

Miocene tectonics and climate forcing of biodiversity, western United States

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ABSTRACT

Ungulate and carnivore diversity patterns since 30 Ma in different regions of the western United States suggest abrupt increased diversification at 17–17.5 Ma, followed by decreases ca. 11 Ma, and stasis thereafter. Although global climate change presumably affects evolution, we hypothesize that widespread extensional tectonism in the western U.S. also helped drive diversity increases ca. 17.5 Ma through a topographically induced increase in floral and habitat diversity. The decreases in diversities ca. 11 Ma, as well as the rapid increase in C4 ecosystems (RICE) worldwide at 7–8 Ma may have responded to climate teleconnections and increased seasonality linked to global cooling and growth of orogenic plateaus, particularly the Tibetan Plateau between 13 and 8 Ma. Thus, biodiversity complexly responds both to climate and to tectonics.

Keywords: paleontology, tectonics, climate change, mammal diversity.

INTRODUCTION

The fossil record in the United States shows major changes in mammalian diversity and grassland evolution since 20 Ma (Webb, 1977, 1983; Janis et al., 2000), yet causes for these changes remain enigmatic. Modern species and habitat diversities correlate with climate (rainfall, which affects productivity; Ritchie and Olff, 1999; mean annual temperature; temperature variability; Simpson, 1964; Badgley and Fox, 2000) and geography (topographic variability or relief and elevation; Simpson, 1964; Badgley and Fox, 2000; Coblenz and Riitters, 2004). For example, modern mammal diversities correlate positively with increased temperature, precipitation, elevation, and topographic variability (Badgley and Fox, 2000), although very high productivity (rainfall) correlates with lower large mammal diversity (Ritchie and Olff, 1999). But do past changes in topography and climate alone explain past changes in faunal diversity? Here we evaluate ungulate and carnivore diversity patterns in the western United States since 30 Ma (Fig. 1) to investigate how biodiversity correlates with tectonic and climatic events, and suggest that tectonics may contribute significantly to diversification in two ways: through the development of topographic (and consequently floral) diversity, and through plateau-induced changes to seasonal climate patterns. Because of links between faunal and floral diversities, we further speculate on tectonic influences on the late Miocene rise of C4 grasslands.

METHODS

In brief, we: (1) used MioMap (Carrasco et al., 2005) as a primary database, augmented with unpublished data from new Oregon collections, and measured (α -) diversity of carnivores

and ungulates at the genus level; (2) grouped geographically proximal sites of similar age over areas smaller than likely habitat patches (a few square kilometers to a few tens of square kilometers; see the GSA Data Repository¹ for justification); (3) used direct age controls for each site; (4) rarefied data (which normalizes diversity to a common sample size, minimizing bias) using number of individual specimens (NISP); and (5) calculated percent area undergoing extension from tectonic syntheses (Atwater, 2006). Note that most large-mammal fossil sites in the Basin and Range were not sufficiently productive, well characterized, and/or well-constrained temporally to support diversity analysis. Age resolution for regional tectonic syntheses is not better than ± 1 m.y. (e.g., Wernicke and Snow, 1998), whereas that of faunal collections varies considerably. Our methods differ from Barnosky et al. (2005) and Davis (2005) in excluding small mammals, and from Janis et al. (2000) in rarefying data. (See the Data Repository for further method details.)

RESULTS

Raw ungulate and carnivore diversities in all areas show much more abrupt increases at 17–17.5 Ma than previously reported, and decreases to lower diversity by 11 Ma (Figs. 2A and 2B). Columbia Plateau and Snake River Plain data suggest diversity stasis thereafter. For ungulates, two-sided t-tests (see Table DR2 [see

¹GSA Data Repository item 2008203, supplemental methods, site and sample characteristics, t-test results, locality information, ungulate and carnivore families and genera, chronologic adjustments, sample diversity vs. area, and Tables DR1–DR3, and Figure DR1, is available online at www.geosociety.org/pubs/ft2008.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

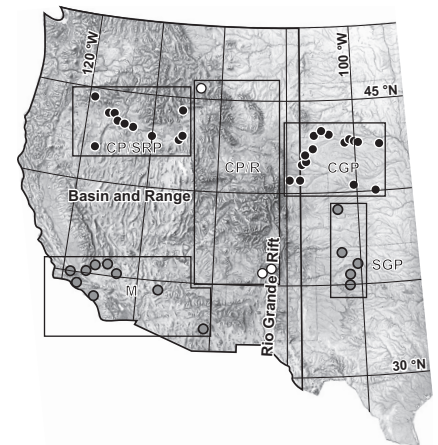


Figure 1. Map of western half of contiguous United States, showing fossil localities used in this study. Thick black border shows modern geographic extent considered in calculating percent of area undergoing extension (see Fig. 2D). Boxes delineate geographic regions of interest. CP/SRP—Columbia Plateau–Snake River Plain; M—Mojave; CP/R—Colorado Plateau–Rockies; CGP—central Great Plains; SGP—southern Great Plains. Basin and Range, and Rio Grande Rift provinces identified for reference.

footnote 1]) show that diversities at 11–17.5 Ma differ significantly from times before and after ($p \leq 0.02$), except for the two data points for pre–17.5 Ma in the Mojave ($p \sim 0.08$). Rarefaction analysis (Fig. 2C) supports these basic conclusions ($p = 0.02$ for pre–17.5 Ma versus 11–17.5 Ma; $p < 1 \times 10^{-5}$ for 11–17.5 Ma versus post–11 Ma). For carnivore raw counts, pre–17.5 Ma versus 11–17.5 Ma differ significantly (t-test $p < 0.01$). Post–11 Ma versus 11–17.5 Ma do not differ significantly ($p = 0.36$), but carnivore counts for post–11 Ma collections are considerably larger than for 11–17.5 Ma collections. Rarefaction was not attempted for pre–17.5 Ma carnivores, because only one site is well characterized for NISP and has an unusually high carnivore-ungulate ratio. Rarefied post–11 Ma versus 11–17.5 Ma data show a significant difference ($p = 0.004$). These geographically widespread trends, further supported by rarefaction analysis, suggest either minimal or uniform taphonomic bias and some widespread driving factors.

The percent area undergoing extension (Fig. 2D) is low until 20.0 Ma, increases abruptly by 17.5 Ma due to extension in the

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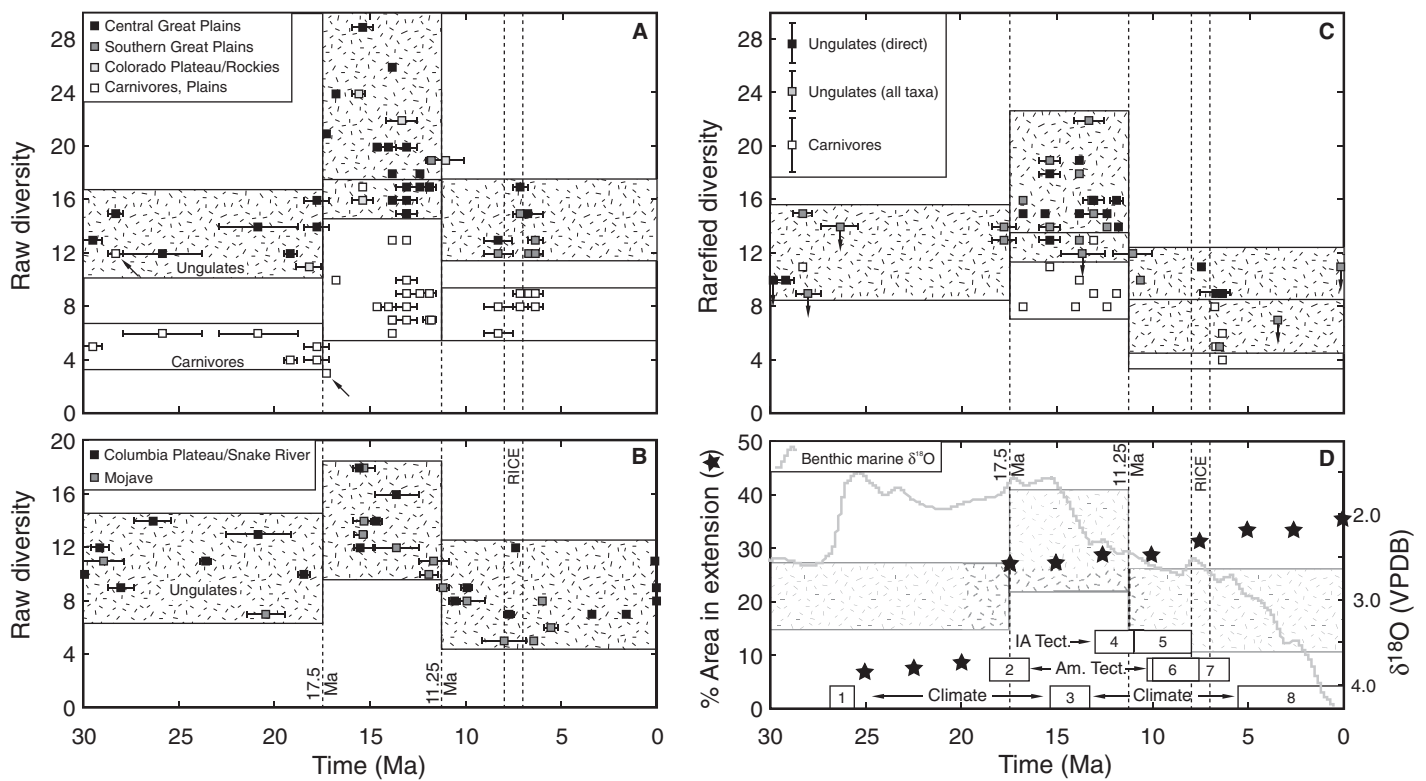


Figure 2. Sample diversity versus time for fossil localities, showing abrupt increase in ungulate and carnivore diversities by ca. 17.5 and ca. 17.0 Ma, respectively, and decline by ca. 11.25 Ma, followed by stasis to the present. Large boxes are meant to delineate broad time periods of increased or decreased diversity; trends may be present within a box. **A:** Central Great Plains (black squares—ungulates; white squares—carnivores), southern Great Plains (dark gray squares), and Rockies (light gray squares). **B:** Columbia Plateau plus Snake River Plain (black squares), and Mojave Desert (dark gray squares). RICE—rapid increase in C4 ecosystems at 7–8 Ma (Cerling et al., 1997). **C:** Rarefied data, showing consistency with raw patterns in A and B. Downward-pointing arrows are limits for collections with insufficient documentation to rarefy data directly, but with more than 400 specimens (so rarefied estimates must be less than unrarefied counts). Error bars in legend are typical 95% confidence limits. **D:** Reference plots of benthic foraminifera $\delta^{18}\text{O}$ (Zachos et al., 2001), percent area undergoing extension (stars), schematic changes in faunal diversity (stippled boxes), and major climatic or tectonic events. 1—late Oligocene warming; 2—initiation of Basin and Range block faulting; 3—mid-Miocene cooling; 4—uplift of northern, northeastern, and eastern sectors of Tibetan Plateau; 5—changes in deformation rates on southern, eastern, and northern margins of Indo-Asian orogen, change in Indian plate motion; 6—rapid uplift of Altiplano, strengthening of California current; 7—rapid uplift of Colorado Plateau, slowdown in rate of extension, central Basin and Range, and change in North America–Pacific relative plate motion; 8—global cooling and Northern Hemisphere glaciations. VPDB—Vienna Peedee belemnite. Dashed lines delineate our inferred major biotic boundaries. IA Tect. and Am. Tect. refer to Indo-Asian and American tectonic events.

Basin and Range, Mojave, Columbia Plateau, and Rio Grande Rift, and rises gradually to the present. The jump at 17.5 Ma corresponds with the apparent increase in raw and rarefied ungulate diversities at 17.5 Ma, and in raw carnivore diversity at 17.0 Ma.

DISCUSSION

High Middle Miocene Diversity: Local Tectonic Forcing?

Many interacting factors influence faunal assemblages, and some workers have argued for strong correlations between climate and faunal diversity changes in the Great Plains and western U.S. (e.g., Retallack, 2007), especially to explain high diversities during the mid-Miocene climatic optimum ca. 15–16 Ma. In contrast, (1) the largest shifts in global climate, ca. 26 and post-7 Ma (e.g., Zachos et al., 2001), are not obviously matched by significant diversity changes (Fig. 2); (2) the highest rarefied ungulate and carnivore diversities postdate the mid-Miocene climatic optimum (Fig. 2C); and (3) faunal diversity

clearly decreased between ca. 12 and ca. 7 Ma when global climate records show little overall change (Fig. 2D). Others noted a poor correspondence between faunal patterns and global climate trends (Alroy et al., 2000). Tectonic activity may help explain these disparities. Topographic relief directly correlates with modern species diversity (Simpson, 1964; Badgley and Fox, 2000), because relief creates diverse local habitats capable of supporting diverse faunas. The advent of major regional tectonic events ca. 17.5 Ma, including high-angle extensional faulting, must have abruptly increased topographic and ecosystem diversity, which helped drive faunal diversity increases. We view high-angle block faulting, characteristic of mid-Miocene extension, rather than earlier low-angle faulting as the most effective tectonic cause of topographic diversity.

Even in these extending regions, some data could indicate climate contributions to faunal diversity. For example, Retallack (2007) associated one of the biggest changes to inferred habitats in Oregon between 16 and 18 Ma with

increasing temperature and precipitation. Thus, tectonics, global warming, and increased precipitation could well have acted in concert to result in increased diversity. However, the Great Plains appear to have cooled and dried during the same interval (Retallack, 2007), and the largest change to flora there occurred when open habitat grasses became abundant between 26 Ma (during the late Oligocene warming event) and 20 Ma (Strömberg, 2005), several million years prior to the peaks in diversity. Insofar as the resulting mix of grasslands and forest elements persisted until 10 Ma (Strömberg, 2005), why would Great Plains faunas diversify ca. 17.5 Ma? Noting the Great Plains' proximity to the margins of the Colorado Plateau and Rockies, tectonics emerges as a plausible factor.

Increased elevations or incision upstream of the Great Plains ca. 17.5 Ma is evident from abrupt coarsening of fossil-bearing sediments (Diffendal, 1982), and tectonically driven increases in habitat diversity may have helped drive increased faunal diversity. Short-term

oscillations in climate, already evident on an obliquity (41 k.y.) cycle between 23.6 and 28.7 Ma in Oregon (Retallack et al., 2004), may have cycled faunas between diverse ecosystems in the Rockies and the topographically unremarkable Great Plains. That is, the Great Plains acted as a passive recorder of diversity elsewhere. Cool versus warm climate cycles yielded different habitats and faunas in the Great Plains, sourced by refugia in topographically diverse areas nearby. As most sampling sites include strata spanning tens or hundreds of thousands of years, multiple climate oscillations, habitats, and faunas are likely. This model implies, however, that layer-specific faunal assemblages should be correlated with warm versus cold or wet versus dry climates, and that diversity reflects an area's carrying capacity, not rates of origination, extinction, or immigration. In our model, these latter processes would change which faunas are present, but not their diversity.

Decreased Late Miocene Diversities: Remote Tectonic Forcing?

Topographic variability steadily increased after 17.5 Ma (Fig. 2D), so other factors must have caused decreased faunal diversity after 13–15 Ma. We ascribe this decrease to changes in local climate, productivity, and precipitation seasonality, in turn driven by global climate change and distal tectonics. Between ca. 15 and ca. 8 Ma, flora became more xeric in the western interior and Great Plains (Wing, 1998), implying decreased rainfall and productivity, and more open, less diverse habitats, supporting less diverse faunas (Badgley and Fox, 2000).

Tectonic activity in multiple orogens worldwide plausibly stabilized drier ecosystems and greater precipitation seasonality by 8–13 Ma. The area, rate of uplift, or both for the Tibetan (Molnar, 2005), Altiplano (Garzzone et al., 2006), and Colorado (Sahagian et al., 2002) plateaus increased between 8 and 13 Ma. Whereas activity in orogens may span tens of millions of years, these changes indicate major departures from “background” activity and attainment of new tectonic states. Lateral growth of Tibet as early as 13 Ma and certainly by 11 Ma (Clark et al., 2005; Garzzone et al., 2005) was accompanied by changes to atmospheric circulation patterns, profound changes in foreland sedimentation, changes in major fault movement rates, formation of the Tien Shan Range, and, ultimately, a change in plate motion rates in the Indian Ocean (see summary of Molnar, 2005). The Altiplano underwent rapid uplift at 8–10 Ma (Garzzone et al., 2006), succeeded by a shift in Pacific–South America plate motions. Analysis of bubble size distributions in volcanic rocks of the Colorado Plateau suggests an increase in surface uplift rate, possibly commencing 6–10 Ma (Sahagian et al., 2002), and a reversal in stable isotope trends from the west-

ern interior ca. 10 Ma was ascribed to tectonics (Horton et al., 2004; Kent-Corson et al., 2006). At 8 Ma, the relative motion between the North American and Pacific plates changed (Atwater and Stock, 1998), and the rate of extension in the central Basin and Range slowed by a factor ≥ 2 (Wernicke and Snow, 1998).

Plateaus control climate, both proximally and distally, through their influence on atmospheric circulation patterns, which in turn affect ocean circulation. We propose that uplift of several major orogenic plateaus between 13 and 8 Ma ushered in new large-scale climatic regimes, particularly with respect to seasonal precipitation, that broadly persist today. As early as 13 Ma and certainly by 11 Ma, faunas became less diverse and remained so (Fig. 2), reflecting a permanent shift to mean climate and climate seasonality, drying the western interior and Great Plains. Annual wet-dry seasons favor grasslands, as dry-season fires discriminate against nongrass floras (Keeley and Rundel, 2003, 2005). Open habitat grasses have been present in North America since at least the Oligocene, but in the Great Plains significant forest indicators remained until at least 10 Ma (Strömberg, 2002, 2005), and paleosol types show minor changes between ca. 20 and 8 Ma (Retallack, 2001), indicating that the modern grassland ecosystem formed subsequently. Increased variation in $\delta^{18}\text{O}$ values of paleosol carbonates in the Great Plains by 9 Ma (Fox and Koch, 2004) may indicate an increase in climate seasonality.

These faunal, floral, and climate changes in North America may well be linked to outward growth of the Tibetan Plateau (e.g., Ruddiman and Kutzbach, 1989). Plateau growth likely increased precipitation seasonality (i.e., the disparity between summer and winter precipitation amounts) in Southeast Asia, and strengthened the western Pacific westerlies (Zhisheng et al., 2001). The western Pacific westerlies are linked to the Alaska Gyre and California Current, which strongly influence the wet-dry cycle in western North America; the California Current strengthened at 10–7.6 Ma (Barron et al., 2002). Recently, stronger monsoons correlate with increased drought in the Great Plains (McCabe et al., 2004), and general circulation models further suggest that global cooling intensifies the winter (dry-season) monsoon (Hori and Ueda, 2006). Thus, uplift of the Tibetan plateau, particularly within the context of mid-late Miocene global cooling, is logically linked to drying of the Great Plains as well as western North America overall. These changes helped stabilize grasslands in the Great Plains, allowing them to expand in the middle to late Miocene. Summer dry seasons may well have been present in the western U.S. since 14–15 Ma (Axelrod, 1992), but lateral growth of the Tibetan Plateau at 8–13 Ma likely intensified them, leading to a loss of habitat patchiness and local ecosystem diversity. Faunas responded to this new

climate and ecosystem regime. Lower productivity after 11 Ma yielded less diverse ecosystems and faunas, because of global climate trends and tectonics, both proximal (western U.S.) and distal (Tibetan Plateau).

Our model implies that regions of the world that were tectonically quiescent (e.g., Australia) or that had different tectonic patterns (Europe?) should show different patterns of faunal diversity. The sparse Australian faunal record and active tectonics of the Alpine-Himalayan chain, East African Rift, and Andes in the past ~30 m.y. may confound such investigations.

Late Miocene Rise of C4 Grasslands

We hypothesize that faunal diversity responds to floral diversity, which is strongly affected by tectonics, so our seasonality model for late Miocene mammal diversity has additional implications for the rise of C4 grasslands. C4 grasses evolved by 12 Ma (see Kohn and Cerling, 2002), and perhaps by 25 Ma (Kellogg, 1999; plausibly linked to a global decrease in CO_2 levels in the Oligocene), but they spread rapidly worldwide at 7–8 Ma (Cerling et al., 1997), possibly triggered by a worldwide intensification of seasonal fires (Keeley and Rundel, 2005). In the western U.S., increased seasonality resulted from the northward displacement of summer westerlies to ~38°N, beginning at 11 Ma and strengthening at 7–8 Ma (Kennett et al., 1985; Barron et al., 2002). Tectonics, augmented by global cooling, drove increased precipitation seasonality, intensification of seasonal fires, and rise of grasslands (e.g., Quade et al., 1989). C4 grasses are not abundant everywhere in the western U.S. because of differences in the season of dominant precipitation. The dry season corresponds with summer for the Columbia Plateau and west coast, but with winter for the Great Plains and southwestern U.S., reflecting monsoonal flow associated with the Colorado Plateau and teleconnections to the North Pacific, North Atlantic, Indian monsoon, and Tibetan Plateau. Thus, our hypothesized increase in seasonality favored C4 grasses in the southwestern U.S. and Great Plains, but C3 grasses along the west coast and on the Columbia Plateau. Precipitation seasonality in the three other regions on Earth exhibiting the rapid increase in C4 ecosystems (RICE)—the Indian subcontinent, East Africa and South America—is also affected by the Tibetan Plateau and Altiplano. Abrupt uplift culminating by 7–8 Ma logically drove RICE in these areas, too, although the correspondence between the rise of the Altiplano and Tibet may well be fortuitous.

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REFERENCES CITED

- Alroy, J., Koch, P.L., and Zachos, J.C., 2000, Global climate change and North American mammalian evolution: *Paleobiology*, v. 26, p. 259–288, doi: 10.1666/0094-8373(2000)26[259:GCCANA]2.0.CO;2.
- Atwater, T., 2006, N.E. Pacific and W. North America plate history, 38 Ma to present: Educational Multimedia Visualization Center at the University of California–Santa Barbara, <http://emvc.geol.ucsb.edu/download/nepac.php> (June 2005).
- Atwater, T., and Stock, J., 1998, Pacific–North America plate tectonics of the Neogene southwestern United States: An update: *International Geology Review*, v. 40, p. 375–402.
- Axelrod, D.I., 1992, Climatic pulses, a major factor in legume evolution, in Herendeen, P.S., and Dilcher, D.L., eds., *Advances in legume systematics: Part 4. The fossil record*: Kew, Royal Botanical Gardens, p. 259–279.
- Badgley, C., and Fox, D.L., 2000, Ecological biogeography of North American mammals: Species density and ecological structure in relation to environmental gradients: *Journal of Biogeography*, v. 27, p. 1437–1467, doi: 10.1046/j.1365-2699.2000.00498.x.
- Barnosky, A.D., Carrasco, M.A., and Davis, E.B., 2005, The impact of the species-area relationship on estimates of paleodiversity: *PLoS Biology*, v. 3, article e266.
- Barron, J.A., Lyle, M., and Koizumi, I., 2002, Late Miocene and early Pliocene biosiliceous sedimentation along the California margin: *Revista Mexicana de Ciencias Geológicas*, v. 19, p. 161–169.
- Carrasco, M.A., Kraatz, B.P., Davis, E.B., and Barnosky, A.D., 2005, Miocene Mammal Mapping Project (MIOMAP): University of California Museum of Paleontology, <http://www.ucmp.berkeley.edu/miomap/>.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., and Ehleringer, J.R., 1997, Global vegetation change through the Miocene/Pliocene boundary: *Nature*, v. 389, p. 153–158, doi: 10.1038/38229.
- Clark, M.K., House, M.A., Royden, L.H., Whipple, K.X., Burchfiel, B.C., Zhang, X., and Tang, W., 2005, Late Cenozoic uplift of southeastern Tibet: *Geology*, v. 33, p. 525–528, doi: 10.1130/G21265.1.
- Coblentz, D.D., and Riitters, K.H., 2004, Topographic controls on the regional-scale biodiversity of the south-western USA: *Journal of Biogeography*, v. 31, p. 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: *Global Ecology and Biogeography*, v. 14, p. 479–490, doi: 10.1111/j.1466-822x.2005.00183.x.
- Diffendal, R.F.J., 1982, Regional implications of the geology of the Ogallala Group (upper Tertiary) of southwestern Morrill County, Nebraska, and adjacent areas: *Geological Society of America Bulletin*, v. 93, p. 964–976, doi: 10.1130/0016-7606(1982)93<964:RIOTGO>2.0.CO;2.
- Fox, D.L., and Koch, P.L., 2004, Carbon and oxygen isotopic variability in Neogene paleosol carbonates: Constraints on the evolution of the C4-grasslands of the Great Plains, USA: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 207, p. 305–329, doi: 10.1016/S0031-0182(04)00045-8.
- Garzzone, C.N., Ikari, M.J., and Basu, A.R., 2005, Source of Oligocene to Pliocene sedimentary rocks in the Linxia basin in northeastern Tibet from Nd isotopes: Implications for tectonic forcing of climate: *Geological Society of America Bulletin*, v. 117, p. 1156–1166, doi: 10.1130/B25743.1.
- Garzzone, C.N., Molnar, P., Libarkin, J.C., and MacFadden, B.J., 2006, Rapid late Miocene rise of the Bolivian Altiplano: Evidence for removal of mantle lithosphere: *Earth and Planetary Science Letters*, v. 241, p. 543–556, doi: 10.1016/j.epsl.2005.11.026.
- Hori, M.E., and Ueda, H., 2006, Impact of global warming on the East Asian winter monsoon as revealed by nine coupled atmosphere-ocean GCMs: *Geophysical Research Letters*, v. 33, L03713, doi: 10.1029/2005GL024961.
- Horton, T.W., Sjostrom, D.J., Abruzzese, M.J., Poage, M.A., Waldbauer, J.R., Hren, M., Wooden, J., and Chamberlain, C.P., 2004, Spatial and temporal variation of Cenozoic surface elevation in the Great Basin and Sierra Nevada: *American Journal of Science*, v. 304, p. 862–888, doi: 10.2475/ajs.304.10.862.
- Janis, C.M., Damuth, J., and Theodor, J.M., 2000, Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone?: *National Academy of Sciences Proceedings*, v. 97, p. 7899–7904, doi: 10.1073/pnas.97.14.7899.
- Keeley, J.E., and Rundel, P.W., 2003, Evolution of CAM and C4 carbon-concentrating mechanisms: *International Journal of Plant Sciences*, v. 164, p. S55–S77, doi: 10.1086/374192.
- Keeley, J.E., and Rundel, P.W., 2005, Fire and the Miocene expansion of C4 grasslands: *Ecology Letters*, v. 8, p. 683–690, doi: 10.1111/j.1461-0248.2005.00767.x.
- Kellogg, E.A., 1999, Phylogenetic aspects of the evolution of C4 photosynthesis, in Sage, R.F., and Monson, R.K., eds., *C4 plant biology*: San Diego, California, Academic Press, p. 411–444.
- Kennett, J.P., Keller, G., and Srinivasan, M.S., 1985, Miocene planktonic foraminiferal biogeography and paleoceanographic development of the Indo-Pacific region: *Geological Society of America Memoirs*, v. 163, p. 197–263.
- Kent-Corson, M.L., Sherman, L.S., Mulch, A., and Chamberlain, C.P., 2006, Cenozoic topographic and climatic response to changing tectonic boundary conditions in western North America: *Earth and Planetary Science Letters*, v. 252, p. 453–466, doi: 10.1016/j.epsl.2006.09.049.
- Kohn, M.J., and Cerling, T.E., 2002, Stable isotope compositions of biological apatite: *Reviews in Mineralogy and Geochemistry*, v. 48, p. 455–488.
- McCabe, G.J., Palecki, M.A., and Betancourt, J.L., 2004, Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States: *National Academy of Sciences Proceedings*, v. 101, p. 4136–4141, doi: 10.1073/pnas.0306738101.
- Molnar, P., 2005, Mio-Pliocene growth of the Tibetan Plateau and evolution of east Asian climate: *Palaeontologia Electronica*, v. 8, 2A, 23 p.
- Quade, J., Cerling, T.E., and Bowman, J.R., 1989, Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan: *Nature*, v. 342, p. 163–166, doi: 10.1038/342163a0.
- Retallack, G.J., 2001, Cenozoic expansion of grasslands and climatic cooling: *Journal of Geology*, v. 109, p. 407–426, doi: 10.1086/320791.
- Retallack, G.J., 2007, Cenozoic paleoclimate on land in North America: *Journal of Geology*, v. 115, p. 271–294, doi: 10.1086/512753.
- Retallack, G.J., Wynn, J.G., and Fremd, T.J., 2004, Glacial-interglacial-scale paleoclimatic change without large ice sheets in the Oligocene of central Oregon: *Geology*, v. 32, p. 297–300, doi: 10.1130/G20247.1.
- Ritchie, M.E., and Olff, H., 1999, Spatial scaling laws yield a synthetic theory of biodiversity: *Nature*, v. 400, p. 557–560, doi: 10.1038/23010.
- Ruddiman, W.F., and Kutzbach, J.E., 1989, Forcing of late Cenozoic Northern Hemisphere climate by plateau uplift in southern Asia and the American West: *Journal of Geophysical Research*, v. 94, p. 18,409–18,427, doi: 10.1029/JD094iD15p18409.
- Sahagian, D., Proussevitch, A., and Carlson, W., 2002, Timing of Colorado Plateau uplift: Initial constraints from vesicular basalt-derived paleoelevations: *Geology*, v. 30, p. 807–810, doi: 10.1130/0091-7613(2002)030<0807:TOCPUI>2.0.CO;2.
- Simpson, G.G., 1964, Species density of North American Recent mammals: *Systematic Zoology*, v. 13, p. 57–73, doi: 10.2307/2411825.
- Strömberg, C.A.E., 2002, The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: Preliminary results concerning the evolution of hypsodonty: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 177, p. 59–75, doi: 10.1016/S0031-0182(01)00352-2.
- Strömberg, C.A.E., 2005, Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America: *National Academy of Sciences Proceedings*, v. 102, p. 11,980–11,984, doi: 10.1073/pnas.0505700102.
- Webb, S.D., 1977, A history of savanna vertebrates in the New World: Part I: *North America: Annual Review of Ecology and Systematics*, v. 8, p. 355–380, doi: 10.1146/annurev.es.08.110177.002035.
- Webb, S.D., 1983, The rise and fall of the late Miocene ungulate fauna in North America, in Nitecki, M.H., ed., *Coevolution*: Chicago, University of Chicago Press, p. 267–306.
- Wernicke, B., and Snow, J.K., 1998, Cenozoic tectonism in the central Basin and Range; motion of the Sierran–Great Valley block: *International Geology Review*, v. 40, p. 403–410.
- Wing, S.L., 1998, Tertiary vegetation of North America as a context for mammalian evolution, in Janis, C.M., et al., eds., *Evolution of Tertiary mammals of North America*: Cambridge, Cambridge University Press, p. 37–65.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: *Science*, v. 292, p. 686–693, doi: 10.1126/science.1059412.
- Zhisheng, A., Kutzbach, J.E., Prell, W.L., and Porter, S.C., 2001, Evolution of the Himalaya–Tibetan plateau since late Miocene times: *Nature*, v. 411, p. 62–66, doi: 10.1038/35075035.

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