

Paleobiology

**Diversity dynamics of mammals in relation to tectonic and climatic history:
comparison of three Neogene records from North America**

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Abstract.—In modern ecosystems, regions of topographic heterogeneity, when compared with nearby topographically homogeneous regions, support high species densities of mammals and other groups. This biogeographic pattern could be explained by either greater diversification rates or greater accommodation of species in topographically complex regions. In this context, we assess the hypothesis that changes in landscape history have stimulated diversification in mammals. Landscape history includes tectonic and climatic processes that influence topographic complexity at regional scales. We evaluated the influence of changes in topographic complexity and climate on origination and extinction rates of rodents, the most diverse clade of mammals.

We compared the Neogene records of rodent diversity for three regions in North America. The Columbia Basin of the Pacific Northwest (Region 1) and the northern Rocky Mountains (Region 2) were tectonically active over much of the Cenozoic and are characterized by high topographic complexity today. The northern Great Plains (Region 3) have been tectonically quiescent, with low relief, throughout the Cenozoic. These three regions have distinctive geologic histories and substantial fossil records. All three regions showed significant changes in diversification and faunal composition over the Neogene. In the montane regions, originations and extinctions peaked at the onset and close, respectively, of the Miocene Climatic Optimum (17–14 Ma), with significant changes in faunal composition accompanying these episodes of diversification. In the Great Plains, rodents showed considerable turnover but infrequent diversification. Peak Neogene diversity in the Great Plains occurred during cooling after the Miocene Climatic Optimum. These histories suggest that climatic changes interacting with increasing topographic complexity intensify macroevolutionary processes. In addition, close tracking of diversity and fossil productivity with the stratigraphic record suggests either large-scale sampling biases or the mutual response of diversity and depositional processes to changes in landscape history.

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Introduction

In modern terrestrial ecosystems, species diversity increases with diminishing seasonality of temperature (Hawkins et al. 2003), increasing biome area (Rosenzweig 1995), and for many groups, increasing topographic complexity. Montane regions, rift valleys, and dissected plateaus support greater diversity than their adjacent lowlands (Simpson 1964; Cracraft 1985; Badgley 2010). These patterns are so pervasive today that it is tempting to consider them as fundamental properties of the biosphere (see, for example, Crame 2001). However, seemingly basic biogeographic gradients may appear quite different during well-sampled intervals of earth history. For example, Rose et al. (2011) documented virtually

constant diversity over more than 30 degrees of latitude for Paleocene mammals of western North America, despite a paleotemperature gradient of similar slope (although different absolute values) to that of the present day. For Miocene rodents of midlatitude North America, the topographic diversity gradient was absent more often than it was present (Finarelli and Badgley 2010). Rodent diversity peaked during the middle Miocene, when widespread tectonic activities coincided with global warming during the Miocene Climatic Optimum (MCO). In addition, Northern Hemisphere latitudinal temperature gradients in the middle to latest Miocene were much shallower than the modern gradient, accord-

ing to a global data set of Miocene floras (Pound et al. 2012).

These contrasts have important implications for understanding biogeographic processes. First, modern interglacial diversity gradients do not appear to be persistent features of global biogeography, and processes inferred from present-day distributions may not fully represent processes acting across deep time. Second, contrasts between older Cenozoic and modern diversity gradients suggest that particular episodes in landscape and climatic history have stimulated processes of diversification. Thus, geohistorical records are essential for understanding these processes, which include speciation, extinction, and shifting geographic ranges.

Here, our goals are to (1) evaluate diversification (changes in origination, extinction, and faunal composition) in rodents over the Neogene, (2) test hypotheses about responses of rodent diversity to changes in landscape and climate, and (3) compare three regional records of North American landscape, climate, and diversity over the same time period. We focus on rodents because they exhibit high taxonomic and ecological diversity, life habits that are often intimately connected to geological substrates, and a good fossil record. In addition, the geographic ranges of rodents, and other small mammals, occur on the scale of the regions that we evaluate, whereas larger mammals, such as ungulates and carnivores, typically have much larger geographic ranges. Many aspects of present-day landscapes around the world formed as a result of tectonic or climatic events during the Miocene (Potter and Szatmari 2009). We evaluate changes in diversity and faunal composition through time, assessing how each record supports or falsifies hypotheses about evolutionary responses to landscape history.

The Three Regions

In North America, the species density (number of species per unit area) of extant mammals is much greater over the tectonically active region (Rocky Mountains to the Pacific) than in the tectonically passive region (Great Plains to the Atlantic). This contrast is evident at both regional (Simpson quadrats: 225 km ×

225 km; Simpson 1964; Badgley and Fox 2000) and sub-continental spatial scales (Finarelli and Badgley 2010). High diversity in the tectonically active portion of North America is a consequence of high spatial turnover of species over topographically complex landscapes, close proximity of many bioclimatic zones on steep mountains, and heterogeneous habitats at smaller spatial scales (Coblentz and Riitters 2004; Qian et al. 2009). Over the tectonically passive region, bioclimatic zones are more continuous, species' geographic ranges are larger, and spatial turnover is lower (Badgley 2010). During the Miocene, however, active-region diversity substantially exceeded that of the passive region only during the MCO, an interval that was also characterized by widespread tectonic activity (Finarelli and Badgley 2010).

Here we investigate diversification at a finer scale, focusing on three regions (subsets of the active and passive regions in Finarelli and Badgley 2010) with different tectonic and climatic histories. These regions are (1) the Columbia Basin of the Pacific Northwest, centered on Oregon and southern Washington, (2) the northern Rocky Mountains, centered on southwestern Montana and eastern Idaho, and (3) the northern Great Plains, centered on Nebraska (Table 1, Fig. 1). These regions have different geologic and vegetation histories through the Neogene (Leopold and Denton 1987; Christiansen and Yeats 1992) and substantial fossil records of both small and large mammals from at least the Oligocene to Recent (Carrasco et al. 2005; Graham and Lundelius 2010).

Region 1 extends from the Cascade Mountains to the eastern boundary of Oregon and Washington, including the northwestern edge of the Great Basin (Fig. 1). Fossil localities occur in alluvial sediments alternating with basalt flows and ash layers (Orr and Orr 2009). Over the last 40 Myr, volcanism has influenced this region, including intrusive and extrusive magmatism in the Cascades to the west and eruption of flood basalts over much of the eastern Columbia Plateau (Hooper et al. 2002; Mitchell and Montgomery 2006). Volcanism associated with the Yellowstone hotspot began in southeastern Oregon during the early

TABLE 1. Geographic data and modern mammal diversity for three regions in different tectonic provinces. Each region encompasses approximately 90,000 km² (about 13,900 mi², equivalent to four quadrats from Badgley and Fox 2000).

	Region 1: Oregon	Region 2: Montana	Region 3: Nebraska
Location			
Latitude	42.7 to 46.8°N	44.6 to 46.4°N	40.7 to 43.6°N
Longitude	-117.7 to -120.9°W	-111.5 to -113.4°W	-103.9 to -105.2°W
Topography			
Mean elevation	1350 m	2100 m	800 m
Mean relief	2800 m	2250 m	600 m
Macroclimate			
Mean ann. temperature	8.4°C	2.6°C	9.0°C
Mean ann. precipitation	400 mm	500 mm	550 mm
No. mammal species	124 (89–103/quad)	100 (81–88/quad)	82 (66–71/quad)
No. without bats	108 (78–89/quad)	86 (69–77/quad)	68 (59–64/quad)
No. rodent species	55 (31–43/quad)	39 (26–35/quad)	29 (25–27/quad)
Dominant rodent families	Muridae, Sciuridae	Muridae, Sciuridae	Muridae, Sciuridae, Heteromyidae

middle Miocene (Pierce and Morgan 1982). Major formations include the John Day Group, Columbia Plateau basalts, and the Mascall, Ellensburg, Rattlesnake, and Ringold Formations (Tedford et al. 2004). Geologic and paleobotanical evidence suggests the presence of high elevation and relief in the Cascades of northern Washington during the Miocene, whereas relief in the southern Cascades of southern Washington and Oregon was insufficient to create a strong rain shadow to the east until the late Miocene (Mitchell and Montgomery 2006). Thermochronometry (Reiners et al. 2002) and source analysis of

volcaniclastic sediments (Smith et al. 1988) indicate rapid exhumation and erosion of the southern Cascades between 8 and 12 Ma. Increasing elevation and relief imply increasing topographic complexity and the associated bioclimatic heterogeneity. Countering these influences were recurrent flood basalts, potentially reducing habitable areas over hundreds of square kilometers at low elevation. Fossil floras indicate that diverse mesic forests with conifers and hardwoods dominated the Columbia Basin over most of the Miocene (Leopold and Denton 1987). Indicators of dry summers increased in latest Miocene to

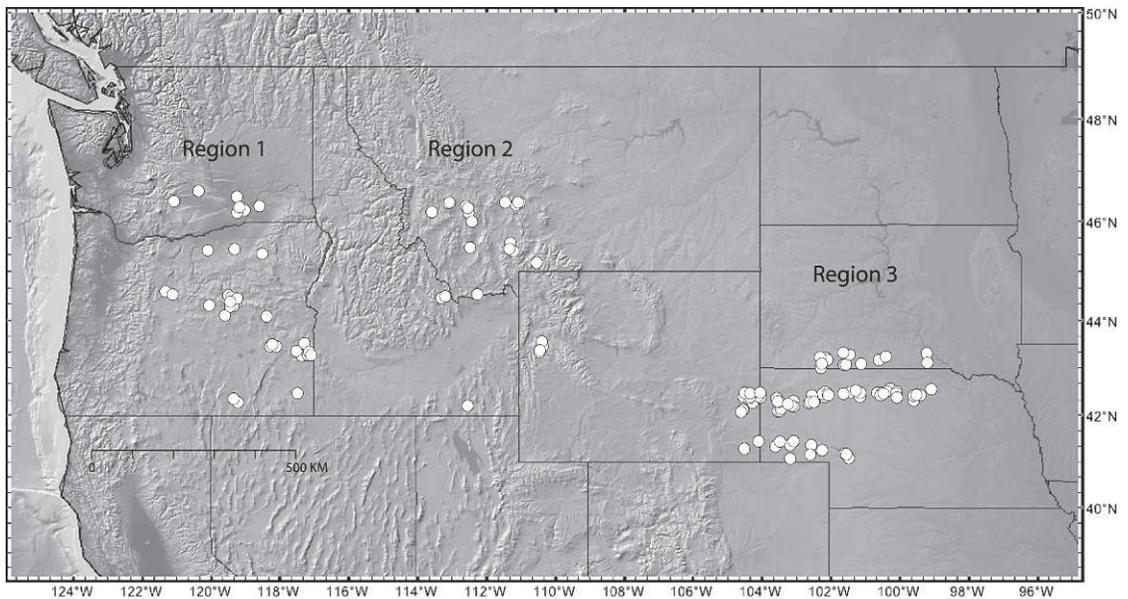


FIGURE 1. Map showing distribution of fossil localities in three regions representing different tectonic provinces. Base map from Geomapapp, www.geomapapp.org.

Pliocene floras, suggesting that the Cascades did not impose a substantial rain shadow until after 8 Ma. Today this region has a mean elevation of over 1300 m, with high relief (Table 1) and steep environmental gradients, especially eastward from the Cascades. Biomes include temperate rainforest on the west side of the Cascades, montane conifer forest on the east side of the Cascades, and semi-desert in central and eastern parts of the region (Verts and Carraway 1998). Small mountain ranges separate desert basins in the eastern half of the region. Mammal diversity in Region 1 is high (124 species) for this latitude, with high spatial turnover among small mammals. Muridae (deer mice and woodrats) and Sciuridae (tree and ground squirrels) are the dominant rodent families, with notable diversity in the Heteromyidae (pocket mice and kangaroo rats) in the eastern deserts.

Region 2 lies within the northern Rocky Mountains tectonic province (Fig. 1). Fossil localities occur in volcanoclastic and alluvial sediments in intermontane basins that formed early in the Cenozoic (Fields et al. 1985; Hanneman and Wideman 1991). Extensive Cretaceous to Eocene volcanism across the region became intermittent and localized by the early Miocene, and then intensified regionally from the late Miocene to present as the Yellowstone hotspot migrated to its present position. Major fossiliferous sequences include the Renova Formation (Eocene to early Miocene) and the Sixmile Creek Formation (middle to late Miocene) as well as coeval formations in several intermontane basins, including the Colter, Deep River, Madison Valley, and Hepburn's Mesa Formations (Fields et al. 1985; Tedford et al. 2004). The regional mid-Tertiary unconformity, between the Renova and Sixmile Formations and their equivalents, signaled extensional faulting and tilting of early Cenozoic strata (Barnosky et al. 2007). The timing of this unconformity overlapped the onset of the MCO. Paleobotanical data indicate that the MCO in Region 2 was a humid interval interrupting long-term Neogene aridification. Montane conifer forest and sage scrub, similar to the modern vegetation, dominated much of the Neogene (Leopold

and Denton 1987). The warmer, wetter MCO climate may have contributed to the regional unconformity, through increased erosion causing exhumation of earlier strata and further enhancing uplift (Thompson et al. 1982). Following the middle Miocene, erosion increased relief, establishing the dissected basins of the modern landscape (Fields et al. 1985; Elliott et al. 2003). Today, this region has the highest mean elevation and lowest mean annual temperature of the three regions (Table 1). Mammal diversity, including rodents, is intermediate (100 species) between those of Regions 1 and 3, with Muridae and Sciuridae dominating the rodent faunas.

Region 3 lies within the northern Great Plains up to, but not including, its junction with the front range of the Rocky Mountains (Fig. 1). Although this region has been tectonically quiescent since the late Mesozoic, it has been influenced by the changing topography of the adjacent montane region (Swinehart et al. 1985). Cenozoic eolian and alluvial sediments blanketed Region 3, alternating with episodic erosion and dissection of a plains landscape. Eolian volcanic and alluvial deposition dominated the late Oligocene to early Miocene Arikaree Group from sources in northern Colorado. A major erosional period ca. 19 Ma, marking the onset of Rocky Mountain uplift, separated deposition of the Arikaree and Ogallala groups (Swinehart et al. 1985; Tedford et al. 2004). Alluvial siliciclastics from river systems draining mountains in Wyoming and Colorado dominate the middle Miocene to Pliocene Ogallala Group. Renewed incision since ca. 5 Ma has increased relief along river valleys. A series of unconformities in the stratigraphic record match intervals without fossil localities in the rodent record. $\delta^{18}\text{O}$ values in equid teeth increased by $\sim 4\%$ between 18 and 12 Ma, then steadily decreased by the same magnitude from 12 to 5 Ma, suggesting middle Miocene warming and aridity followed by late Miocene cooling with increased humidity (Passey et al. 2002). Paleofloras indicate the presence of prairie grasses, forbs, and scattered trees over the Neogene (Leopold and Denton 1987). Paleosol carbon isotopes (from Nebraska to Texas) indicate that C_4 grasses

persisted on the landscape throughout the Miocene (at 12–34% of biomass), increasing to >30% of biomass around the Miocene/Pliocene boundary, with a rise to modern levels (>80% of biomass) in the Quaternary (Fox and Koch 2003; Fox et al. 2012). Carbon isotopes from equid teeth signify increased consumption of C_4 vegetation by some species in the latest Miocene and Pliocene, with considerable interspecific variation (Passey et al. 2002). Today, Region 3 has the lowest mean elevation and relief, and the warmest mean annual temperature, of the three regions (Table 1). The predominant vegetation is short-grass prairie, with riparian woodland. Diversity is lower in Region 3 than in either montane region for mammals in general (82 species) and rodents in particular. In addition, extant rodent diversity in Region 3 is lower than peak diversity during the richest intervals of the Neogene. Sciuridae, Muridae, and Heteromyidae dominate modern rodent faunas.

The three regions have several geohistorical features in common. Regions 1 and 2 both experienced faulting and volcanism associated with Basin and Range extension (Hanneman and Wideman 1991), and share volcanism and localized uplift along the track of the Yellowstone hotspot (Pierce and Morgan 1982; Hooper et al. 2002). Regions 2 and 3 share indications of middle Miocene regional uplift that resulted in widespread erosional unconformities and changes in sediment sources (Fields et al. 1985; Swinehart et al. 1985; Christiansen and Yeats 1992). All three regions share depositional sequences and sequence boundaries in common from the late Eocene through the Neogene, with time-transgressive unconformities at some sequence boundaries (Hanneman and Wideman 2006).

Concepts and Hypotheses

The hypothesis that landscape history influences mammalian diversification is multifaceted and encompasses several elements. We use the term “landscape history” here to include changes in topography, both vertically and horizontally, as well as climate. Topographic complexity can increase as a result of tectonic uplift and erosion or from erosion causing isostatic uplift (Molnar and England

1990). Either mechanism increases relief at the regional scale. Strong positive feedbacks make it difficult to disentangle tectonic and climatic influences on topography. Furthermore, topographic change alters regional temperature gradients and orographic precipitation via the thermal lapse rate. Global temperature change affects the magnitude of the thermal lapse rate; e.g., global warming reduces the lapse rate (Poulsen and Jeffery 2011). These factors can influence the magnitude of bioclimatic gradients along mountain slopes. Tectonically passive regions may experience the effects of uplift in adjacent regions in the form of regional tilting or sediment flux from the active region.

We evaluated predictions of the landscape-history hypothesis for both topographically complex (tectonically active) and topographically simple (tectonically passive) regions. Predictions emphasize the influence of changes in topography and climate on diversification. Topographic complexity by itself did not result in a sustained topographic diversity gradient at sub-continental scales in western North America over the Miocene (Finarelli and Badgley 2010). Here, we focus on the regional scale, large enough to encompass species ranges, at least for many small mammals, and evaluate diversification at a temporal scale long enough for speciation to occur. The first prediction emphasizes tectonic processes as the primary influence on landscape change and the next two emphasize climatic changes over active and passive regions.

1. In tectonically active regions, episodes of uplift and increased relief should stimulate diversification, with originations exceeding extinctions. Greater topographic complexity and longer elevational gradients should promote allopatric speciation from vicariance due to geographically fragmented habitats and from adaptation to new bioclimatic zones at high elevation. Newly uplifted habitats in tectonically active regions represent opportunities for colonization without competition from incumbent biotas. The combination of fragmentation and new ecological oppor-

tunity has the potential to stimulate speciation. Greater regional and local endemism should result. Passive regions should not show corresponding changes in diversification. This prediction would be falsified if an episode of tectonic activity were observed without a corresponding increase in active-region diversification.

2. Global warming, if significant and sustained across time scales of 10^5 – 10^6 years, should cause an increase in diversity in active regions. (Milankovitch climatic triggers may also operate [e.g., van Dam et al. 2006] and should be accentuated in topographically complex regions.) As bioclimatic zones move upward in elevation, regional diversity should become concentrated in mountains, as it is today. Fragmentation of geographic ranges across mountain ranges should promote speciation. Extinction of small, isolated montane populations may enhance regional faunal turnover, in combination with increased regional origination. Endemism should increase at the scale of mountain ranges and regions. In the passive region, faunal change should occur primarily via shifting geographic ranges, resulting in increased turnover, without net diversification, and low regional endemism. This prediction would be falsified if diversity and endemism in the active region did not increase or if increased faunal turnover was not observed during periods of global warming.
3. Global cooling, if significant and sustained, should reduce the number of bioclimatic zones at high elevation in topographically complex landscapes. (A counteracting factor would be the associated increase in the thermal lapse rate.) Active-region diversity should decline through downslope expansion of low-diversity, high-elevation bioclimatic zones and reduced orographic gradients. The speciation rate should decline with more continuity among habitats and greater population connectivity. As geographic ranges expand at lower elevation, endemism should decline within the active region. If the modern North American record is representative of underlying

macroecological processes, then decreased active-region endemism should still exceed passive-region endemism. The passive region should experience immigration from adjacent high-elevation regions and emigration as geographic ranges shift in response to cooling and associated changes in precipitation, resulting in increased faunal turnover. This prediction would be falsified if diversity and endemism in active regions did not decline and if increased turnover was not observed in passive regions coincident with sustained global cooling. Table 2 summarizes potentially testable predictions. More generally, the hypothesis of landscape history driving diversification is falsified if diversity changes in active and passive regions parallel one another throughout intervals of changing tectonic or climatic history.

A complicating factor is the response of the stratigraphic record to tectonic and climatic changes. As such, changes in the number and spatial distribution of fossil localities can reflect changes in original diversity as well as in the recording mechanism itself (Peters 2006a, 2008). The continental stratigraphic record is likely to document geomorphic and diversity responses to episodes of tectonic activity or climate change, but may provide a poor or intermittent record of tectonic or climatic stability—circumstances that should feature low rates of sediment accumulation if not unconformities. We evaluated indicators of a macrostratigraphic pattern—correlations among sampling, formation boundaries, and diversity—as well as changes in paleoenvironment and faunal composition that would not be expected to occur as a consequence of changes in sampling intensity alone.

Data and Methods

Rodent Occurrence Data

Fossil rodent occurrences were extracted from the NeoMap database (available at <http://www.ucmp.berkeley.edu/neomap/>), which combines the principally Miocene coverage of the MioMap fossil-mammal database (Carrasco et al. 2005, <http://www.ucmp>).

TABLE 2. Predicted changes in diversity metrics under different scenarios of landscape history due to changes in tectonic and climatic conditions. A, tectonically active region; P, passive region; $O(i)$, number of originations; $E(i)$, number of extinctions; $d(i)$, per-lineage diversification rate; $t(i)$, per-lineage turnover rate.

Landscape history	Predicted response in mammal diversity
Tectonic activity	A: Increase in $O(i)$, $d(i)$. Increase in endemism. P: Background $d(i)$. Low endemism.
Global warming	A: Increase in $O(i)$, $d(i)$, $t(i)$. Increase in endemism. Change in faunal composition. P: Increase in $O(i)$, $E(i)$, $t(i)$ but not $d(i)$. Low endemism. Change in faunal composition.
Global cooling	A: Increase in $E(i)$, $d(i)$, $t(i)$. Decrease in endemism. Change in faunal composition. P: Increase in $O(i) > E(i)$, $t(i)$ but not $d(i)$. Low endemism. Change in faunal composition.

berkeley.edu/miomap/) with the Plio-Pleistocene coverage of the Faunmap and Neotoma fossil-mammal databases (Graham and Lundelius 2010, <http://www.ucmp.berkeley.edu/faunmap/>). We collated species occurrences for fossil localities for each region, then tallied species occurrences in each region, omitting indeterminate identifications, to document diversity and faunal composition from 25 to 2 Ma, corresponding approximately to the Miocene and Pliocene epochs (Gradstein et al. 2004). We retained occurrence data for earlier and later intervals to avoid introducing edge effects for diversification metrics. For each species, we used the temporal resolution of fossil localities in the NeoMap database to establish first and last appearances, adopting the earliest and latest possible dates for each species from the locality age ranges (as in Finarelli and Badgley 2010). For Region 3, we augmented NeoMap occurrences and age estimates for fossil localities with data from Martin et al. (2008). Our final data set consisted of 939 species occurrences representing 282 unique rodent species recorded from 327 fossil localities (Table 3). Diversity data by time interval for each region are given in Supplementary Tables 1–3.

There is a clear overprint of sampling intensity on the patterns of species richness

TABLE 3. Number of fossil localities, rodent species and occurrences by region. We omitted indeterminate identifications and binned localities and species into 1-Myr intervals spanning 25 to 2 Ma.

	Region 1: Oregon	Region 2: Montana	Region 3: Nebraska
Localities	80	53	194
Species	85	67	130
Occurrences	279	140	520

through our study interval. For each region, at least some million-year time intervals have no fossil data. For example, in Region 1, there are no fossil localities from the beginning of the MCO interval (17–14 Ma), and the high diversity observed after this sampling gap could reflect a gradual trend of increasing diversity leading up to and during the first part of the MCO. In Region 2, sampling is poor for several million years prior to the peak in diversity during the MCO. To what extent can we be confident of the observed patterns from each region? In order to understand diversity changes in light of variable sampling, we performed a random subsampling procedure modified from the Shareholder Quorum Subsampling method of Alroy (2010a,b). We constructed rarefaction curves for the three regions by calculating the total target sampling intensity (species-locality occurrences) implied for each quorum level (corrected for rare taxa). We plotted mean diversity ± 2 standard deviations (SD) from 1000 iterations at each sampling target for each region. Complete details of this method are provided in online supplementary information.

Rates of Origination and Extinction

As in previous analyses (Finarelli and Badgley 2010), we divided the study interval into 1-Myr time bins. Large changes in sampling intensity can produce an overabundance of short-lived taxa from highly sampled intervals (e.g., Badgley and Gingerich 1988), and to avoid such sampling biases in estimates of origination and extinction rates, we excluded “singleton” taxa (those observed in a single time interval) (Foote 2000a, 2001, 2003). We estimated per-lineage rates of origination

(p') and extinction (q') for each time bin i in each region by

$$p'(i) = \text{Ln} \left[\frac{N_{bt}(i) + N_{Ft}(i)}{N_{bt}(i)} \right] \quad (1a)$$

and

$$q'(i) = \text{Ln} \left[\frac{N_{bt}(i) + N_{bL}(i)}{N_{bt}(i)} \right] \quad (1b)$$

(Alroy 2000; Foote 2000a,b, 2001).

Here, N_{bt} is the number of taxa surviving from time bin $i-1$ to $i+1$ ("bottom-top" boundary crossers), N_{Ft} is the number of taxa first appearing in bin i and surviving to bin $i+1$ ("First-top" crossers), and N_{bL} is the number of taxa surviving from time bin $i-1$ and also appearing last in bin i ("bottom-Last" crossers). Equations (1a) and (1b) are algebraically equivalent to those in Finarelli and Badgley (2010), but we have changed our terminology to be consistent with Foote (2000a,b). We applied a continuity correction to N_{Ft} and N_{bL} , adding 0.5 to either count if it was 0 in a given interval (Finarelli 2007).

Rates of Diversification and Turnover

Finarelli and Badgley (2010) calculated per-lineage net diversification as

$$d(i) = \frac{N_t(i) - N_b(i)}{N_{bt}(i)} \quad (2a)$$

where N_t and N_b are total top and bottom boundary crossers, respectively. Using the terminology of equation (1), this expression is equivalent to

$$d(i) = \frac{N_{Ft}(i) - N_{bL}(i)}{N_{bt}(i)}. \quad (2b)$$

Therefore, net diversification, $d(i)$, is the difference between originations and extinctions in each bin i , scaled to the diversity passing through i (see also Foote 2000a). Expressing $d(i)$ as a function of p' and q' ,

$$d(i) = e^{p'(i)} - e^{q'(i)}. \quad (3)$$

To assess statistical significance in $p'(i)$, $q'(i)$, and $d(i)$, we bootstrapped the temporal durations of fossil taxa with replacement, randomly assigning first appearances within the observed temporal range for 5000 replicates

(Peters 2006b; Finarelli and Badgley 2010), and calculated estimates of origination, extinction, and diversification of the bootstrapped values. Confidence intervals around observed values were taken as 2 SD of the mean of the bootstrap distribution.

In the present analysis, we introduce a turnover metric, $t(i)$, defined as

$$t(i) = \frac{N_{Ft}(i) + N_{bL}(i)}{N_{bt}(i)} \quad (4)$$

For all species (excluding singletons) observed in time interval i , we want to compare the set of species that passed through both the upper and lower boundaries of the interval (the unchanged portion of the faunal list: N_{bt}) with those that did not pass through (the changed portion of the list: N_{Ft} and N_{bL}). As such, $t(i)$ is an odds-ratio of the changing and static portions of the fauna (Sokal and Rohlf 1995) and can distinguish intervals with substantial originations and extinctions (high turnover), even when there is little net diversity change. Following equation (3), relating $t(i)$ as a function of $p'(i)$ and $q'(i)$ gives

$$t(i) = e^{p'(i)} + e^{q'(i)} - 2. \quad (5)$$

Diversification rate statistics by time interval for each region are given in Supplementary Tables 4–9.

Assessing significance for $t(i)$ differs from the procedures for the other metrics. Intervals of high diversification (positive or negative) must possess high numbers of taxa that do not pass through one interval boundary. However, nearly balanced, but absolutely large, $p'(i)$ and $q'(i)$ should produce high turnover with $d(i) \approx 0$. Therefore, what is relevant is $t(i)$ in excess of the amount of change necessitated by $d(i)$. For the case in which extinction rate is 0 with net positive diversification, $d(i)$ and $t(i)$ are equal (equations 2b and 4) and $d(i) - t(i) = 0$. Here, $d(i)$ is driven solely by originations. As we manipulate extinction rates, as $q'(i)$ increases, the relative contribution of the extinction rate to $t(i)$ increases. It is this relative contribution that we want to test. (A similar argument can be made for the absolute value of $d(i)$ in the case of negative diversification with origination rate = 0.) A test statistic that determines whether the

difference between $d(i)$ and $t(i)$ is significantly different from 0 is given by

$$\delta(i) = |d(i)| - t(i). \quad (6)$$

From this relationship, if $d(i) \geq 0$, then

$$\begin{aligned} \delta(i) &= \left(\frac{N_{Ft}(i) - N_{bL}(i)}{N_{bt}(i)} \right) - \left(\frac{N_{Ft}(i) + N_{bL}(i)}{N_{bt}(i)} \right) \\ &= \left(\frac{-2N_{bL}(i)}{N_{bt}(i)} \right); \end{aligned} \quad (7a)$$

if $d(i) < 0$, then

$$\begin{aligned} \delta(i) &= - \left(\frac{N_{Ft}(i) - N_{bL}(i)}{N_{bt}(i)} \right) - \left(\frac{N_{Ft}(i) + N_{bL}(i)}{N_{bt}(i)} \right) \\ &= \frac{-2N_{Ft}(i)}{N_{bt}(i)}. \end{aligned} \quad (7b)$$

Expressing $\delta(i)$ as a function of $p'(i)$ and $q'(i)$ gives

$$\text{if } d(i) \geq 0, \text{ then } \delta(i) = -2e^{q'(i)} + 2 \quad (8a)$$

and

$$\text{if } d(i) < 0, \text{ then } \delta(i) = -2e^{p'(i)} + 2. \quad (8b)$$

Assignment of the case of zero net diversification to equations (7a) and (8a) is arbitrary. As with the previous metrics, significance for $\delta(i)$ was assessed using 5000 bootstrap replicates (Peters 2006; Finarelli and Badgley 2010). Bootstrap results are given in Supplementary Table 10.

Comparing Rodent Diversity and Composition among Regions

We performed pairwise Mann-Whitney tests on the distribution of total diversity counts (excluding singletons) among 1-Myr time intervals to determine whether standing diversity differed significantly among regions. Pairwise F -tests were performed to test for regional differences in the variance of diversity. For both procedures, we employed Bonferroni correction, multiplying observed p -values by three for simultaneous tests (Sokal and Rohlf 1995). We also compared the similarity of species-level taxonomic composition of

modern and paleofaunas with the Jaccard index, J (Legendre and Legendre 1988):

$$J = \frac{a}{a + b + c}, \quad (9)$$

where a is the number of species shared between two regions, b is the number of species unique to the first region, and c is the number of species unique to the second region. We evaluated changes in faunal composition at the species level using Analysis of Similarity (ANOSIM, Clarke 1993). This method compares within-group ranked distances to between-group ranked distances; significance was assessed through 10,000 bootstrap replicates, as implemented in the PAST computer program (version 2.08, Hammer et al. 2001), using the Jaccard distance metric. We performed two ANOSIM comparisons: (1) pre-MCO intervals against intervals in the MCO and (2) MCO intervals against post-MCO intervals. In all cases we excluded intervals with no species records. This resulted in three MCO intervals (17–16 Ma, 16–15 Ma, and 15–14 Ma) for Regions 2 and 3, but only two for Region 1 (17–16 Ma excluded).

Change in Faunal Composition within Regions

We evaluated change in faunal composition within each region with a multinomial likelihood method (Finarelli and Badgley 2010). Within each region, rodent species were grouped by family. Minor rodent families (few species and occurrences) were combined in an “Other” category. Between adjacent 1-Myr time intervals, we tested compositional similarity in terms of the proportional contribution of each family-level group to total diversity. For each time interval, we calculated the multinomial likelihood of the proportions for each family by using (1) the empirical proportions observed in that interval and (2) the proportions of the preceding interval. The log-likelihood (LnL) of the multinomial distribution is given by

$$\text{LnL}(i) = \sum_j a_j \ln(p_j) \quad (\text{Edwards 1992}), \quad (10)$$

where a_j is the count of species in family j , and p_j is the proportion of total species in interval i assigned to family j . Summing over j families gives the LnL for interval i . This value was

then compared with the LnL calculated using count data for interval i and proportions from interval $i-1$. The proportions for interval i always give the highest likelihood for interval i , with increasingly divergent proportions between intervals creating greater log-likelihood differences. We considered a LnL difference greater than 2.0 as a threshold for significant faunal change (Edwards 1992).

Sampling Effects

The data set includes species and occurrences at fossil localities but often without associated specimen numbers. We calculated the correlation (Spearman's r) between the number of localities and both raw range-through diversity for each time interval and diversity without singletons. Numbers of sampled localities per time interval are given in Supplementary Table 11. We also calculated correlations for the first differences (change in localities versus change in diversity between adjacent intervals). We omitted intervals with no localities because such intervals represent gaps in the fossil record rather than the absence of species.

Results

Diversity Comparisons and Sampling Effects

Rodent diversity and rate metrics for each region are given in Figures 2–4 and Supplementary Tables 1–9. Raw diversity per Myr in Region 1 (Fig. 2A) reached about half of modern rodent diversity (Table 1) during the richest intervals. In contrast, the richest intervals of Regions 2 and 3 (Figs. 3A, 4A) matched or exceeded modern rodent diversity of those regions. Overall, per-interval diversity was not significantly different between the montane Regions 1 and 2 (means of 9.7 and 6.4 species per Myr interval, respectively), but Great Plains diversity (Region 3, mean of 17.9 species per interval) was significantly greater than in both Regions 1 and 2 (Table 4). All three regions showed substantial variability in diversity, but the variances were not significantly different among regions (Table 5).

All three regions showed a positive correlation between diversity and the number of sampled localities (Table 6). Raw diversity

showed significant correlations with the number of localities for all regions, whereas diversity excluding singletons was significantly correlated for Regions 2 and 3, but not Region 1. When we considered first differences in diversity and sampling, only Region 3 showed a significant correlation (for both raw and no-singleton diversity; Table 6). Figures 2–4 illustrate the strong correspondence between formation boundaries (Figs. 2E, 3E, 4E) and intervals with no localities or a substantial change in the number of localities compared with the preceding interval. However, formation boundaries and depositional hiatuses were not the only contexts in which the number of fossil localities was at or near zero, suggesting that facies characteristics or outcrop exposure could also have constrained fossil productivity.

Rarefaction curves enable us to judge how robust the major patterns of diversity change are to different levels of sampling. The overall shape of the diversity curves was preserved in each of the subsampling quorum levels, although a notable flattening of the diversity peaks occurs at severely reduced sampling levels (e.g., $q = 0.25$ of total sampling effort; Supplementary Fig. 1). The large MCO diversity peaks in the tectonically active regions (1 and 2) appear to be robust to sampling, as does the immediate post-MCO diversity peak in the tectonically passive region (3).

Comparison of rarefaction curves among the three regions reveals that sampling-corrected diversity in Region 2 (Montana) was significantly higher than diversity in the other regions during the MCO (16–15 Ma and 15–14 Ma), despite Region 2 being relatively poorly sampled (Fig. 5). The MCO diversity peak observed in the Rocky Mountains therefore likely represents a genuine increase in species richness, and not simply an artifact. In the two time bins immediately following the MCO (14–13 Ma and 13–12 Ma), diversity increased in Region 3 (Great Plains), such that it was indistinguishable from that of Region 2 (Fig. 5). Region 1 (Oregon) showed significantly lower diversity than did Regions 2 and 3 during these intervals, despite exhibiting an overall sampling intensity similar to the more species-rich Region 3. From 12 Ma to 10 Ma,

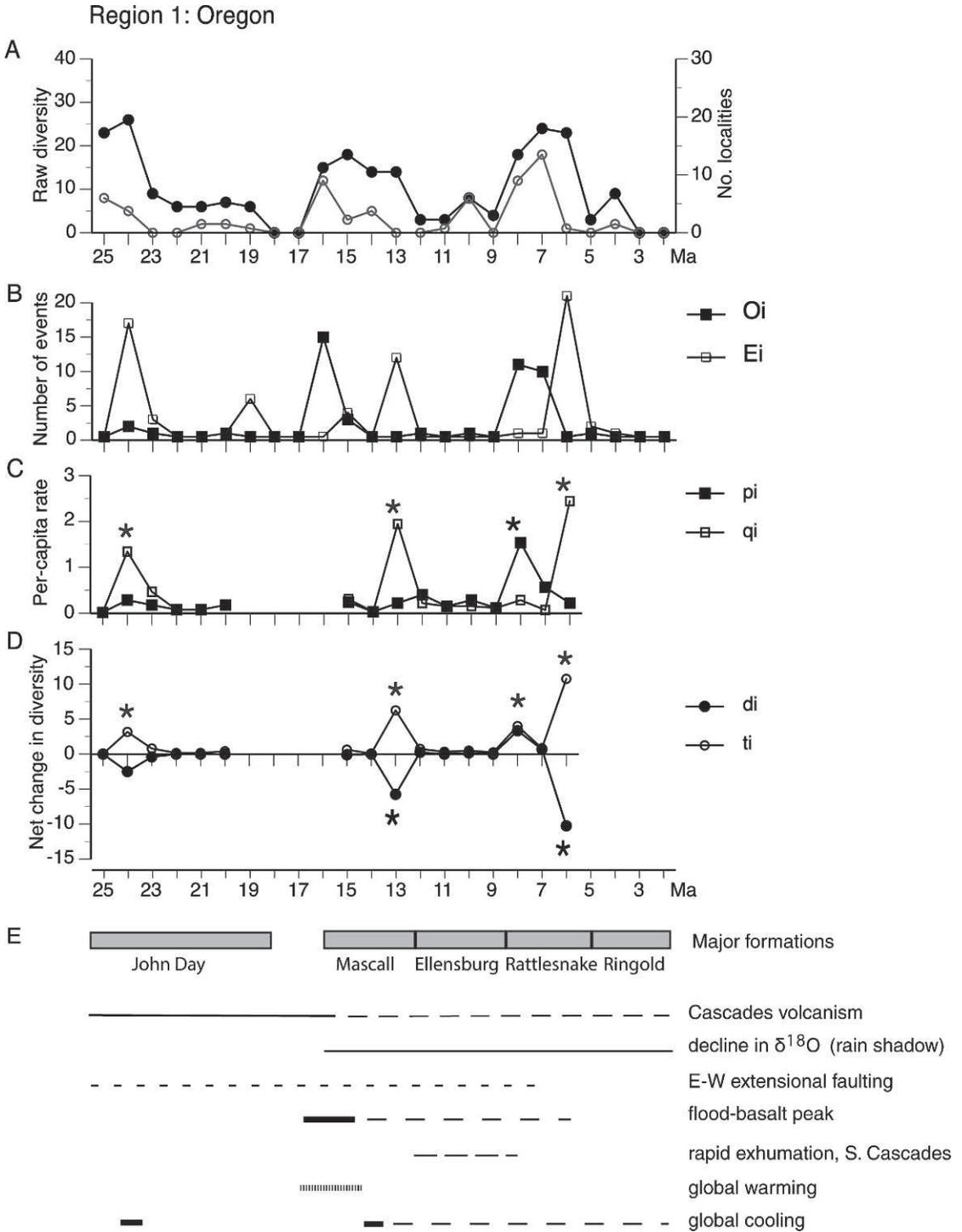


FIGURE 2. History of rodent diversity and landscape in Region 1 (Columbia Basin ≈ “Oregon”) based on sources in text. A, Species diversity of rodents (range-through diversity including singletons) per 1-Myr interval (solid black symbols) and number of fossil localities in the NeoMap database per 1-Myr interval (open gray symbols). B, Number of origination (black) and extinction (gray) events per Myr based on range-through diversity excluding singletons. C, Per capita rate of origination $p'(i)$ (black) and rate of extinction $q'(i)$ (gray) per Myr for range-through diversity excluding singletons. D, Net diversification rate $d(i)$ and turnover rate $t(i)$. In C and D, asterisks mark intervals with significant values of the respective diversity metrics; see text for discussion. E, Highlights of Neogene tectonic and climatic history for Region 1.

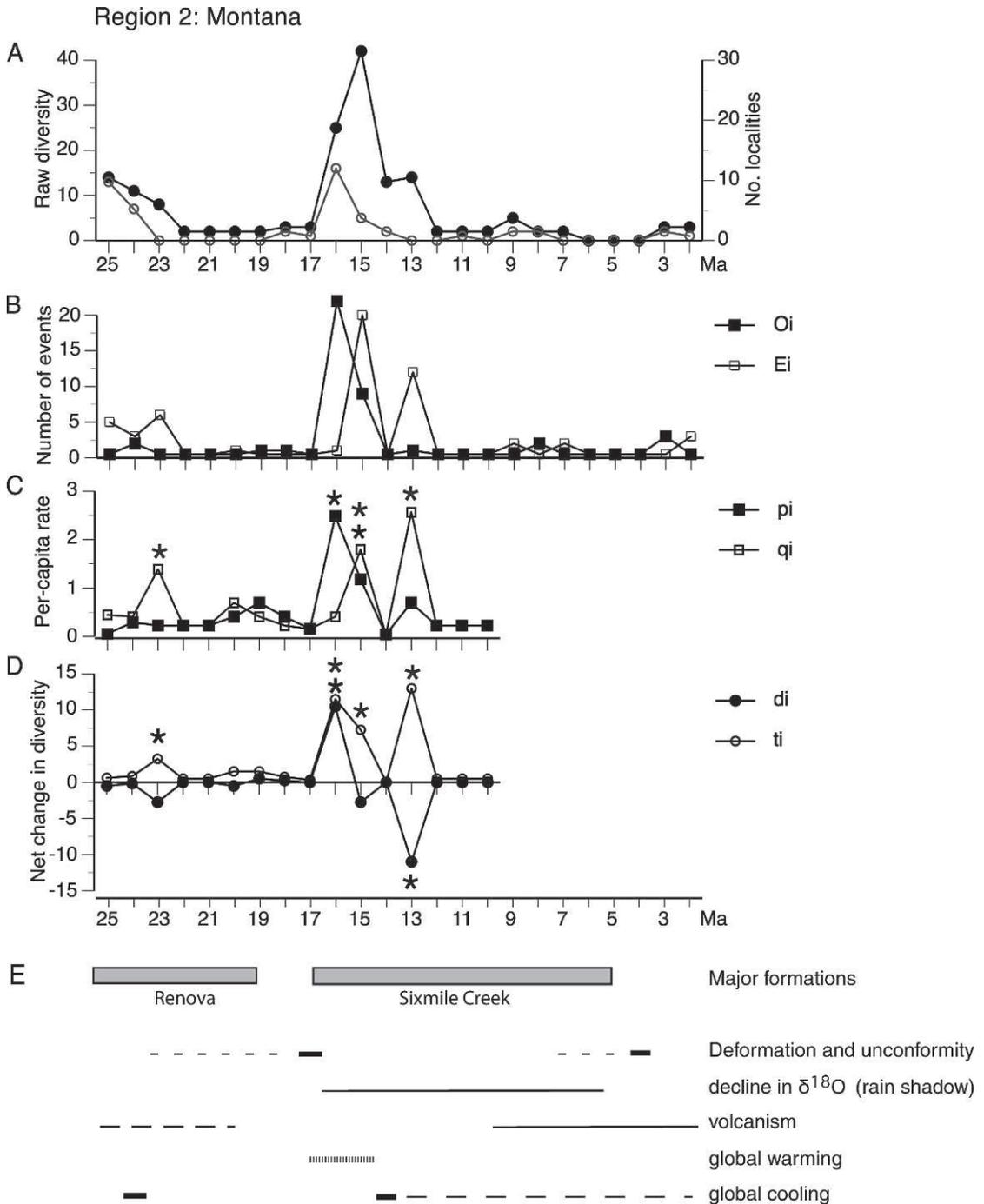


FIGURE 3. History of rodent diversity and landscape in Region 2 (northern Rocky Mountains \approx “Montana”) based on sources in text. A, Species diversity of rodents (solid black symbols) and number of fossil localities (open gray symbols) per 1-Myr interval. B, Number of origination (black) and extinction (gray) events per Myr. C, Per capita rate of origination $p'(i)$ (black) and rate of extinction $q'(i)$ (gray) per Myr. D, Net diversification rate $d(i)$ and turnover rate $t(i)$. In C and D, asterisks mark intervals with significant values. E, Highlights of Neogene tectonic and climatic history for Region 2. See Figure 2 for further details.

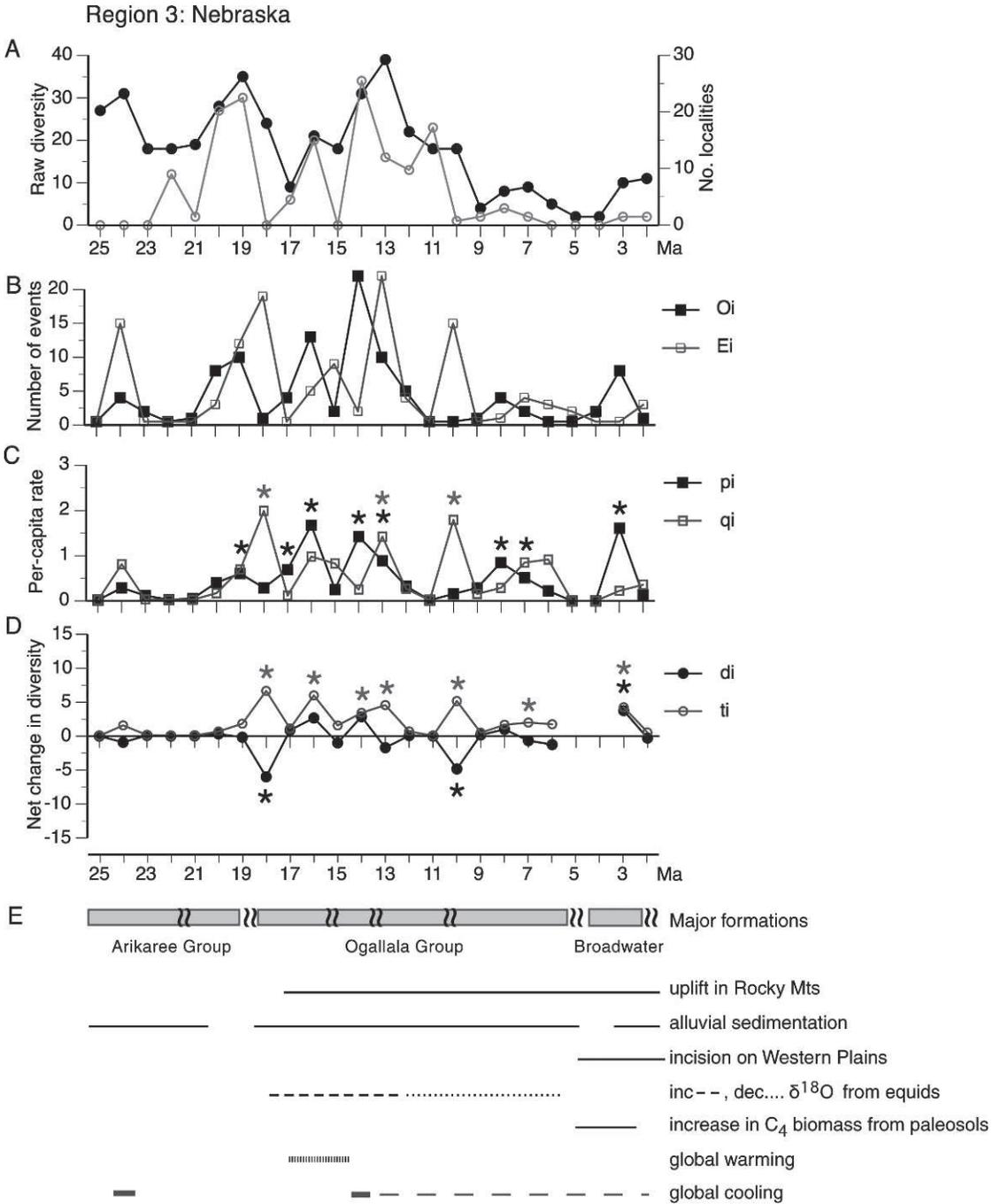


FIGURE 4. History of rodent diversity and landscape in Region 3 (northern Great Plains ≈ “Nebraska”) based on sources in text. A, Species diversity of rodents (solid black symbols) and number of fossil localities (open gray symbols) per 1-Myr interval. B, Number of origination (black) and extinction (gray) events per Myr. C, Per capita rate of origination $p'(i)$ (black) and rate of extinction $q'(i)$ (gray) per Myr. D, Net diversification rate $d(i)$ and turnover rate $t(i)$. In C–D, asterisks mark intervals with significant values. E, Highlights of Neogene tectonic and climatic history for Region 3. See Figure 2 for further details.

TABLE 4. Pairwise Mann-Whitney tests for species diversity (singletons excluded) by time interval for the three regions. Diversities were compared for 23 sampled time intervals between 25 and 2 Ma. Mann-Whitney U statistic below the diagonal, and Bonferroni-corrected p -values (multiplied by 3, to account for three simultaneous tests) above the diagonal. Significant values (at $p < 0.05$) given in bold.

	Region 1	Region 2	Region 3
Region 1	—	0.166	0.023
Region 2	177.5	—	<0.001
Region 3	143.0	91.0	—

Region 3 showed significantly higher diversity than in either of the active regions. By the end of the Miocene (e.g., from 7 to 6 Ma), diversity was greater in Oregon than on the Great Plains (Fig. 5).

Diversification and Landscape History

Rodent diversification history in each region is shown in Figs. 2B–D, 3B–D, and 4B–D (see also Supplementary Tables 4–9). In Region 1 (Oregon), the only significant origination rate, $p'(i)$, was at 8 Ma (Fig. 2C). Despite the largest number of originations occurring at 16 Ma (Fig. 2B), the lack of boundary-crossing taxa from 17 Ma makes $p'(i)$ undefined in this interval (eq. 1a). The largest extinction peaks (Fig. 2B) coincided with significant extinction rates, $q'(i)$ (Fig. 2C). Two intervals of significant diversification rate, $d(i)$, occurred at 13 Ma and 6 Ma, both dominated by extinction (Fig. 2D). These and two additional intervals, at 24 Ma and 8 Ma, also exhibited significant turnover. Changes in diversity generally tracked changes in the number of localities (Fig. 2A), although some intervals with few localities still exhibited high diversity. In terms of geohistory (Fig. 2E), uplift of the Cascade Range and E–W extensional faulting occurred over much of the Neogene (Christiansen and Yeats 1992). Columbia River flood-basalt eruptions peaked between 17 and 14 Ma (Hooper et al. 2002). This interval corresponded to the warm MCO and overlapped an episode of montane uplift (Kohn et al. 2002; Takeuchi and Larson 2005). Relief in the southern Cascades increased during accelerated exhumation from 12 to 8 Ma (Reiners et al. 2002). Rapid global cooling between 14 and 13 Ma was succeeded by gradual cooling

TABLE 5. Pairwise F -tests for diversity (singletons excluded) by time interval for the three regions. Variance in diversity was compared for the 23 sampled time intervals between 25 and 2 Ma. Bonferroni-corrected p -values (multiplied by 3 to account for three simultaneous tests) above the diagonal, and F -statistic below the diagonal. None of the p -values are significant.

	Region 1	Region 2	Region 3
Region 1	—	1.000	0.867
Region 2	1.102	—	0.921
Region 3	1.582	1.556	—

(Zachos et al. 2001, 2008) and aridification east of the northern Cascades (Takeuchi and Larson 2005), although paleofloras indicate that forests dominated much of the Columbia Basin until the Pliocene (Leopold and Denton 1987). On the central Snake River Plain, between Regions 1 and 2, pollen spectra indicate the presence of sagebrush steppe, similar to modern vegetation, at 12 Ma and through the late Miocene (Davis and Ellis 2010). The interval with concentrated tectonic and climatic changes, 17 to 14 Ma, coincided with the largest peak in originations and was followed by an interval of significant decline in diversification rate at 13 Ma. The late Miocene (9–7 Ma) increase in diversity and interval of significant $p'(i)$ and $t(i)$ at 8 Ma coincided with increasing relief in the southern Cascades.

In Region 2 (Montana), the stratigraphic record documents late Oligocene through late Miocene time, with a gap from 19 to 17 Ma (Fig. 3A,E) (Fields et al. 1985; Hanneman and Wideman 1991). High peaks in origination (Fig. 3B) coincided with the significant $p'(i)$ at 16 Ma and 15 Ma (Fig. 3C), and peaks in extinction (Fig. 3B) corresponded to three intervals of significant $q'(i)$ at 23 Ma, 15 Ma, and 13 Ma (Fig. 3C). Significant $d(i)$ occurred at 23 Ma (from extinctions), 16 Ma (from originations), and 13 Ma (from extinctions) (Fig. 3D), and significant turnover rates coincided with significant diversification at 16 Ma and 13 Ma; that is, $t(i)$ significantly exceeded that required by the significant $d(i)$ in these intervals. The turnover rate was also significant at 15 Ma, without significant diversification (Fig. 3D). From 12 to 2 Ma, both the number of localities and diversity

TABLE 6. Spearman rank correlation between number of localities and species diversity per Myr for three regions. Time intervals with 0 fossil localities were omitted. Entries in bold are statistically significant at $p < 0.05$.

	R1: Oregon		R2: Montana		R3: Nebraska	
	Raw diversity	No singletons	Raw diversity	No singletons	Raw diversity	No singletons
Raw data						
r	0.554	0.452	0.781	0.735	0.698	0.695
n	14	14	11	11	15	15
2-tailed p	0.040	0.105	0.005	0.012	0.004	0.004
First differences						
r	0.542	0.401	0.376	0.377	0.650	0.595
n	13	13	10	10	14	14
2-tailed p	0.056	0.175	0.283	0.283	0.012	0.025

were very low, without significant diversification metrics. In Region 2, a depositional hiatus separated the late Oligocene to early Miocene from middle to late Miocene deposits (Fig. 3E). Gradual uplift and extension from 23 to 18 Ma changed to deformation, resulting in a regional-scale unconformity from 17.3 to 16.7 Ma (Fields et al. 1985; Barnosky et al. 2007). A similar pattern occurred from the late Miocene to middle Pliocene (Elliott et al. 2003). Geochemical and paleobotanical indicators of aridity were widespread in early Miocene sections of the Renova Formation and throughout the middle to late Miocene Sixmile Creek Formation (Thompson et al. 1982; Fields et al. 1985; Leopold and Denton 1987). The interval of overlapping deformation and global warming (17 to 14 Ma) coincided with a significant increase in both originations and extinctions. Diversity peaked at over 40 species by 15 Ma (Fig. 3A), with the highest diversification and turnover rates occurring between 16 and 13 Ma. During the MCO, diversification and turnover were driven principally by originations. In contrast, during the subsequent cooling episode, $d(i)$ and $t(i)$ were driven mainly by extinctions (Fig. 3D). As would be expected with high turnover in the absence of net diversification, the high $t(i)$ value at 15 Ma included both elevated extinctions and originations.

Region 3 (Nebraska) exhibited the greatest fluctuation in species diversity of all three regions (Fig. 4). The largest peaks in origination occurred at 19 Ma, 16 Ma, and 14 Ma (Fig. 4B). Four peaks in extinction occurred at 24 Ma, 18 Ma, 13 Ma, and 10 Ma. Six intervals exhibited significant $p'(i)$ (Fig. 4C): the highest

of these occurred at 16 Ma, 14 Ma, and 3 Ma, although only the youngest $p'(i)$ corresponded to a significant positive diversification rate (Fig. 4D). Three intervals had significant $q'(i)$ (Fig. 4C): those at 18 Ma and 10 Ma corresponded to significant negative diversification rates (Fig. 4D). Although origination and extinction rates were more volatile in Region 3, the magnitudes of these rates were lower than in the other regions. Turnover rates were significant during seven intervals (Fig. 4D), peaking at 18 Ma, coincident with the onset of deposition of the Ogallala Group. Some intervals with significant $p'(i)$ or $q'(i)$ corresponded to increases or decreases, respectively, in the number of localities per interval. Importantly, some did not. Three intervals with both significant $d(i)$ and $t(i)$ corresponded to substantial change in the number of localities. An additional three intervals of significant $t(i)$, without significant $d(i)$, also coincided with large change in the number of localities. Although some of this pattern could be taken as consistent with the expectations of sampling bias inducing spurious extinctions or originations at a boundary interval, we would not expect to see elevated turnover with static diversity (that is simultaneous increase in both) as a sampling effect.

Most time intervals with few to no fossil localities corresponded to unconformities between formations (Fig. 4A,E), and origination peaks aligned with depositional periods. Uplift in the Rocky Mountains was the primary source for clastic deposits of the Ogallala Group (Swinehart et al. 1985), whereas tilting and incision on the western plains from the end of the Miocene to the present time (McMillan et al.

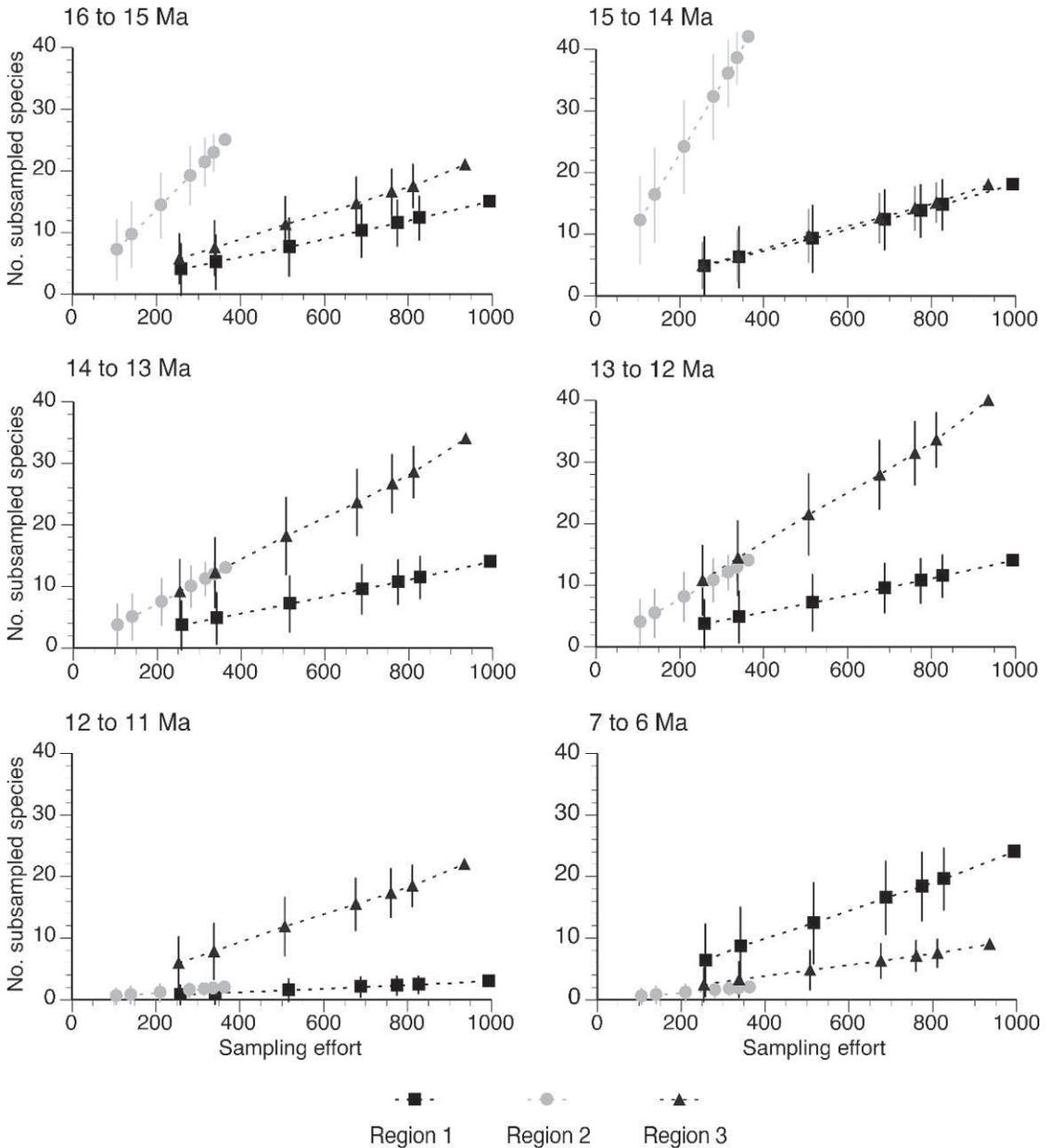


FIGURE 5. Rarefaction curves for Regions 1, 2, and 3 based on Shareholder Quorum Subsampling for six 1-Myr time intervals. Each rarefaction curve depicts the mean value of 1000 iterations for six quorum levels, q , corrected for rare taxa: ($q = 0.25, 0.33, 0.50, 0.67, 0.76, \text{ and } 0.80$) for each region. Error bars represent two standard deviations about the mean. Data are plotted at the implied number of species occurrences for each quorum level. The curves demonstrate that the major changes in diversity within and among regions are apparent even at fairly low sampling intensity.

2002) coincided with lower fossil productivity and rodent diversity. The contrast in source and substrate between the Arikaree Group and the Ogallala Group does not correspond to a significant change in diversity but does coincide with significant changes in faunal composition

(see below). The warm MCO coincided with significant origination and turnover rates but not with significant extinction or diversification rates. The interval of rapid cooling (beginning 14 Ma) witnessed significant origination and turnover as well.

TABLE 7. Jaccard index of similarity for pairwise comparisons of the three regions. Values above the diagonal are for modern faunas, and values below the diagonal are for faunas at 16 Ma, when diversity was high in each region. Number of species in each region, extant faunas: R1 = 55, R2 = 39, R3 = 29; fossil faunas: R1 = 15, R2 = 25, R3 = 21.

	Region 1	Region 2	Region 3
Region 1	—	0.40	0.13
Region 2	0.00	—	0.40
Region 3	0.00	0.07	—

Faunal Composition

Rodent paleofaunas differed substantially in taxonomic composition among the three regions, and, within each region, paleofaunas also differed from modern rodent faunas. Extant faunas show moderate similarity at the species level between Regions 1 and 2 and Regions 2 and 3, but low similarity between Regions 1 and 3 (Table 7). For paleofaunas at 16 Ma, an interval of fairly high diversity in all three regions (Figs. 2–4), Region 1 showed no similarity with Region 2 or 3, and Regions 2 and 3 had very low similarity. In evaluating these comparisons, we need to acknowledge differences in temporal scale and taxonomic practices, as well as incomplete sampling of paleofaunas. Nonetheless, the low inter-region similarity at 16 Ma is striking. For the Neogene record of each region, species composition prior to the MCO differed significantly from subsequent species composition (Table 8), suggesting that the middle Miocene witnessed substantial restructuring of small mammal faunas.

Paleofaunas of the three regions differed from each other at the family level (Figs. 6–8). Six families (Sciuridae, Mylagaulidae, Muridae, Heteromyidae, Geomyidae, and Castor-

idae) dominated Neogene diversity for all three regions, with each region possessing unique minor families and changes in family-level diversity. In Region 1, geomyids and allomyids had high diversity from 25 to 18 Ma but disappeared in the middle Miocene (Fig. 6), whereas murids, heteromyids, and castorids were minor components of the early Miocene rodent fauna and then increased from the middle to late Miocene. Sciurid diversity waxed and waned over the Neogene in Region 1. Likelihood ratios of change in faunal composition revealed three intervals of significant change in composition: 23 Ma (significant increase in mylagaulids), 16 Ma (significant increase in sciurids), and 7 Ma (significant increase in heteromyids). It is striking for this region that none of the significant changes in faunal composition correspond to intervals in which significant rate metrics were observed.

In Region 2, geomyids and aplodontids dominated the early part of the record, declining in diversity as sciurids and heteromyids became the major constituents of middle Miocene rodent faunas (Fig. 7). Neither heteromyids nor sciurids were present in Region 2 prior to 16 Ma, which corresponded to a significant change in composition, as well as significant peaks in $p'(i)$ (Fig. 3C), $d(i)$, and $t(i)$ (Fig. 3D). A smaller, but still significant, peak in compositional change occurred at 3 Ma. Other peaks in extinction and origination rates (Fig. 3C) and diversification and turnover rates (Fig. 3D) did not correspond to changes in faunal composition.

In Region 3, geomyids and castorids dominated the record from 25 to 18 Ma, with mylagaulids, heteromyids, and castorids dom-

TABLE 8. Results of an Analysis of Similarity (ANOSIM) as implemented in PAST (ver. 2.08) using the Jaccard similarity index. Comparisons are for (1) pre-MCO intervals against intervals in the MCO (17–14 Ma) and (2) MCO intervals against post-MCO intervals. We performed 10,000 bootstrap replicates to assess significance (Bonferroni-corrected p -values multiplied by 2 to account for two comparisons per region). Significant values (at a corrected level of $p < 0.05$) are given in bold. In all three regions, species composition during the MCO was significantly different from that prior to the MCO, but was not different from subsequent intervals.

	Pre-MCO intervals vs. MCO		MCO vs. post-MCO intervals	
	ANOSIM R	p	ANOSIM R	p
Region 1	1.000	0.049	0.115	0.414
Region 2	0.652	0.037	0.232	0.256
Region 3	0.987	0.012	0.439	0.606

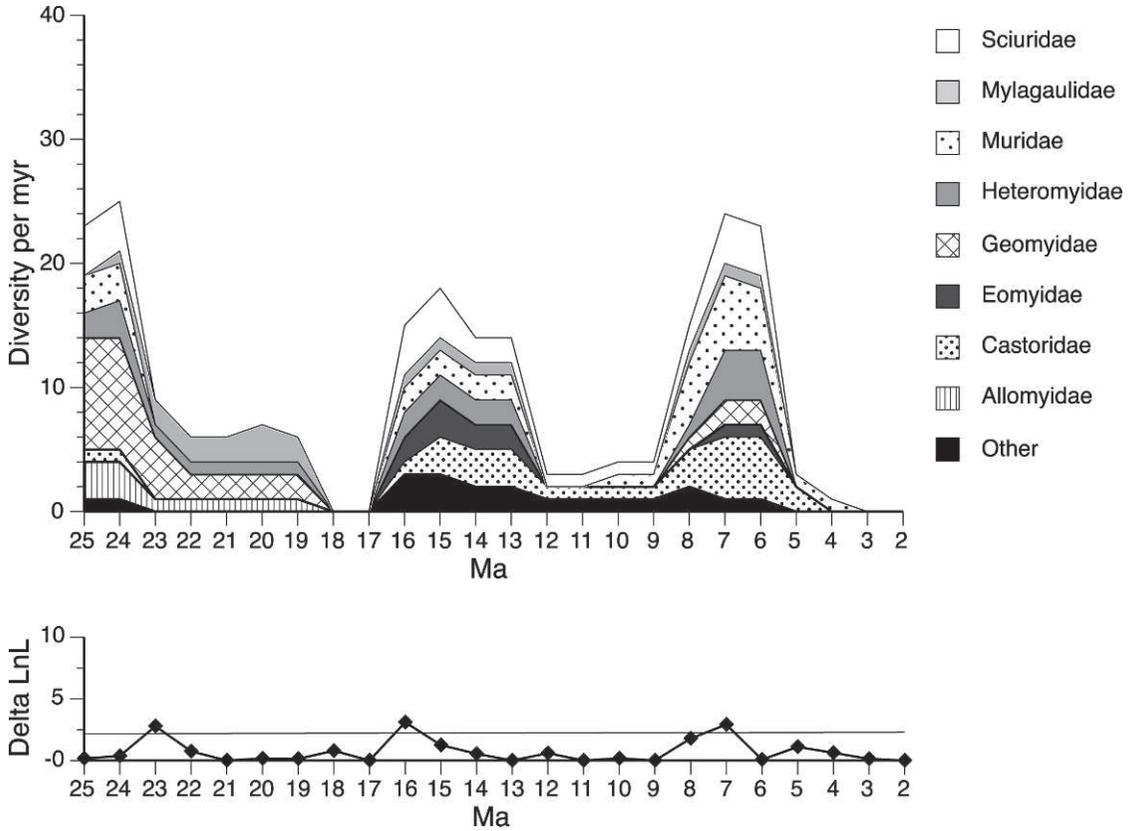


FIGURE 6. Changes in family-level species composition of rodent faunas, Region 1. Diversity excludes singletons. A, Stacked-diversity of species in rodent families. Families with few species over the Neogene were lumped into "Other." B, Log-likelihood ratios of faunal composition comparing adjacent 1-Myr intervals. Likelihood ratios greater than 2.0 represent significant change in faunal composition for that time interval. See text for discussion. The rodent families contributing to the three intervals of significant faunal change are heteromyids and sciurids; omitting these families from the analysis removed all significant changes in family-level diversity.

inating the middle Miocene (Fig. 8). During the Pliocene, murid species outnumbered all other families combined. Likelihood ratios indicate a significant change in faunal composition at 14 Ma, influenced by a spike in heteromyid diversity. Smaller significant peaks occurred throughout the Nebraska record, with each peak reflecting substantial changes in one or two families. Changes in faunal composition comprised idiosyncratic fluctuations in the six major families of Region 3 (Heteromyidae, Castoridae, Mylagaulidae, Sciuridae, Muridae, and Eutypomyidae). The largest peak of faunal change at 14 Ma coincided with significant $p'(i)$ (Fig. 4C) and $t(i)$ but not significant $d(i)$ (Fig. 4D). Two other peaks occurred at 16 Ma, which coincided with the highest $p'(i)$ (Fig. 4C) and significant

$t(i)$ (Fig. 4D), and at 12 Ma, which did not coincide with any significant diversity metrics.

An intriguing aspect of Neogene rodent faunal histories involves evidence of shifts or expansions in geographic range (Table 9). Each region shared 12–16% of its species with at least one other region between 25 and 2 Ma; some of these shared species appeared earlier in one region than in the others. These apparent range expansions represent 8.4% of species from Region 1, 13.4% of species from Region 2, and 5.4% of species from Region 3. Notably, Region 3 had the highest species richness, yet the lowest proportion of apparently dispersing species, indicating a greater degree of endemism. We tallied immigration and emigration among the three regions. Dispersal events appear clustered in time for

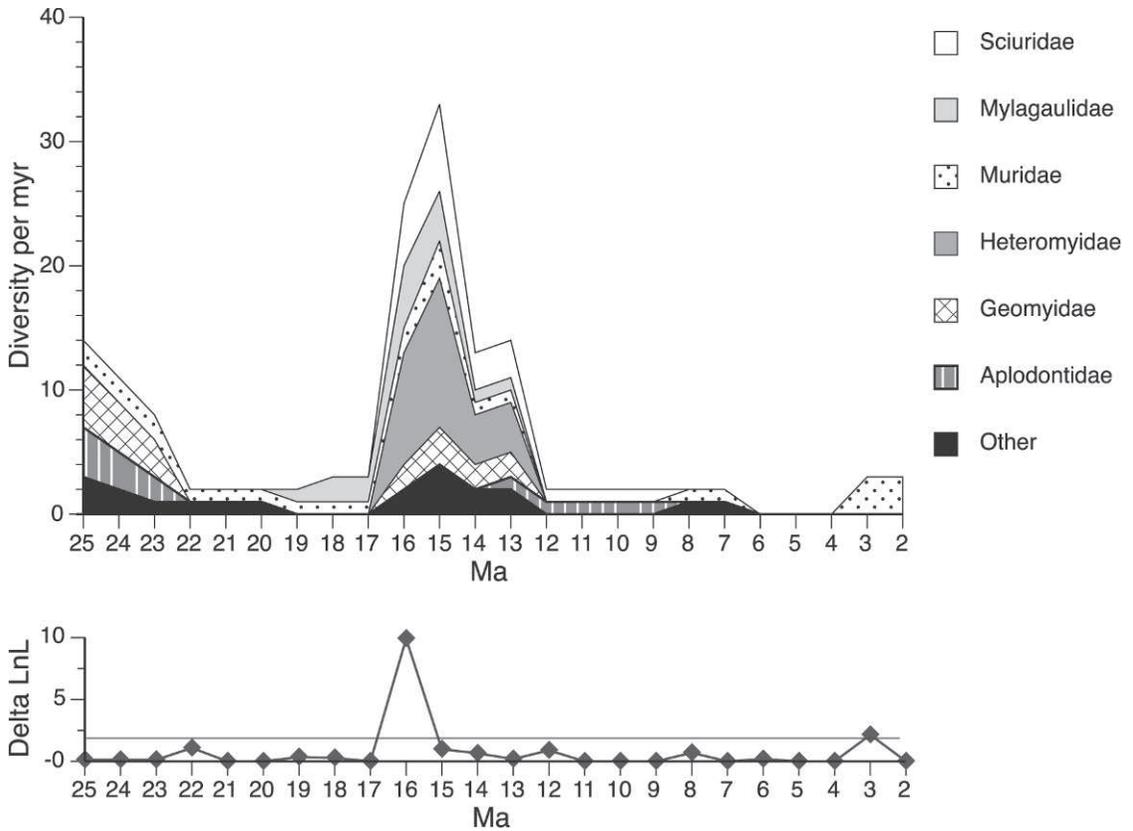


FIGURE 7. Changes in family-level species composition of rodent faunas, Region 2. Diversity excludes singletons. A, Stacked-diversity of species in rodent families. Families with few species over the Neogene were lumped into "Other." B, Log-likelihood ratios of faunal composition comparing adjacent 1-Myr intervals. Likelihood ratios greater than 2.0 represent significant change in faunal composition for that time interval. See text for discussion. The rodent families contributing to the main interval of significant faunal change are heteromyids and sciurids; omitting these families from the analysis removed all significant changes in family-level diversity.

each region, primarily during the MCO: at 15 Ma for Regions 1 and 2, and at 16 Ma for Region 3 (Table 9). We caution that these patterns should, as yet, only be taken as suggestive, because sample sizes are small and all three records exhibited sensitivity to sampling. In addition, several species in the data set belong to lineages that represent intercontinental immigrants into North America during the study interval (Tedford et al. 2004). These include the genera *Petauristodon* at 18.8 Ma (Sciuridae [Goodwin 2008]), *Copemys* at 17.5 Ma (Cricetidae = Muridae, Lindsay 2008), *Leptodontomys* at 17.5 Ma (Eomyidae [Flynn 2008]), and *Promimomys* at 6.7 Ma (Arvicolidae = Muridae [Martin 2008]). Species from at least some of these lineages occurred in all three regions studied.

Discussion

Regional Histories

Each region showed substantial changes in species diversity over the Neogene. The specific patterns were unique to each region, although some features of diversification and faunal composition occurred in common. Interestingly, fossil rodent faunas differed more in composition across these regions than do the modern faunas, at both the species (Table 7) and family levels (Figs. 6–8), implying greater provincialism in Neogene than in Recent rodent faunas. Although the apparent provincialism could have arisen from different workers concentrating in different field areas, recent evaluations of several widespread

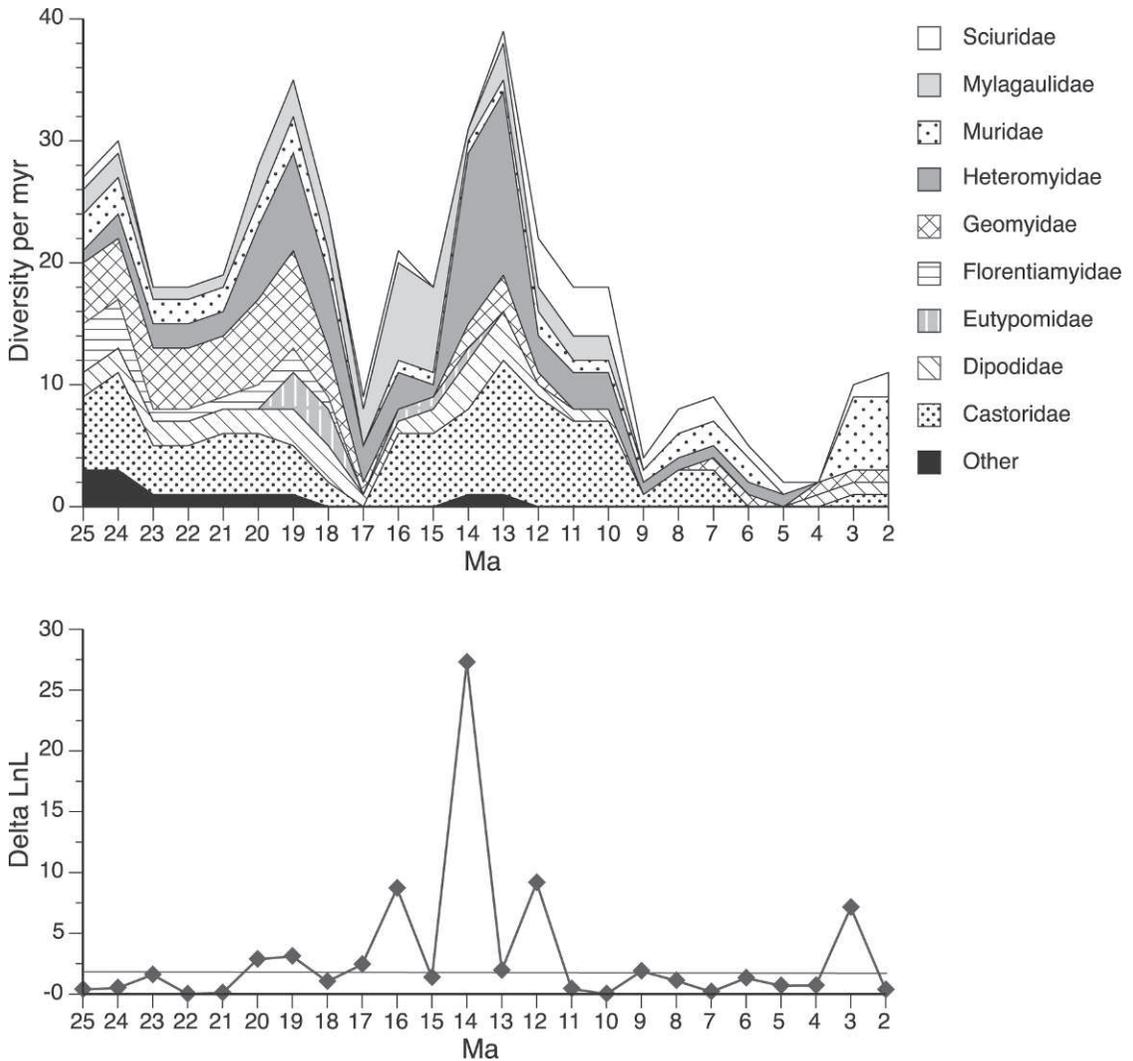


FIGURE 8. Changes in family-level species composition of rodent faunas, Region 3. Diversity excludes singletons. A, Stacked-diversity of species in rodent families. Families with few species over the Neogene were lumped into "Other." B, Log-likelihood ratios of faunal composition comparing adjacent 1-Myr intervals. Likelihood ratios greater than 2.0 represent significant change in faunal composition for that time interval. See text for discussion. Six rodent families contributed to the intervals of significant faunal change. Heteromyids and mylagaulids contributed to the largest peak of faunal change, at 14 Ma.

groups support this geographic pattern (e.g., Korth 2000; Hopkins 2007; Martin et al. 2008).

Correlations between diversity and the number of fossil localities are striking in all three regions, although not all are significant (Table 6, Supplementary Table 11). The number of sampled localities generally tracked the deposition of local or regional formations or hiatuses, and such a strong macrostratigraphic pattern prompts us to question whether the observed temporal variation in diversity is merely a

result of sampling, or whether both diversity and fossil productivity were responding to changes in landscape history (Peters 2006a; Peters and Heim 2011). Time intervals with no fossil localities represent the clear overprint of sampling on the fossil record. On the other hand, we observed significant changes in diversity metrics and faunal composition across intervals with stable numbers of fossil localities in all three regions, implying that faunal changes do contain evolutionary signals.

TABLE 9. Number of species unique to each region, and to overlapping regions, and timing of inferred range expansion between regions for species with stratigraphic ranges that overlap or occur within the interval from 25 to 2 Ma.

	Region 1	Region 2	Region 3
Total species	85	67	130
Species found only in region	72	56	115
Species shared with at least one other region	13	11	15
Dispersing species: those first appearing in region and appearing later in other regions*	7	9	7
Dispersing species as proportion of total	0.082	0.134	0.054
R1→R2	2		
R1→R3	3		
R1→R2→R3	2		
R2→R1		4	
R2→R3		5	
R3→R2			4
R3→R1			3
R1→other region(s)	24–23 Ma: 1 18–17 Ma: 1 15–14 Ma: 3 10–9 Ma: 1 7–6 Ma: 1		
R2→other region		15–14 Ma: 4 14–13 Ma: 1 11–10 Ma: 1 8–7 Ma: 3	
R3→other region			16–15 Ma: 4 15–14 Ma: 1 11–10 Ma: 1 4–3 Ma: 1

* Does not include species whose temporal ranges overlap the 25–2 Ma study interval, but whose dispersal event falls outside the interval.

If diversification simply reflected sampling, then originations and extinctions should both cluster around gaps in the stratigraphic record (Holland 1995; Peters 2006a). The number of fossil localities, as a measure of rock record and fossil productivity, was positively correlated with originations for Regions 2 and 3, yet was not significantly correlated with extinctions in any region (Table 10, Supplementary Table 11). The pattern is strongest in Region 3 (Nebraska), yet even here, we observed significant changes in faunal composition (Fig. 8) counter to the expected response of sampling artifact. The asymmetry between originations and extinctions in relation to fossil productivity suggests that the regional diversity histories are more than a product of sampling biases.

Fossil productivity and originations could be causally linked in the montane regions through the creation of new habitats and the fragmentation of species geographic ranges caused by tectonic or isostatic uplift increasing relief. Alternatively, tectonism could increase preservation potential via increased rates of

sediment transport and deposition, in which case originations would actually reflect greater fossil productivity. In tectonically stable regions, episodes of sediment accumulation could stimulate originations through the localized fragmentation of populations across large expanses of floodplain habitats or, as with active regions, could increase preservation potential. In contrast, the low correlations between extinction rate and fossil productivity suggest that extinctions were caused by factors independent of depositional processes. Such hypotheses could be evaluated further by using ecomorphology, abundance, and geographic ranges to determine whether regional first and last appearances represent speciation and extinction or range shifts.

If overall diversity patterns were the result of preservation or collecting artifacts, then we would not expect the patterns to persist after subsampling. However, the overall shape of the diversity peaks remained unchanged by reducing the sampling effort in all three regions, even under drastic reductions in the number of sampled localities (Supplementary

TABLE 10. Spearman rank correlation between number of fossil localities—as an indicator of sampling effort, fossil productivity, and sediment accumulation—and diversity metrics that are sensitive to sampling. “Raw data” indicates observed number of fossil localities per time bin measured against observed diversity metrics. “First diff.” is the first difference between adjacent time bins. Two-tailed p -values were multiplied by 5 (Bonferroni correction) to account for multiple tests (each diversity metric). Entries in bold indicate significant rank correlation for a corrected $p < 0.05$. Note that originations show significant correlations whereas extinctions do not. NS, no singletons; see text for other abbreviations.

Diversity NS	No. of originations N_{FT}	Origination rate $p'(i)$	No. of extinctions N_{bL}	Extinction rate $q'(i)$
Region 1: Oregon				
Raw data ($n = 23$)				
r_s	0.646	0.523	0.337	0.051
p	0.004	0.052	0.579	1.000
First diff. ($n = 22$)				
r_s	0.317	0.402	0.046	-0.203
p	0.753	0.318	1.000	1.000
Region 2: Montana				
Raw data ($n = 23$)				
r_s	0.664	0.567	0.124	0.290
p	0.003	0.024	1.000	0.898
First diff. ($n = 22$)				
r_s	0.344	0.528	0.188	-0.108
p	0.585	0.058	1.000	1.000
Region 3: Nebraska				
Raw data ($n = 23$)				
r_s	0.415	0.575	0.569	0.039
p	0.245	0.021	0.023	1.000
First diff. ($n = 22$)				
r_s	0.370	0.676	0.671	-0.311
p	0.450	0.003	0.003	0.794

Fig. 1). In addition, rarefaction curves generated by the subsampling routine demonstrate significant diversity differences among regions (Fig. 5, Supplementary Fig. 2). As such, the subsampling analysis indicates that the variable fossil productivity within and among regions over the study interval has not obscured significant changes in rodent diversity in each region (Supplementary Fig. 2).

In the montane regions, regional tectonic episodes were accompanied by significant diversity changes. In Region 1, the largest peak in originations (16 Ma) coincided with the peak in eruption of Columbia River flood basalts and the MCO (Fig. 2B) (we note that $p'(i)$ cannot be calculated for this interval, so this pulse is not reflected in $d(i)$). The late Miocene peak in $p'(i)$ coincided with increased exhumation and relief in the southern Cascades. Significant $q'(i)$ (at 24 Ma, 13 Ma, and 6 Ma: Fig. 2C) occurred in intervals with large declines in localities compared to the previous interval, and two significant intervals of $d(i)$ (13 Ma and 6 Ma) reflect these extinctions (Fig. 2D). Although these extinction peaks may

represent low fossil productivity, significant turnover $t(i)$ (at 24 Ma: Fig. 2D) suggests that this change was not a sampling artifact. Global cooling after 24 Ma could explain extinction and faunal change during this interval. Among the three intervals of significant change in faunal composition (Fig. 6), the earliest at 23 Ma followed global cooling, the largest at 16 Ma occurred during the MCO, and the latest at 7 Ma followed southern Cascade uplift and the appearance of xeric elements in Columbia Basin floras.

Region 1 supports the predictions of rodent diversification following tectonic activity and global climate change (Table 2). Late Oligocene warming coincided with the highest Neogene diversity at 24 Ma, followed by cooling and significant extinctions. A middle Miocene peak of flood basalts and global warming coincided with a peak of originations at 16 Ma, accompanied by significant change in species composition. A major peak of extinctions at 13 Ma followed cooling at 14 Ma. Late Miocene intervals of origination at 8 Ma and extinction at 6 Ma bracketed signifi-

cant faunal change at 7 Ma, when strong orographic gradients were established. Changes in diversity and faunal composition occurred at times of tectonic or climatic change, but sampling effects may have contributed to these changes as well.

Region 2 showed a strong association between changes in landscape history and rodent diversity, although sampling was uneven (Fig. 3). Two intervals of significant origination rates $p'(i)$ during the MCO at 16 Ma and 15 Ma followed uplift and a regional unconformity at 17 Ma. The $p'(i)$ at 16 Ma contributed to the only interval with a significant, positive diversification rate. High $p'(i)$ at 15 Ma coincided with a high extinction rate, resulting in significant $t(i)$ but not $d(i)$ (Fig. 3C,D). Diversity declined from 14 to 12 Ma, as global cooling resumed, with peak extinction rates and the largest negative diversification occurring during this interval. Sampling may have exerted a strong influence on diversity metrics, as increases and decreases in diversity closely followed increases and declines in the number of fossil localities (Fig. 3A). However, significant turnover and change in faunal composition, involving increase in sciurid and heteromyid species, occurred within the middle Miocene interval (Fig. 7), and the highest diversity occurred during an interval with only a few fossil localities, suggesting that factors beyond sampling were involved.

Region 2 also supports the predictions for the effects of landscape change on diversification. The increase in diversity, positive $d(i)$, and change in faunal composition at 16 Ma coincided with warming following uplift and erosion. The major decline in diversity and negative $d(i)$ at 13 Ma followed cooling, although faunal composition did not change significantly then.

In Region 3, the more volatile changes in diversity were of lower magnitude than the fewer, larger changes in the montane regions. Origination and extinction rates were all <2.0 (Fig. 4C); likewise, significant $d(i)$ and $t(i)$ values in Region 3 were lower than in Regions 1 and 2. During the MCO, peaks in the number of originations at 16 Ma and 14 Ma coincided with sufficient extinctions to pro-

duce significant turnover without significant diversification (Fig. 4D). The largest number of originations, at 14 Ma, coincided with rapid cooling following the MCO and substantial change in faunal composition, dominated by an influx of heteromyids (Fig. 8). Although $q'(i)$ at 13 Ma was significant, enough originations occurred to render $d(i)$ non-significant. Two significant intervals of diversification at 18 Ma and 10 Ma could be due to sampling effects, as they coincided with large declines in fossil localities and no changes in faunal composition (Fig. 8). In contrast, the significant diversification at 3 Ma coincided with significant change in composition.

These patterns in Region 3 are consistent with predictions of global warming and cooling in a landscape of low topographic complexity (Table 2)—high turnover with low diversification. Although diversity tracked changes in the frequency of fossil localities, the numerous significant changes in family-level composition from the early to middle Miocene suggest that a series of environmental changes affecting substrates, vegetation, and seasonality were also influencing faunal composition and diversity.

Common Patterns across Regions

Although each region featured a unique history of landscape changes and rodent diversity, all three regions exhibited some patterns and inferred processes in common.

Influence of Uplift and Erosion.—The highest frequency of originations occurred during intervals of intensified tectonic activity in the montane regions—during the peak of flood-basalt eruptions in the Oregon region and immediately after deformation and uplift in the Montana region. In the Nebraska region, the largest decline in diversification, peak of extinction rate, and highest turnover rate at 18 Ma occurred at the hiatus between the Arikaree and Ogallala formations. There, a temporal gap was accompanied by substantial change in sediment sources and depositional mode (Swinehart et al. 1985). In all three regions, rodent diversity tracked major changes in the stratigraphic record. Although we have not evaluated other mammal groups from these regions, we would expect rodents

to be more sensitive than ungulates or carnivores to changes in substrate composition and areal extent, since most rodent habitats are closely linked to landscape features such as topsoil depth and prevalence of rocky areas.

Influence of Climatic Change.—All three regions showed the expected responses in diversification during the MCO. Regions 1 and 2 had a spike in originations early in the warm interval and a spike of extinctions during subsequent cooling. In Region 3, the highest number of originations occurred during cooling after the MCO. Significant changes in faunal composition occurred during the MCO, when a uniquely early Miocene rodent fauna was replaced by a more modern assemblage of rodents in terms of both faunal proportions at the family-level (Figs. 6–8) and species-level similarity (Table 8). Compositional changes also occurred during the warming phase of the MCO in Regions 1 and 2, and during the warming and cooling phases in Region 3. Thus, the faunal response to the MCO differed in the montane regions than in the plains. Although we cannot unambiguously discriminate between speciation and immigration in the origination data, the high degree of endemism (even within the two active regions) would imply that dispersals formed a minor component in the origination rates. Dispersal among regions occurred with greater frequency during the MCO than at any other time. Species originating on the plains dispersed into the montane regions earlier (16 to 15 Ma) than species originating in the montane regions dispersed into another montane region or onto the plains (15 to 14 Ma). Range expansions at 16 Ma from the plains into the montane regions were an expected consequence of global warming. From 15 to 14 Ma, species dispersed among all three regions, with an equal number of exchanges between the two montane regions as onto the plains—suggesting that this interval was a time of unusual mobility. Thermal lapse rates are expected to be lower under regimes of higher global temperature (Poulsen and Jeffery 2011), with shallower elevational gradients that may have facilitated range expansion. However, missing from these dispersal records is the

expected response to global cooling, in which a cluster of species from the montane regions should have appeared in the Nebraska record ca. 14 Ma during the peak of originations.

Conclusion

Rodent diversification through the Neogene differed substantially between the tectonically active regions of the intermontane west and the tectonically passive Great Plains. Although all three regions showed macrostratigraphic tracking between the stratigraphic sequence and diversity, this relationship is not expected to affect diversity patterns differentially between the active and passive regions. Changes in landscape, when sustained over the time scales of speciation and extinction, should influence speciation, extinction, and immigration rates, thereby influencing regional diversity gradients. Our original hypothesis, that topographic complexity promotes diversification in mammals, is supported with an important qualification: the interactive effects of concurrent climatic and topographic changes stimulate diversification.

Earlier studies of western North America highlighted the middle Miocene as an interval of increased diversity in mammalian faunas. Webb and Opdyke (1995) noted significant immigrations and major changes in ecological structure of North American mammal faunas in the early middle Miocene. Alroy et al. (2000) evaluated the link between global temperature change and rates of origination, extinction, turnover, and diversification for North American mammals through the Cenozoic. Their analysis, performed at the scale of the entire continent, failed to find coherent associations between diversity dynamics and climate change. In a comparison of the effects of biotic interactions (Red Queen) and physical perturbations (Court Jester) as drivers of macroevolutionary change, Barnosky (2001) documented increase in diversity and change in faunal composition of Oligocene to late Miocene mammalian faunas from the northern Rocky Mountains (our Region 2) during the MCO. In a subsequent study comparing the Pacific Northwest, the northern Rocky Mountains, and the northern Great Plains (approximately the three regions in this

study), Barnosky and Carrasco (2002) evaluated changes in mammalian diversity in relation to global temperature change. Although raw diversity increased during the MCO, there was little change during a late Oligocene warming event; species richness per locality varied little with global temperature except in the Rocky Mountain region. Evidence for high beta diversity during the MCO in the Rocky Mountains prompted their suggestion that tectonic activity could stimulate diversification. Kohn and Fremd (2008) noted that increased extensional tectonism in the intermontane west coincided with increased diversity of ungulates and carnivores in both montane regions and the Great Plains. They proposed that the increased diversity of the Great Plains was a spillover effect from proximity to the Rocky Mountains. Figueirido et al. (2012) identified several evolutionary faunas for Cenozoic mammals of North America; their Miocene fauna showed peak diversity at the MCO. Janis et al. (2000) also noted extraordinary diversity of ungulate browsers in the early middle Miocene.

Building on previous analyses of faunal dynamics in the Neogene of North America, we have framed this study in terms of specific expectations of the effects of tectonic activity and climate change on faunal dynamics; metrics of diversity and faunal composition that permit evaluation of originations, extinctions, and turnover—the functional components of diversification; and a focus on rodents, the most diverse clade of mammals across these regions today. Three principal results emerge from our analysis. (1) Diversification has a topographic signature, which in turn is related to tectonism. Increases in topographic complexity, whether resulting from extension, volcanism, or exhumation, coincided with increases in origination in the intermontane west. In contrast, during periods of low regional tectonism, rodents did not diversify more rapidly in montane regions than in the plains. (2) Climate and tectonism interact to intensify macroevolutionary processes. Increases in rodent diversity were most pronounced when tectonic activity coincided with global warming. Global warming and cooling on the time scale of mammalian

speciation rates, as exemplified during the MCO, coincided with changes in diversity in both montane and plains faunas. Peak diversity on the plains lagged peak diversity in the montane regions, consistent with an interpretation of species flux on the plains during global cooling as diversity declined in montane regions. (3) The correspondence between intervals of low diversity and sedimentary hiatuses or low frequency of localities exemplifies a kind of continental macrostratigraphy. Although this pattern serves as a warning of potential large-scale sampling biases, its configuration in the three study regions suggests that the stratigraphic record may convey an environmental signal relevant to macroevolution.

Much remains to be learned about mammalian diversification in relation to landscape history. Additional targeted sampling of fossiliferous sequences in the intermontane west and the Great Plains would increase sample sizes and fossil localities for further investigation of sampling effects, dispersal versus speciation scenarios in faunal comparisons among regions, and more robust estimates of diversity. Integration of paleoenvironmental information from facies analysis, stable-isotope ecology, and faunal composition would indicate how species changed in microhabitat occupation over time and space. Ecomorphological analyses of mammalian lineages and faunas would permit evaluation of ecological responses to specific changes in landscape history. Finally, integration of phylogenetic and phylogeographic analyses with the spatial and temporal distribution of lineages in the fossil record would facilitate more detailed tests of the impacts of landscape history on macroevolution.

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