constraints are derived from the mammalian record (Table 2), and the isotope-sampling localities are in geographic proximity to the localities used to construct faunal diversity records. We present oxygen isotope analyses of 130 lacustrine, fluvial, and paleosol carbonate samples from eight sedimentary basins in the northern Rocky Mountain region. Using these data as well as published oxygen and hydrogen data from additional locales, we determine estimates of oxygen isotope values of paleo-meteoric waters, and bin these according to North American Land Mammal Ages (NALMA) (Table 1).

We collected fluvial, paleosol, and lacustrine carbonate from sedimentary sections with age controls based on tephrachronology, vertebrate fossils, and K/Ar, Ar/Ar, and paleomagnetic dating (Table 2). When stratigraphy and sedimentology was established by previous studies, samples were keyed into these stratigraphic sections. If previous studies had not established stratigraphy and sedimentology, stratigraphic sections were measured at the meter scale and sedimentary environment, lithology, and stratigraphic evolution were recorded. Samples were taken every 1–5 m depending on lithology.

Fresh surfaces of carbonate samples were sampled using a dental drill and analyzed at the Stanford University Stable Isotope Biogeochemistry Laboratory. Between 0.2 and 7.0 mg of powdered sample was placed in sealed vessels, flushed with helium, and then reacted with anhydrous phosphoric acid at 72 °C. The evolved CO_2 was sampled using a Gas-Bench inlet system, and then analyzed in a Finnigan MAT Delta Plus XL mass spectrometer. Measurements of NBS-19 and internal laboratory standards show that precision for oxygen isotope measurements is <0.2‰.

Estimates of paleoprecipitation oxygen isotope values ($\delta^{18}O_{ppt}$) were calculated using the equations of Kim and O'Neil (1997, carbonates) and Sheppard and Gilg (1996, smectites), and hydrogen isotope values were calculated using the equation of Capuano (1992, smectites) to correct for the temperature-dependent isotopic fractionation that occurs between water and mineral. The equation of Friedman et al. (1993) was used to correct for fractionation of deuterium that occurs as water diffuses into volcanic glass. In order to estimate fractionation temperature in the

Table 2
Age constraints for samples.

Locality	Constraint type	Reference
Bannock Basin	Tephrachronology	Carney et al. (2002); Long et al. (2004)
Hoback Basin	Vertebrate fossils	Dorr et al., 1977
Jackson Hole	Vertebrate fossils	Sutton and Black (1972); Barnosky (1984); Leopold et al. (2007)
Gravelly Range	Vertebrate fossils	Luikart (1997)
Jefferson Basin	Vertebrate fossils	Vuke et al. (2004)
Madison Basin	Vertebrate fossils, K/Ar	Vuke (2003)
Wind River Basin (south)	Vertebrate fossils, paleomagnetic data	Munthe (1979); Prothero and Sanchez (2004)
Wind River Basin (north)	Vertebrate fossils, k/ar	Love (1978)
Sage Creek Basin	Vertebrate fossils, paleomagnetic data	Tabrum et al. (1996)
Hagerman	Vertebrate fossils, ar/ar	Hart and Brueseke (1999)

past, we modified modern mean annual temperatures (NCDC and National Climatic Data Center Climate Normals, 2012) using mid-latitude North American terrestrial paleotemperature estimates from Wolfe (1994). Although these temperatures are likely lower than the actual temperature of soil carbonate formation (e.g. Breeker et al., 2009; Passey et al., 2010; Peters et al., 2013; Quade et al., 2013), any offset induced by our use of MAT's should be internally consistent.

In cases where only δD values were measured, δ^{18}O estimates were calculated assuming that samples parallel the global meteoric water line.

For our mammalian diversity estimates, we used data from the MIOMAP database (Carrasco et al., 2005) and methods explained in Barnosky et al. (2005) and in the Supplementary Text to calculate sample-standardized diversity and geographic-sampling area for each relevant time bin in the CP/SRP and NRM. To guard against erroneously recognizing diversity peaks that could result from sampling areas of different sizes, we examined the data not only by rarefying occurrences to account for differing sample sizes, but also in two ways designed to detect species–area effects. First, we divided each diversity value by geographic sampling area. Second, we used the species–area relationship (SAR) previously determined for Neogene mammals (Carrasco et al., 2009) and assessed how far and in what direction observed richness in each time period and region deviated from expectations of the SAR. We also examined alpha diversity and numbers of sites contributing to species richness in the CP/SRP and NRM, using methods explained in Barnosky and Carrasco (2002). No standardization methodology was applied to correct for the unequal time bins sampled because previous work (Barnosky et al., 2005) has shown that there is no correlation between bin length and the number of localities per bin. In addition, the subdivisions of the NALMAs (Table 1) that we used are definable precisely because there is limited turnover during each time interval. Thus, these time bins are well-suited for comparing diversity through time.

4. Results

4.1. Isotopes

Oxygen and carbon isotope data are shown along with published isotope results from Horton et al. (2004), Takeuchi and Larson (2005), Kent-Corson et al. (2006), and Mulch et al. (2008) in Supplementary Table 1, with groupings determined by NALMA (Tedford et al., 2004; Table 1). Oxygen isotope values measured in this study range from 7.0 to 17.5‰ (SMOW), and carbon isotope values range from −15.7 to 2.7‰ (PDB).

Study areas south of the Snake River Plain that have been published previously (Horton et al., 2004; Mulch et al., 2008; Chamberlain et al., 2012) contain isotopic data obtained from carbonate, chert, glass, and smectite. In these samples, carbonate and chert samples are in disequilibrium with smectite samples (Horton et al., 2004) as has been observed in other studies comparing carbonate and smectite oxygen isotope values (Stern et al., 1997; Poage and Chamberlain, 2002). However on the large spatial scales relevant to our analysis, samples display similar isotopic trends with similar magnitudes through time (see Fig. 3). This offset between carbonate and chert oxygen isotope values as compared to smectite oxygen isotope values is systematic, and observed in all of the binned NALMAs.

There are several characteristics that can be noted based on the spatial distribution of $\delta^{18}O_{ppt}$ (Fig. 2). First, oxygen isotope values vary spatially in each time interval. Second, $\delta^{18}O_{ppt}$ values adjacent to active volcanic centers of the Yellowstone hotspot are generally more negative than in other sample localities, and $\delta^{18}O_{ppt}$ values in the wake of the Yellowstone hotspot are generally more positive than other sample localities. This can be seen by referring to Fig. 3, which shows data through time in grouped locales (for instance South of the Snake River Plane) spanning the time period of hotspot passage. Finally, although there are several localities in which $\delta^{18}O_{ppt}$ is anomalously negative or

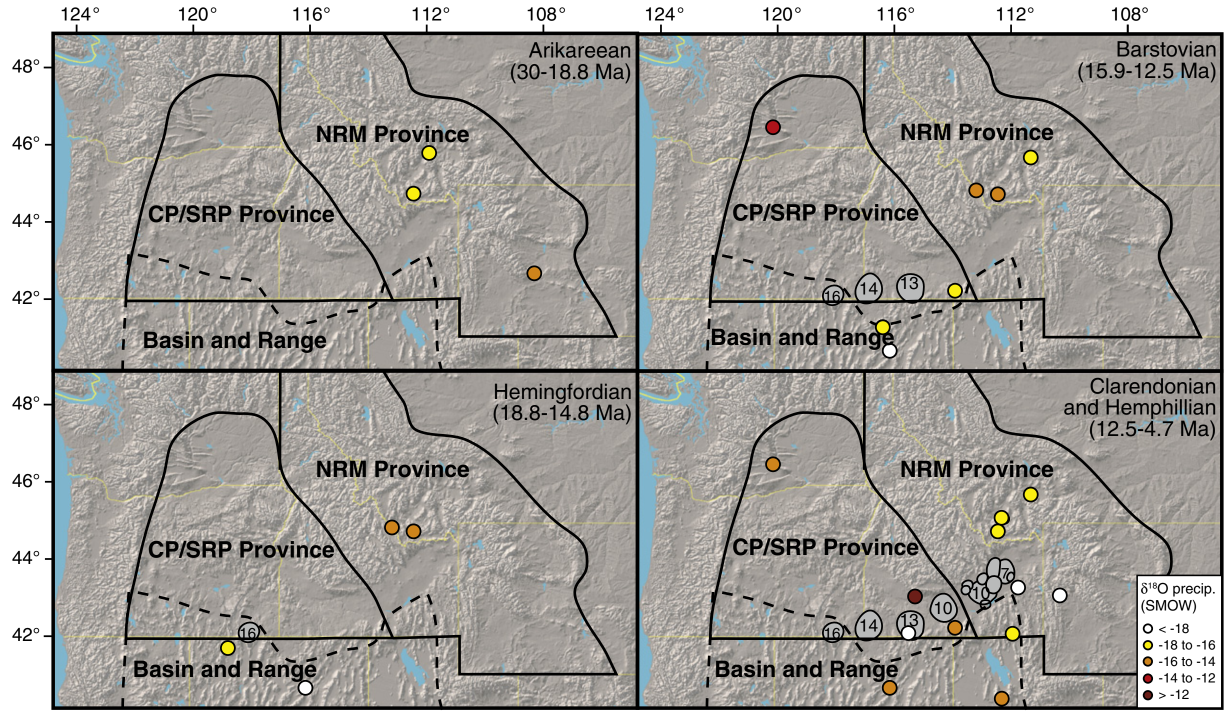

Fig. 2. Average paleoprecipitation δ^{18}O values through time arranged by North American Land Mammal Ages. Age-appropriate eruptive centers of the Yellowstone hotspot are shown by gray circles, with ages rounded to the closest Ma (from Anders and Hemming, 2004). To prevent the proportion of smectite vs. calcite and glass samples in each age group from influencing observed isotopic trends, we have adjusted smectite sample values by subtracting 3.5‰ (the average difference between the two sample groups) from all smectite sample values. By doing this we correct for the systematic offset between the values, which does not change significantly through time. We in no way suggest that estimates of $\delta^{18}O_{ppt}$ obtained from smectite samples are less legitimate than those obtained from glasses and carbonate, but simply aim to make estimates of $\delta^{18}O_{ppt}$ from different sample types comparable through this stratigraphy. We have not adjusted $\delta^{18}O_{ppt}$ from the eastern Washington stratigraphy because these samples are all of the same type.

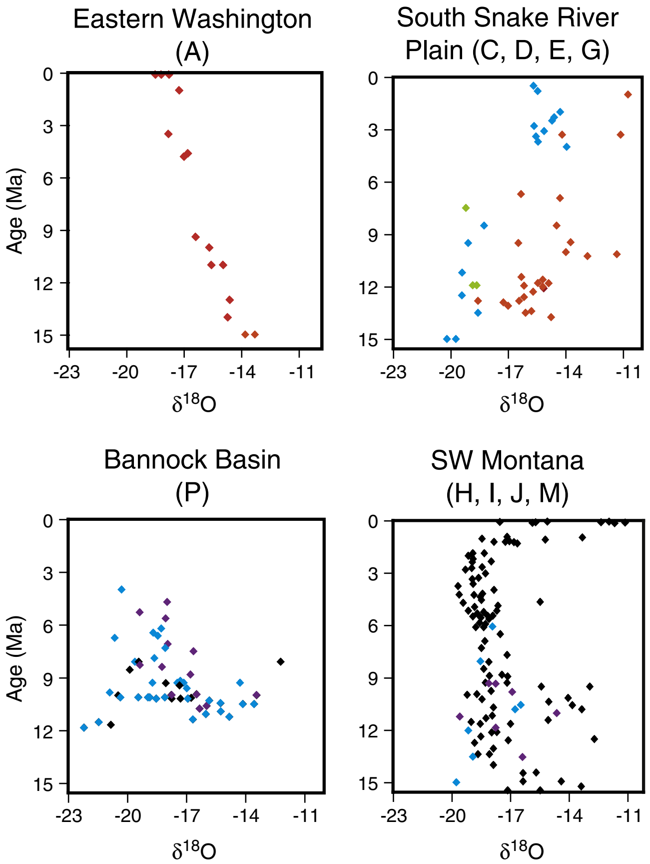

Fig. 3. Oxygen isotope records of paleoprecipitation (in SMOW) calculated from calcite (shale/limestone blue; sandstone/conglomerate cement purple; paleosol carbonate/calcareous ash black; smectite red; and glass green). Letters in parentheses refer to locales in Fig. 1.

positive compared to other sample localities during a single time slice, the Jackson Hole locality consistently has extremely negative $\delta^{18}O_{ppt}$ between the Arikareean and Clarendonian/Hemphillian (Fig. 2).

Fig. 3 shows oxygen isotope data in study locales where a relatively complete proxy record of $\delta^{18}O_{ppt}$ exists. This figure highlights several points. Most notably, the variability of $\delta^{18}O_{ppt}$ varies at each sample locality, and individual localities show localized trends in $\delta^{18}O_{ppt}$ through time. In the CR/SRP region, $\delta^{18}O$ decreases through time in Eastern Washington, but increases in the study areas south of the Snake River Plain. In the northern Rocky Mountain Region, oxygen isotope values generally increase through time in the Jackson area, but decrease in Bannock Basin and southwestern Montana, yet with considerable intra-sample variability.

4.2. Mammal diversity

While mammalian fossil remains are not available for many time periods in both provinces, the available data suggest that the sampling-corrected species richness values may have been out of phase in the CP/SRP and NRM (Fig. 4). Species richness values corrected for sample-size only, and those that maximally correct for a species–area effect by dividing species richness by sampling area, both indicate an earlier diversity peak in the NRM than in the CP/SRP. The NRM peak is between 15 and 16 Ma (Early Barstovian) and the CP/SRP peak is near 14 Ma (Late Barstovian). The earlier peak in the NRM is also evident when the rarefied species richness values are plotted on Cenozoic species–area relationships (SAR) (Fig. 5); for the NRM the Early Barstovian point shows the most positive deviation from the expected relationship (Fig. 5A, B), whereas for the CP/SRP the Late Barstovian point plots highest above the expectations (Fig. 5A, C). It is notable that NRM

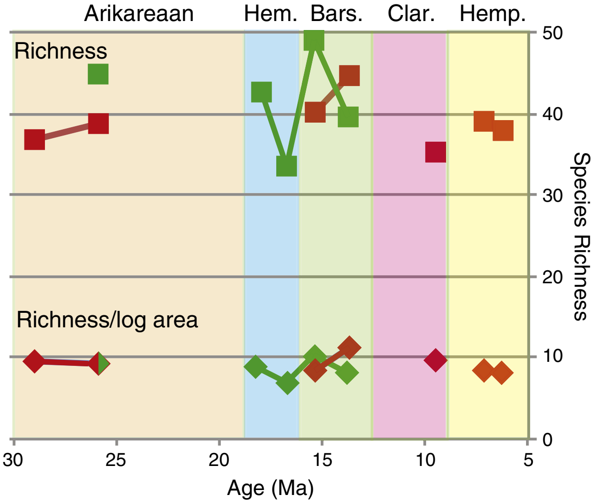

Fig. 4. Species richness fluctuations indicated by using rarefied species richness (top) and rarefied species richness divided by geographic area from which the sample came (bottom). Note by both methods, NRM (green) species richness is low when CP/SRP (red) richness increases in the late Barstovian.

species richness decreases at the same time that it increases in the CP/SRP. Species richness falls between 14 and 10 Ma in the CP/SRP; however, the data are insufficient to track richness in the NRM during that time. There are no clear age-related patterns in alpha diversity (mean species number in communities) per time period for either the CP/SRP (Fig. 6) or the NRM (see Figs. 6 and 7 in Barnosky and Carrasco, 2002).

5. Interpretation

5.1. Oxygen isotope proxy records

The oxygen isotope records examined in this study are derived from a number of types of archives, including fluvial, paleosol, and lacustrine carbonate, and authigenic smectite from altered tuffs and paleosols. Each of these environments has a number of factors that uniquely influence the recorded isotopic values in the environments, including drainage basin area and type, seasonality of mineral precipitation, and alteration of waters by processes such as evaporation. Thus data from each environment and in each sample locale at each point in time should be interpreted in its own context. In most cases, the data included in this study has been interpreted in this local context in previous publications. However, the goal of this paper is to examine long-term, large-scale isotopic trends on a regional scale. In order to accomplish this, we allow that much of the isotopic variation between different samples at individual sample localities and between sample localities is likely due to differences in sedimentary environments and local influences. We have attempted transparency by making sample depositional environment and lithology clear, and referring readers to primary literature regarding individual localities. With natural variability in mind, we assert that long-term, large-scale isotopic trends can be interpreted as long as readers are fully aware that isotopic records from authigenic minerals are influenced by local as well as regional factors.

Although oxygen isotope records preserved in authigenic minerals can result from numerous factors, including diagenesis, detrital contamination, and climatic change, we deem these to be unlikely to affect the first-order trends on the oxygen isotope records presented in this study.

Diagenetic effects are most likely to occur when sedimentary rocks have experienced significant burial temperatures and pressures, most often due to deep burial in basins with high sediment accumulation rates. The sedimentary sections sampled for this study have not experienced significant burial, due to their relatively young age, and we sampled known stratigraphic sections that lack significant (or eroded) thicknesses of younger rocks. In most cases, primary sedimentary

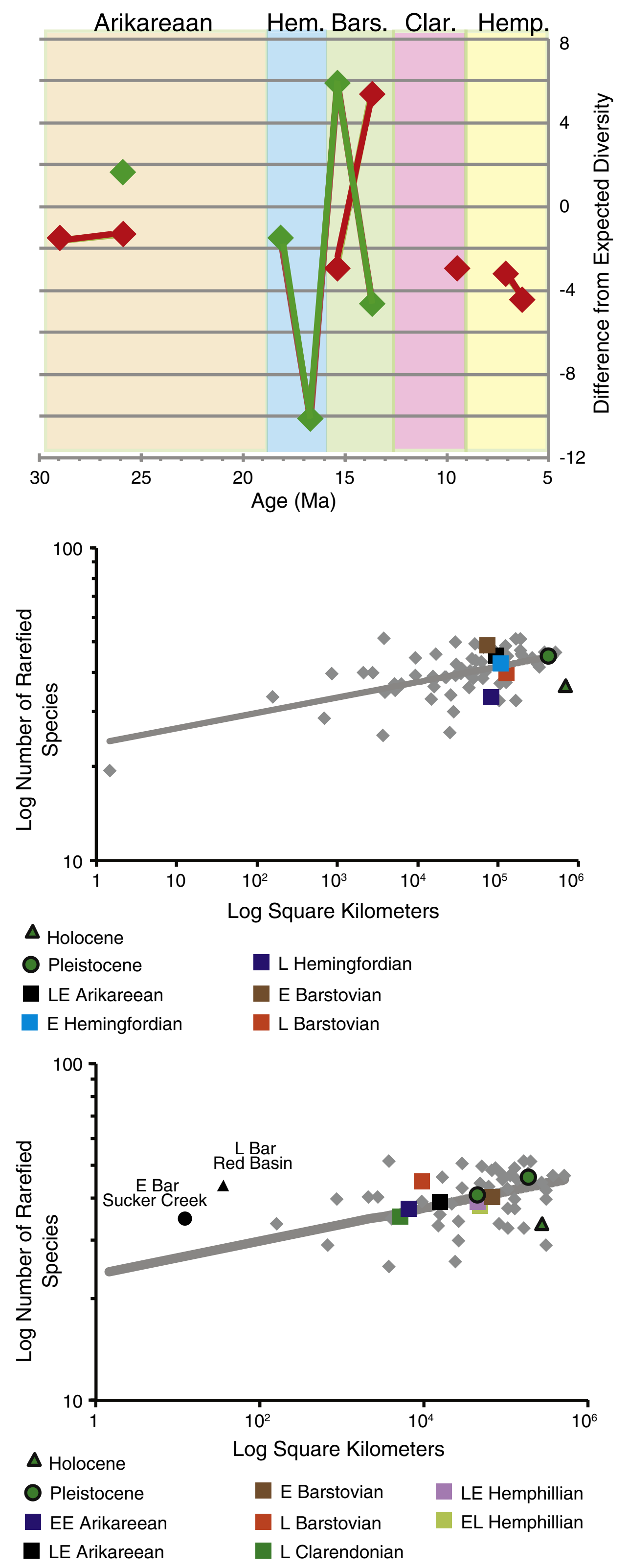

Fig. 5. a. Deviation of species richness from expected values based on the species-area relationship for the Cenozoic (top); Species richness in the NRM per time period compared to the SAR for the entire Cenozoic (middle); Species richness in the CR/SRP per time period compared to the SAR for the entire Cenozoic (bottom).

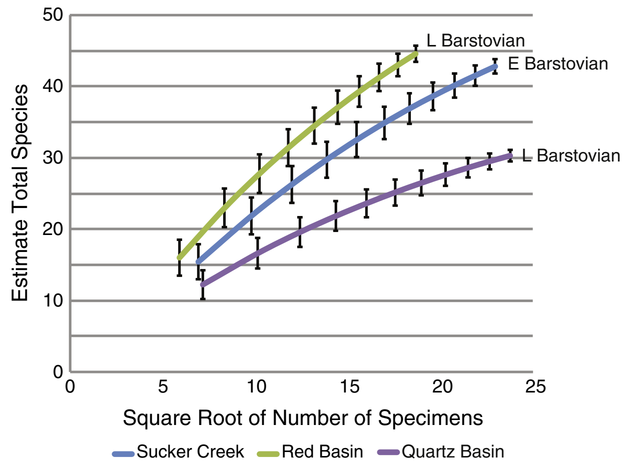

Fig. 6. Alpha diversity at early and late Barstovian sites in the CP/SRP. Red Basin and Sucker Creek (including the Devil's Gate localities) are interpreted to sample relatively more arid microhabitats than Quartz Basin, suggesting that the habitat sampled, rather than geologic age, is a better correlate with diversity in these faunas.

features are extremely well-preserved and samples lack sparry calcite that is typically due to secondary crystallization. As discussed below, some sample localities where we might expect evaporative effects to alter oxygen and carbon isotope values in fact show this covariance, suggesting that these are primary isotopic values. Finally, in many study areas samples from similar periods of time were taken from different formations in different locations. The consistency between locations also suggests that samples did not undergo diagenesis.

However, the sedimentary units in Jackson Hole are unique in that the Arikareean to late Barstovian Colter Formation records volcanic activity proximal to the study area itself, and some units even have evidence of hot emplacement (Barnosky, 1984). Anomalously low oxygen isotope values in the Jackson Hole area beginning in the Arikareean (Chamberlain et al., 2012) could well be the result of diagenesis, and so we have not included samples from Jackson Hole prior to the Hemphillian in this analysis.

Detrital carbonate can also influence oxygen isotope values of authigenic carbonate. There are several lines of evidence that detrital carbonate did not significantly alter $\delta^{18}O$ values in most sample areas. First, in the study areas south of the Snake River Plain, in many study locales isotope data are available both from carbonate and smectite samples. These values are in disequilibrium (Horton et al., 2004) as has been observed in other studies comparing carbonate and smectite oxygen isotope values (Stern et al., 1997; Poage and Chamberlain, 2002), but have similar isotopic trends with similar magnitudes. Because smectite would not be subject to the same detrital influences as carbonate, this suggests that the carbonate samples have not been significantly altered by detrital carbonate. Furthermore, carbonate oxygen isotope values are more negative than those of smectite, an offset opposite from what would be expected if detrital carbonate (usually marine) had contaminated samples.

In other study areas, some samples are from lacustrine carbonate, which should not experience detrital effects. In many study areas, these lacustrine carbonates are associated with periodic paleosol or detrital sedimentary units. Because these samples have similar oxygen isotope values (Supplementary Table 1), we interpret that detrital effects were not significant in most study areas.

Climate can affect oxygen isotope values because temperature affects isotopic fractionation of precipitation and mineral–water oxygen isotope exchange during formation of minerals. However, in the case of this study, the relatively high spatial resolution of and isotopic variability between sites allow us to rule out climate as a major influence. This isotopic record spans periods of climate change including the MMCO, but no major systematic changes are seen in these isotopic records. This is likely because temperature effects are generally small (0.35‰/ °C; O'Neil et al., 1969; Rozanski et al., 1993) relative to the larger changes that can occur due to evaporation (e.g., Horton and

Chamberlain, 2006; Davis et al., 2009) and change in elevation of drainage area (Poage and Chamberlain, 2001). Climate has likely influenced oxygen isotope records through evaporative effects, which can increase both oxygen and carbon isotope values. Oxygen and carbon values of carbonates covary in some intervals in selected sample locales from this study and others (including Carlon-Pinyon samples in the Chadronian, Jefferson samples in the Arikareean, and Madison samples in the Barstovian (Supp. Fig. 1)) and to first order we take covariation as evidence that evaporation has likely altered the oxygen isotope record. Evaporative effects seem to occur diachronously between sections, and are not pervasive through any one stratigraphic section sampled as would be expected if regional climate drove evaporation. Given the lack of indication that regional climate drove evaporation, we interpret pulses of evaporation to record the local balance between the rate basins are supplied with water and sediment, and the rate at which accommodation space is formed (Carroll and Bohacs, 1999). However, a group of eight samples from the Bannock Basin study area have been excluded from this study because of their anomalously high oxygen isotope values, and the covariance between oxygen and carbon isotope values, suggesting evaporative effects in a closed lake environment to be the predominant influence on oxygen isotope values.

Given these arguments, we conclude that the oxygen isotope records presented in this study to first-order reflect the long-term averaged oxygen isotope composition of meteoric waters in the study localities, and thus the oxygen isotopic composition of precipitation and drainages reaching the study localities, as modified by any evaporative effects.

5.2. Mammal diversity

Constructing paleodiversity curves from the fossil record is fraught with sampling problems, the most notable being numbers of localities per time interval, numbers of specimens per locality, and the size of the geographic area sampled per time bin. The procedure used for constructing Fig. 4 corrects for these known biases as much as possible. Nevertheless, Barnosky et al. (2005) pointed out that the high species richness in the CP/SRP at ~14 Ma (late Barstovian), especially in the area-corrected data, conceivably could result from the fact that at that time period the fossils come from collecting sites that are geographically close to one another (~9321 km^2), with most data from two very rich sites (Red Basin and Quartz Basin in southeastern Oregon), whereas the ~15 Ma sites (early Barstovian) are a composite of localities distributed across a broader region (~68969 km^2). Smaller geographic ranges, such as those of the late Barstovian, will tend to increase diversity levels relative to large ones when the data is area-corrected. Such a taphonomic influence does not seem likely to be the only explanation, given the presence of a late Barstovian diversity peak whether or not species richness is divided by area. However, given the small geographic area sampled in the late Barstovian, if the Red Basin and Quartz Basin collecting regions were sampled from markedly different habitats, this could inflate the late Barstovian diversity levels relative to the early Barstovian regionally widespread regions. Compared to Red Basin, the Quartz Basin is characterized by a disproportionately large number of insectivore species, fewer carnivores and large ungulates; higher proportions of castorids, eomyids, and murids; and lower proportions of heteromyids, mylagaulids, and sciurids (see Supplementary Table 2). This overall pattern suggests that Quartz Basin samples more mesic microhabitats, whereas Red Basin samples more arid ones. Taxonomic differences also seem to exist when the early Barstovian localities are compared to the late Barstovian ones. In general, the early Barstovian has a better representation of large ungulates (~47% of the total represented species), whereas the late Barstovian has a better representation of small mammals (~69% of the represented species) (see Supplementary Table 3).

However, the other side of the taphonomic argument is that both mesic and arid microhabitats are represented in both early and late Barstovian sampling sites, and that taphonomic biases explain the differing small vs. large mammal proportions. One early Barstovian collecting region, Sucker Creek (OR), which includes the Devil's Gate localities, has a sample that can be reasonably compared with the late Barstovian Red Basin sites in that Sucker Creek samples predominantly arid microhabitats judging by the high frequencies of heteromyids and dipodids (arid indicators). Similar to Red Basin, Sucker Creek predominantly has a small-mammal fauna and has multiple collecting localities that can be aggregated for rarefaction analysis to determine alpha diversity (Fig. 6). This comparison suggests that late Barstovian arid sites (e.g., Red Basin) have higher species richness than their early Barstovian counterparts (e.g., Sucker Creek), and that both early and late Barstovian arid sites have higher species richness than late Barstovian mesic ones (e.g., Quartz Basin). That arid CP/SRP late Barstovian sites tend to have higher-than-normal species richness is also suggested by their position on the Cenozoic species–area relationship (Fig. 5C) with Red Basin being relatively more species rich than Sucker Creek.

Even though there is only enough data to evaluate alpha diversity from three collecting sites, there are no notable differences in alpha diversity that clearly correlate with temporal interval in the CP/SRP (Fig. 6), which is consistent with earlier interpretations for the NRM (Barnosky and Carrasco, 2002). Therefore, whole-province species richness per time interval likely reflects increasing or decreasing beta diversity, rather than broad shifts in alpha diversity.

6. Discussion

6.1. Topographic history of the Northern Rocky Mountain Region

The isotopic records presented in this study offer two main findings in regard to the topographic evolution of the study region. First, there is considerable variation between $\delta^{18}O_{ppt}$, both spatially in individual time slices (Fig. 2), and in the evolution through time in individual basins (Fig. 3). This observation suggests that the study areas had mainly unconnected drainage systems, with isotopic histories reflecting individual changes in surface elevation, relief, and climate for each study area. We interpret this to indicate that the landscape has been segmented through the entire range of time examined in this study.

Second, the change to more negative oxygen isotope values near active eruptive centers of the Yellowstone hotspot (Fig. 2) indicates that these centers created significant topographic highs, and most likely reorganized drainages. Determining the magnitude of elevation change associated with the passage of the hotspot is beyond the scope of this study. We would like to point out, however, that $\delta^{18}O_{ppt}$ patterns are consistent with high-elevation sourced waters that reach the basins surrounding the hotspot. The more positive oxygen isotope values in the wake of the hotspot render it likely that these centers eventually subsided to topographic lows. This would cause oxygen isotope values to increase both through the decreased elevation of the drainage area, and the ponding and subsequent evaporation of waters. Individual oxygen isotope stratigraphic sections (Fig. 3) are also consistent with this proposed topographic evolution. For instance, oxygen isotope values in the South Snake River Plain area increase from 15 Ma on, as would be expected with a decrease in the elevation of drainages reaching these study areas as topography subsided in the wake of the hotspot, while the decrease in oxygen isotope values in the Bannock Basin and southwestern Montana is consistent with an increasing input of high-elevation sourced, fresh waters through time as the hotspot approached. While the hotspot likely influenced the evolution of topography and climate in much of the study area, the northern part of the CP/SRP has most likely experienced topographic and climatic change of a different source. The decrease in oxygen isotope values in Eastern Washington has also been interpreted to result from the formation of a rainshadow associated with a Miocene pulse of surface uplift in the Washington and Oregon Cascades (Kohn et al., 2002; Takeuchi and Larson, 2005).

These findings based on isotopic records of topographic changes and drainage reorganizations due to the progression of the Yellowstone hotspot are consistent with other studies that have used detrital compositions of sedimentary deposits in this region to identify paleodrainages. These studies have also found a pattern of drainage reorganization that suggests the movement of a significant topographic bulge associated with the Yellowstone hotspot through this landscape, and the downwarping of topography in the wake of this bulge (e.g., Pierce and Morgan, 1992; Pierce and Morgan, 1999; Link et al., 2005; Beranek et al., 2006; Wegmann et al., 2007).

6.2. Topographic influences on mid-Miocene faunal diversity

The constraints on the topographic evolution of the northern Rocky Mountain region allow us to better understand how changes in topography may have contributed to the fluctuations in mammalian diversity documented in the CP/SRP and NRM provinces.

The diversity background on which our study unfolds had already been affected by earlier events. Here we recognize that these earlier events resulted in a diversity peak that occurred in the NRM between 16 and 15 Ma (early Barstovian). The timing is consistent with previous interpretations that suggest regional uplift and fragmentation of the northern Rockies triggered a speciation pulse by fragmenting species ranges (Barnosky and Carrasco, 2002; Kohn and Fremd, 2008; Badgley, 2010; Finarelli and Badgley, 2010). Also consistent with this fragmented-landscape model are the differences in individual oxygen isotope stratigraphic sections we demonstrate, which suggest that the landscape was highly dissected during the entire time the study spans. Albeit $\delta^{18}O$ records in sedimentary basins along the hotspot track presented here do not provide unequivocal evidence of a simple topographic signal, our data strongly support the notion of topographically separated areas whose dividing line moved eastward in concert with the hotspot. This is concordant with interpretations that observed changes in species richness were due mainly to changes in beta diversity instead of alpha diversity, as physically isolated areas might be expected to each show somewhat independent faunal histories.

The changes in topography that our data indicate resulted from initiation and progression of the Yellowstone hotspot between ~16 Ma and the present also show an interesting pattern in relation to mammalian diversity. As the hotspot apparently raised elevations and dissected the landscape near northeastern Oregon around 14 million years ago, mammalian diversity seems to have increased there mainly through changes in beta diversity, while simultaneously declining in the northern Rockies to the east. After collapse of the bow wave as the hotspot moved east, by 10 Ma species richness declined to lower values in the CP/SNR region. This pattern of topographic change is consistent with a model that invokes speciation in the CP/SNR region as the hotspot dissected topography and raised elevations there, while diversity simultaneously decreased farther east in the Rockies as the uplift to the west emplaced a rain shadow that resulted in an overall loss of productivity in the mountains. The diversity decline in the CP/SNR by 10 Ma could have been related to the SNR collapsing into flatter topography thereby decreasing beta diversity, or to the overall cooling and drying in the region that was underway at that time. It presently is not possible to distinguish which, if either, cause was more important. We present these ideas as a hypotheses to be tested further; if they are upheld, tectonism may be implicated in driving evolution not only at the subcontinental scale (by uplifting and fragmenting major mountain chains) and at the global scale (as topographic features like the Tibetan Plateau reach elevations critical in influencing global climate), but also at the geologically more local scale manifested as uplift from hotspot migration relative to plate movements. Testing these ideas will require more detailed work on the taphonomy and paleoecology of the deposits that comprise the samples from each time period, and a detailed investigation of the effects that the Yellowstone hotspot “bulge” had on isotopes in precipitation.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.07.014.

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