

# Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate

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Continental biodiversity gradients result not only from ecological processes, but also from evolutionary and geohistorical processes involving biotic turnover in landscape and climatic history over millions of years. Here, we investigate the evolutionary and historical contributions to the gradient of increasing species richness with topographic complexity. We analysed a dataset of 418 fossil rodent species from western North America spanning 25 to 5 Ma. We compared diversification histories between tectonically active (Intermontane West) and quiescent (Great Plains) regions. Although diversification histories differed between the two regions, species richness, origination rate and extinction rate per million years were not systematically different over the 20 Myr interval. In the tectonically active region, the greatest increase in originations coincided with a Middle Miocene episode of intensified tectonic activity and global warming. During subsequent global cooling, species richness declined in the montane region and increased on the Great Plains. These results suggest that interactions between tectonic activity and climate change stimulate diversification in mammals. The elevational diversity gradient characteristic of modern mammalian faunas was not a persistent feature over geologic time. Rather, the Miocene rodent record suggests that the elevational diversity gradient is a transient feature arising during particular episodes of Earth's history.

**Keywords:** diversity gradient; Rodentia; diversification; macroevolution

## 1. INTRODUCTION

Modern biodiversity displays striking geographic gradients in species richness at regional to continental scales. Best known is the latitudinal diversity gradient, documented for many clades in continental and marine settings (Hillebrand 2004). A second widespread gradient is the increase in species richness in topographically complex regions, typically mountain ranges, compared with their adjacent lowlands (Simpson 1964; Coblenz & Riitters 2004). Both gradients result from ecological, evolutionary and historical processes (Ricklefs & Schluter 1993; Badgley *in press*). Ecological processes include accommodation of species through spatial and temporal habitat heterogeneity, evolutionary processes include geographic variation in speciation and extinction rates, and historical processes include geological and climatic changes affecting topography, dispersal barriers and habitat continuity. These processes need not be mutually exclusive; they may interact and their interactions may vary over time and space. Here, we evaluate whether macroevolutionary processes differed for Miocene rodents from adjacent regions of different tectonic and topographic histories.

Modern mammalian faunas exhibit a positive correlation between topographic complexity and both local and regional diversity. For example, species density in

North America nearly doubles from the Great Plains to the montane West (Badgley & Fox 2000). Whereas the montane West has experienced episodic tectonism over the last 100 million years (Spencer *et al.* 2008), the Great Plains have remained tectonically stable with low topographic relief throughout the Cenozoic (Sloss 1988). For brevity, we refer to the topographically complex region from the Front Range of the Rocky Mountains to the Pacific coast as the tectonically 'active region' (AR) and the Great Plains to the Mississippi River as the tectonically 'passive region' (PR).

The Miocene Epoch, from 23.3 to 5.3 Ma, was a formative period in the tectonic evolution of western North America. Eruption of the Columbia flood basalts, initiation of the Yellowstone hotspot, extension and downdrop of the Great Basin, transverse faulting in the San Andreas system, rifting in the Snake River Plain and Rio Grande Rift, and uplift of the Colorado Plateau (Dickinson 2006; Spencer *et al.* 2008) occurred or began during the Miocene (electronic supplementary material, table S1). Changes in elevation and relief would have created new habitats, intensified environmental gradients and fragmented formerly continuous ranges, all of which could potentially influence regional origination, extinction and species accommodation. Climatically, the Miocene witnessed long-term cooling interrupted by warm intervals, especially the middle Miocene Climatic Optimum (MCO) (17–14 Ma; Zachos *et al.* 2001).

Rodentia presents a model clade for investigating the geohistorical factors behind modern diversity gradients.

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Rodents comprise over half of the extant species across this area, and the topographic richness gradient is particularly pronounced among rodents (Badgley & Fox 2000). For modern rodents, regional species richness differs strikingly: for species with geographic ranges entirely within one region, AR diversity is more than 300 per cent that of the PR (Badgley *in press*), suggesting differential origination and extinction rates between the two regions. Habitat heterogeneity, fragmentation of geographical ranges and strong selection gradients could plausibly facilitate allopatric speciation in the AR, whereas continuous habitats and fewer barriers to dispersal could inhibit PR speciation, similar to how coral reefs have facilitated speciation in marine environments over evolutionary time scales (Kiefferling *et al.* 2010). The PR could host larger species geographic ranges and facilitate high dispersal, lowering extinction risk. In contrast, topographically complex landscapes could increase extinction risk from smaller, more fragmented ranges (e.g. Guralnick 2006) or buffer risk by increasing the frequency of microhabitat refuges (e.g. Bush *et al.* 2004).

The mammalian fossil record for the Miocene of western North America is exceptional (Carrasco *et al.* 2005), and we employ this record to address four macroevolutionary hypotheses concerning the potential impacts of tectonism, topography and climate change on Miocene rodent diversity. (1) No relationship exists between tectonism (topographic complexity) and origination, extinction or diversification rates. (2) Topographic complexity causes biased origination or extinction rates, resulting in systematically higher AR diversity over long intervals of geologic time. (3) Tectonic activity stimulates diversification, such that during episodes of tectonic activity, a pulse of originations or reduction of extinctions occurs in the AR but not in the PR. (4) Tectonics and topography influence diversity through interactions with global climatic change, with episodes of substantial climatic change driving changes in species richness in both regions (see electronic supplementary materials for elaboration). In principle, each of these hypotheses is testable with a robust fossil record.

## 2. MATERIAL AND METHODS

We obtained rodent occurrence data for fossil localities in the contiguous United States west of the Mississippi River from the MioMap database (Carrasco *et al.* 2005). We compiled data at the species level, omitting indeterminate identifications (e.g. 'sp.'), resulting in 1838 species occurrences from 528 unique fossil localities, with each locality classified as occurring in the tectonically 'active' or 'passive' region. We compiled data in 1-million-year (Myr) time bins and calculated the proportional, per-lineage rates of origination, extinction and net diversification for each time bin, following Foote (2000), and assessed significance of rates through bootstrapping. We evaluated change in the faunal composition of rodent species by family, testing significance through time and across regions with maximum likelihoods (see electronic supplementary material).

## 3. RESULTS

The pattern of Miocene rodent diversity differed between the AR and PR (figure 1), and did not arise from sampling effort (see electronic supplementary material

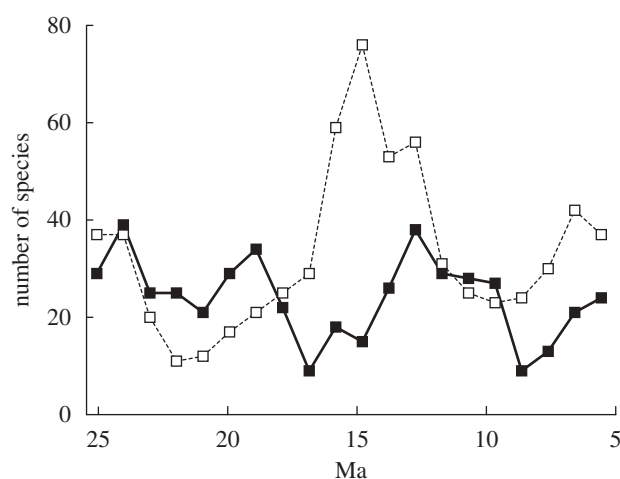


Figure 1. Species richness through time for 1 Myr time bins: active region (white squares, dashed line) and passive region (black squares, solid line). Richness was computed as the standing species richness based on fossil localities in each bin, assuming the range-through of species between first and last occurrences.

for discussion). Two intervals exhibited substantially greater AR diversity, mirroring the modern gradient: a mid-Miocene peak from 17 to 12 Ma and a late-Miocene increase from 9 to 5 Ma. The greatest difference between regions in species richness (61 species) occurred at 16 Ma. However, from 23 to 19 Ma, species richness was greater in the PR and was effectively the same from 25 to 23 Ma and 12 to 9 Ma (figure 1). Median richness per million-year interval was greater in the AR (29.5 versus 25.0 species), although this difference is not significant (Mann–Whitney test, two-tailed  $p = 0.114$ ), and the proportion of bins with greater AR richness (12 of 20) is not significant (sign test, two-tailed  $p = 0.503$ ). Variance in million-year interval richness is significant, even after Bonferroni correction ( $F$ -test, two-tailed  $p = 0.004$ ). Therefore, AR species richness was not systematically greater than PR richness over the Miocene, although AR richness was significantly more volatile.

Median origination and extinction rates were similar between regions. Median AR and PR origination rates ( $p'$ ) were 0.236 and 0.386, and median extinction rates ( $q'$ ) were 0.234 and 0.223, respectively. Bootstrap confidence intervals (CIs) overlap between regions in all but six bins for  $p'$  (electronic supplementary material, figure S2A), and in all but four bins for  $q'$  (electronic supplementary material, figure S2B). Importantly, for both  $p'$  and  $q'$ , instances occur in which either region was significantly greater than the other. For much of the Miocene,  $d(i)$  values are indistinguishable from zero, indicating that diversification was confined to specific episodes. In several cases, both regions exhibited significant net diversification in parallel, most notably increases from 16 to 15 Ma and 7 to 6 Ma, and decreases from 24 to 23 Ma (figure 2a). Significant differences in diversification occurred from 18 to 17 Ma, 14 to 13 Ma and 10 to 9 Ma (figure 2a). From 18 to 17 Ma, PR richness decreased (extinction event: electronic supplementary material, figure S2B) and AR richness increased (origination event: electronic supplementary material, figure S2A). From 14 to 13 Ma, richness increased in the PR (origination event: electronic supplementary

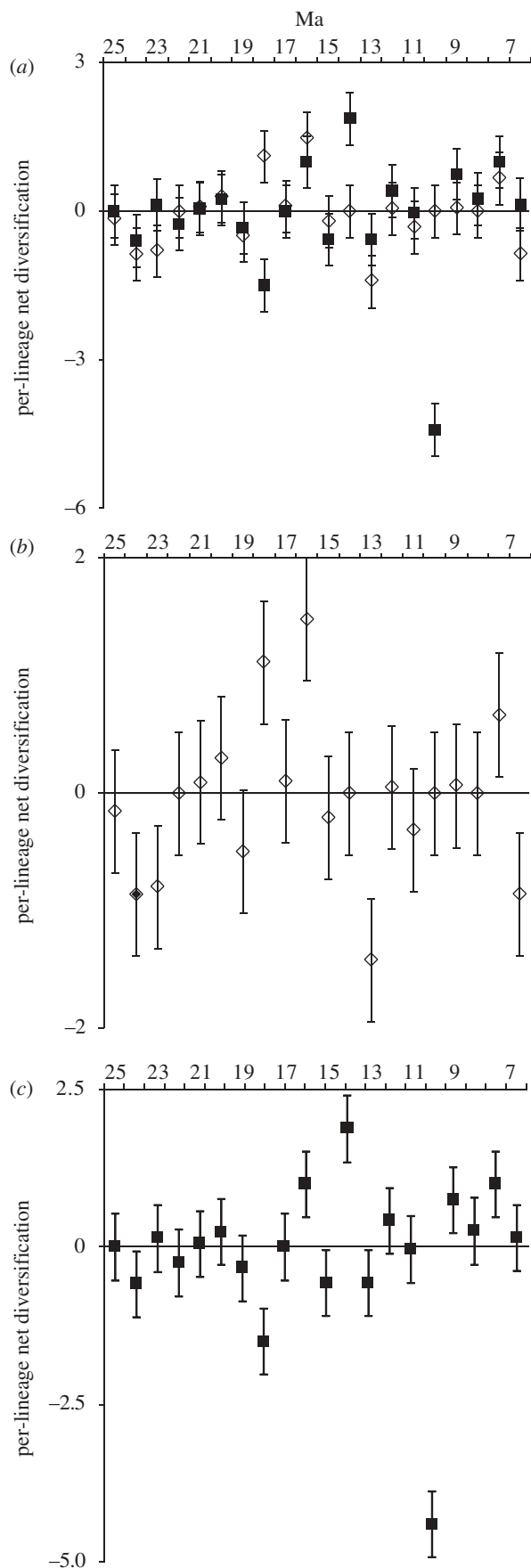


Figure 2. Diversification rates. (a) Per-lineage net diversification per million-year interval, comparing both regions. Bootstrapped confidence intervals are 0.525, and overlap in all but three time intervals. (b) Per-lineage net diversification for the active region. (c) Per-lineage net diversification for the passive region. AR, white diamonds; PR, black squares.

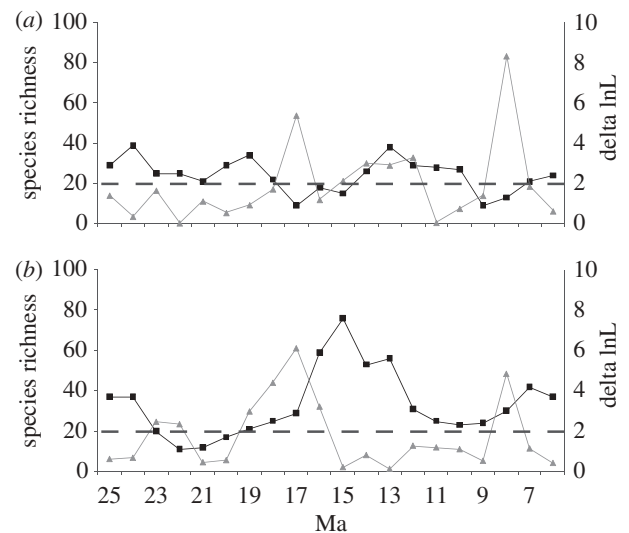


Figure 3. Standing diversity, following figure 1, compared with change in faunal composition: (a) active region, (b) passive region. Log-likelihood difference = 2 given by horizontal dashed line, indicating significantly different composition in that time bin from the preceding bin. Black squares, species richness; grey triangles, delta lnL.

material, figure S2B) but did not change in the AR. From 10 to 9 Ma, PR richness plummeted (extinction event: electronic supplementary material, figure S2B), with no corresponding change in the AR.

Associated with changes in species richness were significant changes in regional taxonomic composition (figure 3; electronic supplementary material, table S3A). Three periods of significant faunal change occurred in the AR, and two in the PR. For the AR, the first occurred from 24 to 22 Ma, coincident with declining species richness and elevated extinction (figure 3; electronic supplementary material, figure S3), with disproportionate declines in Geomyidae and Sciuridae. From 19 to 15 Ma (figure 3a; electronic supplementary material, figure S3), rapid diversification occurred among Heteromyidae, Sciuridae and Muridae. For the PR, the interval from 18 to 12 Ma began with a decline in species richness (figure 3b) and a substantial decrease in the proportions of geomyids and rare archaic groups. Species richness recovered from 17 to 12 Ma, with increasing proportions of heteromyids, sciurids and murids. For both regions, the interval from 8 to 7 Ma was characterized by rapid diversification among murids (electronic supplementary material, figure S3).

#### 4. DISCUSSION

It is unlikely that the fossil record documents the entirety of rodent diversity from the tectonically active region. Many extant species have narrowly defined elevational ranges (e.g. Lenoir *et al.* 2008; Rowe *et al.* in press), and those occupying the highest elevations, far removed from long-term depositional environments, should be under-represented in the fossil record. Even so, the Miocene rodent record displays remarkable variation in species richness and taxonomic composition, permitting evaluation of hypotheses of diversification.

We can falsify two of our four hypotheses. The Miocene rodent record contradicts the hypothesis that

diversification in the active and passive regions is unaffected by regional differences in geologic history. Contra hypothesis 1, the most extreme differences in richness occurred between 17 and 12 Ma, coincident with the interval of greatest tectonic and climatic change. Contra hypothesis 2, greater AR richness was not a persistent feature of the Miocene rodent record. We found no systematic differences in diversity (figure 1), origination and extinction rates (electronic supplementary material, figure S2) or diversification rates (figure 2). These results imply that topographic complexity itself does not generate greater diversity, either through construction of a finer-grained landscape with more varied ecological niches or through fragmentation of species ranges and vicariance.

The Miocene rodent record best supports hypothesis 4. During the MCO (17 to 14 Ma), atmospheric CO<sub>2</sub> reached its highest levels during the last 35 Myr, falling rapidly at approximately 14 Ma and stabilizing by 10 Ma (Tripathi *et al.* 2009). The AR rodent record documents a substantial increase in richness between 17 and 15 Ma, and subsequent decline between 15 and 12 Ma (figure 1), consistent with predictions for warming then cooling. Increased origination rates in both regions at 16 Ma in the middle of the warming interval (electronic supplementary material, figure S2A) are also expected, as is the greater magnitude of originations in the AR. Also expected under global cooling is increased PR richness between 15 and 13 Ma, resulting from both origination within the PR (figure 2) and immigration as species originating in the AR shifted ranges into the PR (electronic supplementary material, table S4).

However, hypothesis 3 cannot be discarded altogether. Tectonism was ongoing in western North America throughout the Miocene, but the interval from approximately 17.5 to 14 Ma involved pronounced uplift, volcanism and extension (Dickinson 2006; Barnosky *et al.* 2007; Spencer *et al.* 2008). During this interval, the AR recorded two substantial spikes in origination rate (electronic supplementary material, figure S2A). Under this hypothesis, PR species richness should remain more or less static, yet from 16 to 13 Ma there were two intervals of significant diversification (figure 2), although the increase in richness was modest in comparison with that of the AR. If tectonic activity drove increased species richness, then any PR change during this interval must have been decoupled from AR processes. At least one such episode did occur. One of the most significant changes in diversity is the drop in PR richness from 10 to 9 Ma (figures 1 and 2), coinciding with increased seasonality across the Great Plains, as signalled by increasing proportions of C<sub>4</sub> grasses in the dominant grassland biome (Fox & Koch 2003). That this decline was not observed in the AR probably reflects the prevalence of forest and woodland vegetation, especially at higher elevations, during the Miocene (Wing 1998).

Three earlier studies of mammalian evolution are particularly relevant to this study. Barnosky & Carrasco (2002) questioned a direct link between diversification and global temperature change. Their study of mammalian species richness from the latest Oligocene through Miocene spanned the northern half of our active and passive regions. Barnosky & Carrasco (2002) found a large richness increase coincident with the MCO, but no

corresponding increase in response to a larger warming event in the latest Oligocene. A notable difference between these warming events was the lower degree of tectonic activity in western North America during the latest Oligocene (Dickinson 2006). Barnosky & Carrasco (2002) also contrasted patterns of changing alpha and gamma diversity. During the late Oligocene warm interval, the northern Rocky Mountains showed increased alpha but not gamma diversity, with low alpha and gamma diversity in the northern Great Plains. During the MCO, the northern Rocky Mountains showed high alpha and gamma diversity, with low alpha but high gamma diversity in the northern Great Plains. This pattern is consistent with our results showing differential response in mammalian richness to global climate change synchronous with topographic change between active and passive regions. Davis (2005) found greater beta diversity among Great Basin mammals relative to the Great Plains, extending from modern faunas into the Pliocene and possibly the late (but not middle) Miocene. This accords with the formation of modern Great Basin physiography; this area was a high plateau through the mid-Cenozoic, sinking by 1–3 km during the Miocene (Spencer *et al.* 2008). Davis (2005) proposed that greater habitat heterogeneity resulting from tectonically driven topographic heterogeneity (Coblentz & Riitters 2004) caused increased beta diversity. Our analysis, however, does not support a general causal relationship between topography and regional diversity. Kohn & Fremd (2008) analysed genus-level richness of Miocene ungulates and carnivores of the western United States, noting a sharp increase in richness at approximately 17 Ma for both the montane West and the Great Plains. They attributed this increase to tectonic extension in the AR, with increased topographic complexity leading to greater species accommodation. Ungulate richness declined by approximately 11 Ma for both regions, which they attributed to global cooling, drying and homogenization of habitats. In their model, PR richness passively reflected changes in AR richness. However, rodent faunal composition differed significantly between regions throughout the Miocene (electronic supplementary material, table S5B) and diversification patterns were significantly different (figure 2). Thus, the rodent record does not support the interpretation that PR richness simply records a filtered version of AR processes.

## 5. CONCLUSION

The modern gradient of higher species richness in topographically complex regions when compared with their adjacent lowlands, prevalent across diverse regions of the world (Badgley *in press*), does not persist over geological time scales. For rodents (this study), ungulates and carnivores (Barnosky & Carrasco 2002; Kohn & Fremd 2008), passive-region species richness exceeded that of the active region over substantial portions of the Miocene. The modern pattern arose twice—once during the middle Miocene and again during the late Miocene. It remains to be seen in the Pliocene record whether the higher active-region richness of the latest Miocene persisted to the present day, or if additional Plio-Pleistocene oscillations occurred before establishment of the modern gradient.

These data falsify the hypothesis that more complex topography promotes higher diversity. The active and passive regions differed substantially in their tectonic history, resulting in vastly different topographies; yet we found no systematic differences in richness or in rates of origination, extinction or diversification. The lack of differences over evolutionary time scales implies that neither the steeper environmental gradients nor habitat fragmentation in topographically complex regions promotes diversification. This finding argues for caution in extending ecological inferences drawn solely from modern biogeographic patterns across large temporal scales. Indeed, the higher gamma diversity (this study) and beta diversity (Davis 2005) in the Great Plains over much of the Miocene suggest that ecosystems in the PR were quite different than are observed today (Janis *et al.* 2000).

The period of greatest disparity between the active and passive regions occurred during the Middle Miocene, coincident with both increased tectonic activity over much of the AR and an interval of global warming. This overlap makes it difficult to parse their respective influences on rodent diversification. Our analysis suggests that an interaction between climatic warming and increasing topographic complexity promoted increased speciation in the active region. Yet it is also possible that increasing topographic complexity resulting from active tectonism alone increased richness, wherein landscape fragmentation enhanced dispersal into novel microhabitats or vicariance among once-continuous populations. When the rate of change in topographic complexity diminished, local extinction of smaller populations decreased regional diversity. Distinguishing between these mechanisms will require evaluation of time intervals and regions in which climate change occurred independently of tectonism, and in which active and passive regions can be contrasted across episodes of tectonic activity in the absence of global climatic changes. One such Neogene record exists in the Miocene Siwalik sequence of northern Pakistan from the Himalayan foreland basin (Barry *et al.* 2002). There, rodent species richness peaked at approximately 14 Ma and declined through the late Miocene (Flynn *et al.* 1998). The similarity with the North American pattern suggests another example of the interaction between climatic change and tectonism. Although the Siwalik record documents a fluvial system in a lowland tectonic setting without an adjacent montane counterpart, it could potentially be compared with the fossil record from the Tibetan Plateau and montane basins of southern China.

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## REFERENCES

- Badgley, C. In press. Tectonics, topography, and mammalian diversity. *Ecography*.
- Badgley, C. & Fox, D. L. 2000 Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *J. Biogeogr.* **27**, 1437–1467. (doi:10.1046/j.1365-2699.2000.00498.x)
- Barnosky, A. D. & Carrasco, M. A. 2002 Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.* **4**, 811–841.
- Barnosky, A. D., Bibi, F., Hopkins, S. S. B. & Nichols, R. 2007 Biostratigraphy and magnetostratigraphy of the mid-Miocene Railroad Canyon Sequence, Montana and Idaho, and age of the mid-Tertiary unconformity west of the continental divide. *J. Vert. Paleo.* **27**, 204–224. (doi:10.1671/0272-4634(2007)27[204:BAMOTM]2.0.CO;2)
- Barry, J. C. *et al.* 2002 Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* **28**, 1–71. (doi:10.1666/0094-8373(2002)28[1:FAECIT]2.0.CO;2)
- Bush, M. B., Silman, M. R. & Urrego, D. H. 2004 48 000 years of climate and forest change in a biodiversity hot spot. *Science* **303**, 827–829. (doi:10.1126/science.1090795)
- Carrasco, M. A., Kraatz, B. P., Davis, E. B. & Barnosky, A. D. 2005. *Miocene Mammal Mapping Project (MIOMAP)*. University of California Museum of Paleontology. See <http://www.ucmp.berkeley.edu/miomap/>.
- Coblentz, D. D. & Rüttgers, K. H. 2004 Topographic controls on the regional-scale biodiversity of the south-western USA. *J. Biogeogr.* **31**, 1125–1138. (doi:10.1111/j.1365-2699.2004.00981.x)
- Davis, E. B. 2005 Mammalian beta diversity in the Great Basin, western USA: palaeontological data suggest deep origin of modern macroecological structure. *Glob. Ecol. Biogeogr.* **14**, 479–490. (doi:10.1111/j.1466-822x.2005.00183.x)
- Dickinson, W. R. 2006 Geotectonic evolution of the Great Basin. *Geosphere* **2**, 353–368. (doi:10.1130/GES00054.1)
- Flynn, L. J., Downs, W., Morgan, M. E., Barry, J. C. & Pilbeam, D. 1998 High Miocene species richness in the Siwaliks of Pakistan. In *Advances in vertebrate paleontology and geochronology* (eds Y. Tomida, L. J. Flynn & L. L. Jacobs), pp. 167–180. National Science Museum Monographs No. 14. Tokyo, Japan: National Science Museum.
- Foote, M. 2000 Origination and extinction components of taxonomic diversity: general problems. In *Deep time: paleobiology's perspective*, *paleobiology* 26 (Supplement to no. 4) (eds D. H. Erwin & S. L. Wing), pp. 74–102.
- Fox, D. L. & Koch, P. L. 2003 Tertiary history of C<sub>4</sub> biomass in the Great Plains, USA. *Geology* **31**, 809–812. (doi:10.1130/G19580.1)
- Guralnick, R. 2006 The legacy of past climate and landscape change on species' current experienced climate and elevation ranges across latitude: a multispecies study utilizing mammals in western North America. *Glob. Ecol. Biogeogr.* **15**, 505–518.
- Hillebrand, H. 2004 On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192–211. (doi:10.1086/381004)
- Janis, C. M., Damuth, J. & Theodor, J. M. 2000 Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc. Natl Acad. Sci. USA* **97**, 7899–7904. (doi:10.1073/pnas.97.14.7899)
- Kiessling, W., Simpson, C. & Foote, M. 2010 Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science* **327**, 196–198. (doi:10.1126/science.1182241)
- Kohn, M. J. & Fremd, T. J. 2008 Miocene tectonics and climate forcing of biodiversity, Western United States. *Geology* **36**, 783–786. (doi:10.1130/G24928A.1)
- Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. 2008 A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768–1771. (doi:10.1126/science.1156831)

- Ricklefs, R. E. & Schluter, D. 1993 Species diversity: regional and historical influences. In *Species Diversity in Ecological Communities* (eds R. E. Ricklefs & D. Schluter), pp. 350–363. Chicago, IL: University of Chicago Press.
- Rowe, R. J., Finarelli, J. A. & Rickart, E. A. In press. Range dynamics of small mammals along an elevational gradient over an 80 year interval. *Glob. Change Biol.* (doi:10.1111/j.1365-2486.2009.02150.x)
- Simpson, G. G. 1964 Species density of North America mammals. *Syst. Zool.* **13**, 57–73. (doi:10.2307/2411825)
- Sloss, L. L. 1988 Tectonic evolution of the craton in Phanerozoic time. In *Sedimentary cover: North American craton*, Geology of North America, vol. D-2 (ed. L. L. Sloss), pp. 25–51. Boulder, CO: Geological Society of America.
- Spencer, J. E., Smith, G. R. & Dowling, T. E. 2008 Middle to late Cenozoic geology, hydrography, and fish evolution in the American Southwest. In *Late Cenozoic drainage history of the southwestern Great Basin and Lower Colorado River Region: geologic and biotic perspectives* (eds M. C. Reheis, R. Hershler & D. M. Miller), pp. 279–299. Special Paper 439. Boulder, CO: Geological Society of America.
- Tripati, A. K., Roberts, C. D. & Eagle, R. A. 2009 Coupling of CO<sub>2</sub> and ice sheet stability over major climate transitions of the last 20 million years. *Science* **326**, 1394–1397. (doi:10.1126/science.1178296)
- Wing, S. L. 1998 Tertiary vegetation of North America as a context for mammalian evolution. In *Evolution of tertiary mammals of North America*, vol. 1 (eds C. M. Janis & K. M. Scott), pp. 37–65. New York, NY: Cambridge University Press.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693. (doi:10.1126/science.1059412)