Biodiversity and Topographic Complexity: Modern and Geohistorical Perspectives

Catherine Badgley¹*, Tara M. Smiley², Rebecca Terry³, Edward B. Davis⁴, Larisa R.G. DeSantis⁵, David L. Fox⁶, Samantha B. Hopkins⁴, Tereza Jezkova⁷, Marjorie D. Matocq⁸, Nick Matzke⁹, Jenny L. McGuire¹⁰, Andreas Mulch¹¹, Brett R. Riddle¹², V. Louise Roth¹³, Joshua X. Samuels¹⁴, Caroline A.E. Strömberg¹⁵, Brian J. Yanites¹⁶

¹Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA
²Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, USA
³Department of Integrative Biology, Oregon State University, Corvallis, Oregon, USA
⁴Department of Geological Sciences, University of Oregon, Eugene, Oregon, USA
⁵Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, Tennessee, USA
⁶Department of Earth Sciences, University of Minnesota, Minneapolis, Minnesota, USA
⁷Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA
⁸Department of Natural Resources and Environmental Science, University of Nevada, Reno, Nevada, USA
⁹Division of Evolution, Ecology, and Genetics, Research School of Biology, Australian National University, Canberra, Australia
¹⁰School of Biology, Georgia Institute of Technology, Atlanta, Georgia, USA
Key words: biogeography, topography, diversity gradient, diversification, paleontological data

Abstract

Topographically complex regions on land and in the oceans feature hotspots of biodiversity that reflect geological influences on ecological and evolutionary processes. Over geologic time, topographic diversity gradients wax and wane over millions of years, tracking tectonic or climatic history. Topographic diversity gradients from the present day and the past can result from the generation of species by vicariance or from the accumulation of species from dispersal into a region with strong environmental gradients. Biological and geological approaches must be integrated to test alternative models of diversification along topographic gradients. Reciprocal illumination among phylogenetic, phylogeographic, ecological, paleontological, tectonic, and climatic perspectives is an emerging frontier of biogeographic research.
Topographic diversity gradients – a general pattern

Across the world today, a disproportionate share of taxonomic diversity occurs within topographically complex regions, such as large mountain ranges and deeply dissected plateaus. Mammals, birds, and angiosperms express this topographic diversity gradient on land, and counterparts occur in the marine realm as well (e.g., 1). Biogeographers have analyzed variation in biologically relevant properties along physical gradients of latitude, elevation, depth, and topographic complexity, although the processes that generate and maintain diversity gradients remain unresolved. Ecological, evolutionary, and geohistorical processes all contribute [2,3], but no agreement has emerged on which processes dominate each gradient, how processes interact, or whether different geographic expressions and geohistorical occurrences of each kind of gradient emerge from a common cause.

Here we focus on changes in taxonomic and ecological diversity that accompany gradients in topographic complexity—a pattern that characterizes the geography of species diversity on continents and in oceans today [4,5]. This topographic diversity gradient (see Glossary) results from interactions among biogeographic, geomorphological, and climatic processes. Biogeographic processes (speciation, extinction, and immigration) give rise to the taxonomic and functional diversity of species and their dynamic patchwork of geographic ranges. Topography, which is shaped by geomorphological processes at local, regional, and plate-tectonic scales, influences the distribution of ranges, biotic interactions, and functional ecological traits. The generation of topographic complexity (Box 1) steepens climatic gradients, increases habitat heterogeneity, and increases surface area within montane regions.
Simultaneously, Earth’s dynamic climate system enhances spatial gradients of temperature, precipitation, wind, and ocean currents. Here we present a framework for evaluating the biogeographic and geohistorical processes that underlie topographic diversity gradients. A case study of North American rodents demonstrates how geological, fossil, phylogenetic, and ecological data can be integrated to test scenarios of diversification in relation to landscape history. Three additional examples illustrate topographic diversity gradients for other taxonomic groups and regions. Topographically complex regions (see Glossary) include many of the world’s diversity hotspots today, harboring a high proportion of species vulnerable to extinction [8]. There is urgent motivation to understand the processes underlying their diversity, with important implications for conservation strategies in the context of current global climate change and biodiversity loss.

The need to integrate landscape and biogeographic history

Topographic diversity gradients can result from the generation of new species or the accumulation of species via dispersal into a topographically complex region. Different rates of biogeographic processes can, in principle, strengthen or weaken a topographic diversity gradient (Box 2). For example, a higher rate of speciation in a tectonically active, montane region could generate more species over time in the montane region compared to lowlands (Box 2A). Alternatively, a brief pulse of accelerated speciation in response to increasing topographic complexity could rapidly increase diversity within the montane region (Box 2B). Or, climatic warming could stimulate geographic-range shifts
to higher elevations, where immigrants and residents could speciate more rapidly than in adjacent lowlands (Box 2C).

Robust testing of hypotheses about processes by which topographic diversity gradients arise, persist, or diminish requires demonstrating precise coincidence and interaction in time and space between causal factors and biogeographic responses. This kind of analysis is only possible with a synthesis of geological and biological data. Four kinds of modern and historical data are needed to formulate and test alternative hypotheses about the origin and maintenance of topographic diversity gradients. Our analytical framework involves systematic evaluation of these four kinds of data in order to address the pertinent questions associated with each.

(1) Landscape history. Topography and relief arise from tectonically driven uplift interacting with climatically driven erosion (Box 1, [9,10]). The timing of changes in topographic complexity (i.e., the regional landscape history) provides the spatio-temporal context for testing models of diversification within mountain ranges compared to adjacent lowlands. Although the broad outlines of Earth's tectonic and climatic history are well known, particularly for the last ~200 Ma since the breakup of Pangaea, the determination of paleo-elevation, relief, and topographic complexity over spatial scales of 10-100 km lie at the frontiers of geological research (e.g., 11-13).

When did topographic complexity arise? How have changes in elevation and relief altered environmental gradients over time?

(2) Diversification history. The net outcome of speciation and extinction of lineages determines the macroevolutionary history of a group across regions of different topographic complexity. Both fossil and modern data are critical for reconstructing
Badgley et al., p. 6

... diversification history, since neither in isolation can fully capture that history. For example, changes in species composition along replicate elevation gradients in different mountain ranges today permit us to evaluate the environmental factors and ecological interactions that support and limit taxonomic and ecological diversity. However, the diversity and distribution of extant species do not indicate how long modern gradients have been present, whether high regional diversity has resulted from the production or the accumulation of diversity, or which extinct species once contributed to the diversity of local communities or clades.

The fossil record documents taxonomic and morphological diversity in space and time, as well as ecological traits in lineages and communities. A dense, spatially explicit regional fossil record provides evidence for geographic distributions, spatial turnover, barriers and connectivity across the landscape, and the magnitude of geographic-range shifts over the duration of a lineage. In phylogenetic context, hypotheses of evolutionary relationships specify a historical sequence of trait acquisition, loss, or transformation, and allow identification of regions and clades with young and old endemic lineages. If montane uplift stimulates speciation, then phylogenies should record a pulse of divergences whose timing matches the onset of uplift. Phylogenies based on extant species can potentially record such pulses (e.g., 14). Phylogenies that combine extant and fossil data provide greater insight by including diversity represented only in extinct lineages.

*Which species ranges were fragmented by montane uplift or rifting and the associated barriers (high elevation, deep canyons)? Is the montane region a source of new species over long periods of time?* Paleontological data for the spatial distribution
of lineages over time within montane regions and adjacent lowlands can establish areas of origin and endemism. Does topographic complexity leave a signature of divergence in phylogenies?

(3) Spatial dynamics. The current geographic distribution of species ranges reflects the responses of populations to environmental factors, interspecific interactions, and barriers to dispersal present today and in the recent past. Placing modern geographic ranges within a geohistorical context is fundamentally important, however, since most species ranges have shifted from their place of origin in response to tectonic, climatic, and biotic history. Barriers to dispersal that have come and gone over the dynamic history of landscapes leave legacy effects in the genetic structure of populations and gaps in geographic distributions. Thus once again, neither modern nor geohistorical data alone can fully capture the role of spatial dynamics in generating diversity gradients. When integrated, however, both data sources can significantly advance our understanding of the development and maintenance of diversity gradients. For example, in the context of landscape history, combining the geography of fossil occurrences with the spatial dynamics of species, as inferred from modern distributions and phylogeographic analyses, can reveal the degree to which dispersal contributes to changes in diversity within topographically complex regions and provide evidence of environmental sorting of species ranges along elevational gradients.

How much does dispersal contribute to diversity in topographically complex regions? How do rates of dispersal change in relation to climatic history?

(4) Ecological traits. The distribution of ecological traits (e.g., body size, feeding habits, life histories, substrate use) within and across lineages, communities, and
ecosystems varies strikingly along present-day environmental gradients [15-18].

Landscape reorganization can spur ecological changes in populations, species, and biotic interactions. Together functional and taxonomic diversity allows assessment of the degree to which changes in community structure accompany the speciation and extinction history of clades. Ecological comparison of diversifying and disappearing lineages can reveal ecological biases in relation to environmental filters structuring diversity. Fossils contribute data about the timing and geography of trait changes.

Do particular ecological traits predispose a group to proliferate in montane regions? Which ecological traits become specialized over time along elevational gradients?

To date, landscape history, diversification history, the spatial dynamics of diversity, and ecological traits have been studied largely in isolation, yet their integration is critical for advancing our understanding of diversity gradients over space and time [3,4]. In order to evaluate the contributions of biogeographic processes to diversity gradients, it is useful to test scenarios of different processes acting separately and in combination (e.g., Box 2). These scenarios demonstrate the historical consequences of different processes and the phylogenetic and geographic diversity patterns that should result. Finally, it is important to evaluate not only the topographically complex region but also adjacent basins or plains for comparison, since the diversity gradient involves changes in diversity in both regions.

Biogeographic processes in topographically complex regions
The dynamic landscape represents the stage on which the biogeographic processes of speciation, extinction, and immigration play out. For example, the rate of species formation and either neutral or adaptive divergence among populations could be elevated in topographically complex regions because of habitat heterogeneity across elevation gradients and numerous opportunities for range fragmentation and isolation of populations by persistent landscape barriers. These circumstances could lead to allopatric speciation at high elevations or on different sides of topographic barriers. Strong environmental gradients with elevation also provide the opportunity for ecological speciation in a population that spans a large portion of the gradient. These speciation processes have been proposed for insects, birds, frogs, mammals, and plants in North and South America (e.g., 19-22). A topographic diversity gradient resulting from higher speciation rates (other processes being equal) would feature many neo-endemic (See Glossary) species in the montane region and increased spatial turnover (beta diversity) [23,24]. Phylogenies would reveal a distribution of species ages skewed towards recent origins in the montane region. In contrast, adjacent lowlands would have few endemics and a greater proportion of older species.

The geographic ranges of species and populations are typically smaller in montane regions than in adjacent lowlands, and small ranges are more vulnerable to extinction [25]. However, complex topography also enhances metapopulation dynamics. A patchwork of similar habitats that are weakly or sporadically connected can serve as sources for recolonization when conspecifics become rare or extirpated [26]. Climate change should enhance these metapopulation processes as species ranges shift to higher or lower elevations. A topographic diversity gradient that resulted from lower
extinction rates in the montane region (other processes being equal) would feature older endemic species. In contrast, adjacent lowlands would have more short-lived species. 

Dispersal could cause a topographic diversity gradient if the immigration rate exceeded the emigration rate from the region. Greater habitat heterogeneity in montane regions could facilitate dispersal and colonization by ecologically diverse species, resulting in tighter species packing. Species could disperse from lowlands via river valleys and gaps in mountain ranges. A topographic diversity gradient that resulted from higher immigration rates would feature few endemics and moderate beta diversity in the topographically complex region because of the influx of widespread species. Adjacent lowlands would have few endemics and low beta diversity. Climate-change episodes should accentuate range shifts: during warm intervals, dispersal should be greater from lowlands into montane regions, with the reverse pattern during cool intervals. The Quaternary fossil record documents such range expansions and contractions between high and low elevations, as well as high and low latitudes, for plants and mammals [27,28]. 

The advent of phylogeography (see Glossary) has enabled the influences of climate and topography on genetic variation to be evaluated for a wide range of animals and plants [29]. For example, during periods of restricted distribution (e.g., when climates limit habitat availability or connectivity), gene flow among isolated populations should cease such that new mutations are no longer exchanged and genetic drift leads to loss of ancestrally shared alleles. Population divergence via this mechanism can be amplified by ecological differences among isolated populations, and changes in ecological attributes are likely to be more pronounced during episodes of climate
change. For Australian arid-region geckos [30] and Southwest Australian Floristic Region plants [31], topographic complexity has been postulated to influence initial population divergence through isolation due to Pliocene climate shifts altering the intervening areas into unsuitable habitats. However, spatial congruence of phylogeographic breaks in multiple taxa does not necessarily indicate that all taxa responded similarly to the same isolating event. A particular topographic feature may have become a barrier or filter to gene flow at different times throughout the evolutionary history of individual taxa [32]. Such temporally discordant but spatially concordant vicariant events have been identified for birds isolated by Neotropical mountains and rivers [33], trans-Beringian small mammals [34], and Central American fishes [35].

A frontier of research concerns the selectivity of evolutionary processes with respect to ecological traits in topographically complex regions. For example, mammalian diet and habitat generalists have larger geographic ranges [36], yet we do not know if those species exhibit higher speciation rates in topographically complex regions, which could result in multiple species with similar dietary and habitat requirements, each occupying a separate region (e.g., [37]). Functional diversity is higher and more variable in montane regions than in lowlands due to greater habitat heterogeneity at small spatial scales [15]. Tracking changes in ecomorphology within species can provide insight about the processes driving speciation, extinction, and dispersal, and how they differ across gradients in topography. Such species-specific trajectories can be assessed with morphometrics, biogeochemical analysis of resource use, and body-size trends through time (Box 3).
North American rodents and landscape history

As a case study, we focus on the Cenozoic history of rodents in North America. We highlight rodents for several reasons: rodents are the most species-rich clade of mammals, with high taxonomic and morphological diversity in modern and ancient ecosystems of North America. Well resolved phylogenetic, phylogeographic, and historical-biogeographic analyses are available for several families that diversified over this time frame (e.g., Heteromyidae, 14; Sciuridae, 37; Mylagaulidae, 38). Also, a dense fossil record based on over 100 years of collecting and describing fossil mammals documents rodent diversity in adjacent regions of contrasting topographic complexity: the intermontane west, a region that has been tectonically active throughout the Cenozoic, compared to the Great Plains, a region of tectonic stability over the same period (Fig. 1). For convenience, we denote these areas as the Active and Passive regions (see Glossary). Today nearly twice as many rodent species per unit area occur in the Active region (Fig. 2A). The spatial turnover of species is also greater there, as many range boundaries follow major physiographic features (Fig. 2B). Integrating landscape history and diversification processes, we can evaluate whether diversification history for clades and regional faunas show changes during particular intervals of tectonic or climatic history (Box 2, Fig. 3), including process-based diversification models that incorporate specific aspects of geologic history (e.g., [39,40]).

During formation of the Basin and Range province over the last 30 myr, a highland extending from British Columbia into northern Mexico [41] was pulled apart into many fault-bounded mountain ranges and intervening basins, expanding the area by over 200
km from east to west [42]. Uplift in the northern and central Rocky Mountains accentuated elevation gradients, and from the middle to late Miocene, volcanic activity formed the Cascade Range. In contrast, the Great Plains were tectonically stable but episodically received blankets of volcanic ash from sources to the west and fluvial sediments from the Rocky Mountains.

The vegetation record from phytolith assemblages documents a climatic drying trend across North America over the last 30 myr via changing proportions of $C_3$ and $C_4$ grasses in relation to forest trees and herbs (Fig. 3). In the Active region, forest indicators constituted over 30% of phytolith assemblages until ca. 17 Ma, then declined as $C_4$ grasses increased. In the Passive region, forest indicators were dominant until about 25 Ma, and grasses became dominant thereafter. Increasing proportions of grass (especially $C_4$ grass) phytoliths indicate that aridification of western North America began earlier in the Passive region than in the Active region.

For long periods, the topographic diversity gradient of North American rodents was weak to nonexistent (Fig. 3). Over the last 34 My, rodent diversity fluctuated substantially in both the Active and Passive regions, with diversity higher in one or the other region at different times. Two diversity peaks coincided with warm intervals—the Miocene Climatic Optimum (MCO, see Glossary) from 17-14 Ma and the Pliocene warm period from 4.0-2.5 Ma.

In addition to changes in species diversity, some intervals showed substantial change in taxonomic composition of regional faunas [43]. Within the Active region, rodents of the Pacific Northwest and the northern Rocky Mountains changed markedly in the number and proportion of species per family during the MCO, including
appearances and disappearances of entire families. In the northern Great Plains, the largest change in taxonomic composition occurred at the end of the MCO. Evidence for geographic-range shifts was greatest in both regions between 16 and 14 Ma. Despite these range shifts, these three regions had low faunal similarity at 16 Ma compared to today. Within the Active region, the middle Miocene witnessed increased diversity within faunas of individual tectonic provinces as well as high spatial turnover. In the Passive region, faunal composition had more taxonomic continuity over time, with high volatility during the middle Miocene. The proportions of species with different tooth-crown heights (Box 3) showed several parallel changes between the Active and Passive regions that track changes in vegetation composition (Fig. 3).

In relation to the scenarios of Box 2, the North American rodent record does not match the mountains-as-cradle model (Box 2A), since diversity was lower in the Active region than in the Passive region for millions of years (Fig. 3). Likewise, the record does not match a mountains-as-museum model (not pictured), since mean species durations did not differ between the Active and Passive regions [44]. North American rodent diversity does match the tectonic-pulse model (Box 2B) during the MCO, when high diversity in the Active region coincided with an interval of widespread tectonic activity that increased topographic complexity [43]. Comparable intervals of intensified tectonic activity did not, however, coincide with older (28-23 Ma) or younger (5-3 Ma) periods of high diversity in the Active region. With regard to the climatic-pulse model (Box 2C), more geographic-range shifts and expansions occurred between 16 and 14 Ma within the Active region and between the Passive and Active regions than during any other part of the Miocene [43]. The Pliocene peak in rodent diversity within the
Active and Passive regions also fits the climatic-pulse model, since warming would stimulate geographic range shifts into both regions. More elaborate scenarios, such as speciation following range expansion along specific dispersal routes (e.g., [45]) could also be tested.

Phylogenetic and phylogeographic analyses complement the fossil record in documenting evolutionary responses of North American rodents to changes in topographic complexity. Among heteromyids (kangaroo rats and pocket mice), deep branching events among genus-level clades occurred during the middle Miocene [14], when rodent diversity peaked across the Active region. Phylogeographic analysis of the Great Basin pocket mouse, Perognathus parvus, has revealed cryptic species whose distributions indicate late Miocene separation of populations by montane barriers in eastern Oregon and the Snake River Plain in southern Idaho [46]. Among chipmunks (Sciuridae), distinct phylogeographic lineages in the yellow-pine chipmunk, Tamias amoenus, occupy specific mountain ranges in the Pacific Northwest and northern Rocky Mountains, with divergences estimated to be at least several million years old [47]. Across the Passive region, the phylogeographic structure of the eastern chipmunk, Tamias striatus, indicates recent population expansion over much of eastern North America from glacial refugia south of the Wisconsinan ice sheet [48].

Topographic complexity and high diversity in other systems

Topographic diversity gradients occur in other groups and contexts beyond North American rodents. Integrating neontological and paleontological insights can reveal the
powerful influence of topographic complexity on biogeographic processes in other systems, such as the three illustrated here.

(1) Inverting the mammalian pattern, the diversity of freshwater fishes of North America today is high in the tectonically passive eastern region and low in the tectonically active montane west [49]. Large rivers, high fluvial connectivity, low stream gradients, warm temperatures, and high precipitation in Appalachian headwaters of the Mississippi Basin support the highest species densities, whereas short, high-gradient rivers with low connectivity and seasonally variable discharge in the montane west support species densities that are lower by an order of magnitude. Speciation rates estimated for six family-level clades with good fossil records across North America do not differ between eastern and western lineages; however, extinction rates were higher for western lineages, evidently associated with tectonic fragmentation of the landscape and numerous montane barriers to recolonization during the Cenozoic.

(2) At the junction of the Pacific, Australian, and Eurasian tectonic plates, long archipelagos, shallow carbonate platforms, and oceanic trenches of the Indo-Australian Coral Triangle host a diversity hotspot for many marine clades, including corals, benthic foraminifera, reef fishes, and mollusks [50]. Strong depth gradients, complex ocean currents, and large islands provide high habitat diversity and barriers to dispersal, even for many species with planktotrophic larvae. A Cenozoic fossil record of corals, foraminifera, and mollusks documents increasing local and regional diversity between 25 and 23 Ma, as the converging Australian, Eurasian, and Pacific plates constricted deep circulation between the western Pacific and Indian oceans [51] and provided new habitats in shallow and deep water, conduits for immigrants via ocean currents, and
numerous island barriers. Over the last 50 myr, the geographic locus of high marine
diversity shifted from the western Tethys (Mediterranean) in the middle Eocene to the
eastern Tethys in the early Miocene to the Indo-Australian region since the Middle
Miocene [52]. As plate collisions produced large expanses of shallow habitats
fragmented by islands and peninsulas, topographic complexity increased and each
diversity hotspot grew.

(3) Of the ~12,500 tree species in Amazonia today [53], the highest local diversity
occurs in western Amazonia and the equatorial Andes [54,55]. Pollen and plant
macrofossils [56] indicate that rainforest was present throughout the Cenozoic, although
the exceptionally high local and regional diversity dates from the early Miocene. The
rising Andes [57] promoted allopatric speciation in the lowlands and ecological
speciation along expanding orographic gradients [20]. Deep river valleys and steep
gradients in slope, soils, and microclimates contributed to high endemism [54]. For
most of the Miocene, an extensive wetland east of the rising Andes would have served
as a barrier to lowland plant distributions. Sediments accumulating in this wetland
contain fossils that document changes in floral and faunal diversity and composition
over the Neogene [58]. Along the eastern Andes, erosion and deposition of fertile
sediments produced distinctive areas for adaptation by plants to different soil types.
High elevations also provided immigration routes for cold-tolerant plants from North
America into northern South America [59]. Subsequent dispersal within the Andes and
Amazonia has overwritten the geographic signature of earlier divergence events.

Implications for conservation
Understanding the ecological and evolutionary drivers of diversity gradients in different landscapes can help guide conservation strategies. Using the geologic record, we can develop broader strategies for conserving landscapes where diversity is actively generated on evolutionary timescales [24,60]. Combining neontological and paleontological analyses can also inform strategies for detecting individual species that are most vulnerable to environmental change [61,62] and the ecological or evolutionary characteristics that increase vulnerability.

Topographically complex regions offer refugia for maintaining diversity under climate warming [63,64]. Predicted warming is high for montane regions over the next 100 years and will lead to loss of high-elevation climates, habitats, and species [65]. By identifying areas that are likely to maintain regional diversity, despite local taxonomic turnover through time, the geohistorical approach adds to the growing body of literature characterizing potential climate refugia for the future [64]. A critical goal of landscape-scale conservation is to establish connectivity among relatively natural areas, promoting dispersal across more anthropogenically altered regions [66,67]. By identifying where turnover occurred when climates changed in the past, the record of past diversity and landscape history can reveal climatic gradients within and between which species were prone to move, making these landscapes conservation targets for the future.

Acknowledgments

We thank the U.S. National Evolutionary Synthesis Center (NESCent) for hosting a catalysis meeting in 2013, at which these perspectives and goals began to develop. For
discussion, we thank J.A. Finarelli, M. Zelditch, and G.R. Smith. Carol Abraczinskas assisted with preparation of figures. Reviewer comments improved the manuscript.

**Reference list**


19 Winger, B.M. *et al.* (2015) Inferring speciation history in the Andes with reduced-representation sequence data: an example in the bay-backed antpittas (Aves;


Barnosky, A.D. et al. (2004) Assessing the causes of Late Pleistocene
extinctions on the continents. *Science* 306, 70–75


horns in the Mylagaulidae (Mammalia: Rodentia). *Proc. R. Soc. B* 272, 1705–1713


Demboski, J.R. and Sullivan, J. (2003) Extensive mtDNA variation within the


Hubbell, S.P. *et al.* (2008), How many tree species are there in the Amazon and how many of them will go extinct? *Proc. Natl. Acad. Sci.* 105, 11498–11504


Species Evolution: A look into the Past (Hoorn, C. and Wesselingh, F.P., eds), pp. 349–359, Blackwell


63 Tzedakis, P.C. et al. (2013) Cryptic or mystic? Glacial tree refugia in northern...


Cotton, J.M. *et al.* (2012) High-resolution isotopic record of C4 photosynthesis in...


**Figure captions**

Figure 1. Geologic history of western North America. Three representative time slices are based on information from [41,42,68]. The tectonically active region (gray shading) consists of several tectonic provinces that have changed in size, elevation, and relief over the last 30 myr. Black arrows refer to increase or decrease in mean elevation; white arrows refer to increase or decrease in relief. The tectonically passive region (yellow shading) has been stable over this time, receiving aeolian and fluvial sediments from the Active region. (A) At 30 Ma, the Active region was narrower than today. The Nevadaplano was starting to break up into the Basin and Range. (B) At 15 Ma, in the middle Miocene, the Basin and Range was expanding rapidly and had higher relief than any time since; volcanic activity in the Pacific Northwest led to growth of the Cascade Range and the Yellowstone hotspot began to migrate eastward. (C) The present-day landscape shows a wider Active region from expansion of the Basin and Range and more subdued tectonic activity.

Figure 2. Present-day diversity for rodents of western North America. Diversity is based on species ranges in NatureServe [69], compiled at a resolution of 0.1°. (A) Species density of rodents. (B) The distribution of overlapping range boundaries for two or more
species. Both species density and spatial turnover are greater in the Active region than the Passive region today.

Figure 3. Climatic and biotic changes in North America through the last 35 myr. The global temperature trend is reflected in the benthic foraminiferal oxygen-isotope record (data from [70]). Notable warming intervals during the middle Miocene were followed by long-term cooling and Quaternary glacial-interglacial cycles. Global climate influenced vegetation (inferred from the phytolith record) differently in the Active (montane west) versus the Passive (Great Plains) regions of North America (data from [71-74]). Although both regions exhibit a Neogene increase in grasses, the decline of forest ecosystems occurred earlier in the Passive region. Between 34–28 Ma, 22–18 Ma, and 2–1 Ma, rodent diversity was higher in the Passive than in the Active region, whereas from 17–13 Ma, 7–5 Ma, and 5–3 Ma, diversity was much higher in the Active region. The contrast in diversity between Active and Passive regions was greatest during the Miocene Climatic Optimum (17–14 Ma). Much of the diversity change among rodents was accompanied by changes in faunal composition [43,44]. Corresponding changes in dietary ecology are demonstrated by the increase in high-crowned species (hypsodont and hypselodont) towards the present (data from J.X. Samuels). This increase preceded the expansion of grasslands in both regions, suggesting that adaptation to more abrasive diets was not driven by grass consumption but rather by volcanic ash in soils or grit on plants.
Box 1. How complex topography is generated

Topography results from the interactions of tectonics, climate, and erosion. Tectonic processes in Earth’s crust and mantle produce high-elevation landscapes, and together erosion and surface uplift generate relief at large spatial scales (≥10^2 km) (e.g., [9]). At convergent plate margins, the development of high surface elevations and relief result either from thickening of the crust, which increases elevation by isostasy [75], or from changes in the density structure of the underlying mantle (e.g., [76]). In extensional regimes (such as the Basin and Range province of western North America), vertical faulting can give rise to significant local relief independent of changes in regional elevation (see Glossary). Climatically driven erosional processes amplify large-scale elevation and relief to generate the complex topography observed in many mountainous regions. A network of river valleys provides a ‘skeleton’ on which such topography continually evolves in response to climatic and tectonic drivers. Adjacent to elevated regions, deposition of eroded material in basins generates relatively smooth landscapes. These different landscape regimes (erosional vs. depositional) provide different magnitudes of topographic complexity and relief (Fig. 1).

A major insight in recent decades is that climatic and tectonic processes interact through the evolution of topography. Essentially, changes in the distribution of mass on Earth’s surface resulting from climatically driven erosion can influence the tectonic forces causing mountain uplift and significant topographic adjustment of a region. Moreover, the building of mountainous topography by tectonics influences local, regional, and even global climate (e.g., [77]). Therefore, understanding the topographic
history of a region requires integrating records of mountain building, paleoclimate, and erosion rates.

Advances in quantifying topographic change have led to discoveries about Earth’s topographic history and rates of topographic change. Reconstructions of past elevations of a region, e.g., from stable isotope paleoaltimetry, are able to detect changes in elevation more precisely than absolute elevations [12]. Estimating rates of erosion and topographic change with thermochronology [13] or numerical landscape models [78] provides ways to test ideas about the relative contributions of tectonics and climate as drivers of topographic change.

Advances in biological and geological inquiries provide an opportunity for a transformative recognition of the interactions of the atmosphere, geosphere, and biosphere. The richness of biosphere - landscape interactions, from biological influences on erosion to topographic influences on evolutionary processes, provides new insights into an integrated-systems view of Earth processes and history.

Figure 1. Landscape-evolution model [79] for an 8-million-year simulation. In this model, half of the domain is underdoing active tectonic uplift (at 0.5 mm per yr), while the other half is subsiding at a rate significantly lower than the uplift. Output is shown for the initial model set-up (A), at 4 million years (B), and at 8 million years (C) of model simulation time. As part of the landscape becomes uplifted, climate-driven processes of erosion, sediment transport, and deposition are modeled with established geomorphic principles. Bedrock erosion dominates in the Active region as the landscape steepens from sustained uplift, leading to development of complex topography. Sediment deposition dominates in the Passive region, leading to a smoother landscape.
Combining data from extant and fossil taxa will be critical for evaluating diversification processes—speciation, extinction, and immigration—within the context of dynamic landscape histories. Diversification rates can be quantified from time-calibrated phylogenetic trees [80] or from fossil species-occurrence data [40, 44]. The generation of large molecular, paleontological, and ecomorphological datasets and their integration with comparative methods makes understanding the history of diversity patterns such as the topographic diversity gradient a tractable prospect.

Here we present three theoretically plausible models for generating a topographic diversity gradient and describe tests from the present-day and fossil records to evaluate them. Extinction rate is constant over time or space in these models; however, variable extinction rates could be tested.

(A) **Mountains as cradle** Speciation rate is stochastically constant but elevated in the tectonically active region (AR) compared to the tectonically passive region (PR).

*Present-day (phylogenetic) test:* Instantaneous rates of speciation for extant taxa are higher in the AR than in the PR.

*Fossil (occurrence-based) test:* Speciation rates are consistently higher in the AR.

(B) **Tectonic pulse** Speciation rate is elevated during an interval of tectonic activity in the AR, but remains constant in the PR.

*Present-day test:* Increase in older branching events during the tectonic pulse. A speciation rate slow-down may appear for extant AR lineages, while rates remain low and time-invariant in the PR.
Fossil test: Speciation rates increase in the AR but not in the PR during the tectonic pulse.

(C) Climate-driven immigration During global warming, immigration into the AR increases.

Present-day test: In likelihood-based biogeographic methods (Lagrange, BioGeoBEARS), model comparison could be used to infer increased immigration rates during certain time periods using a time-stratified analysis.

Fossil test: Distinguishing immigration and speciation events in the fossil record is difficult. Fossil taxa can be integrated into BioGeoBEARS as tips or direct ancestors. Alternatively, fossil coverage over large geographic regions offers the potential to track the geographic distribution of lineages and resolve these distinctions.

Ecomorphological and geographic data can be mapped onto clade history to reconstruct evolutionary and biogeographic processes [81]. For example, state-dependent speciation/extinction (SSE) models offer potential for the comparative study of regional diversification. In SSE models, speciation or extinction rate can vary as a function of a character state (or geographic region) that itself is evolving on the tree [82]. The complexity and flexibility of SSE models also raise challenges [83,84], with some already being addressed [45,85].

Box 2, Figure 1 caption

Three theoretically plausible models (A-C) for generating the topographic diversity gradient of rodents in North America over the Cenozoic. Simulated phylogenies for the Active (blue) and Passive (red) regions for each model are shown in the upper panel,
with corresponding lineage-through-time (LTT) plots in the lower panel. The timing of
speciation (B) and immigration (C) rate shifts is indicated by gray bars. See box text for
descriptions of each model and tests for evaluating model fit to the North American
rodent record.

Box 3. Paleoecological approaches to inferring diet and vegetation

North American rodents possess an array of dietary and locomotor specializations
reflecting variation in diet, substrate use, and habitat selection (e.g., [86]). Below we
summarize major paleoecological approaches to reconstruct mammalian diet and
terrestrial vegetation (Fig. 1). Integrating these data—from individuals, populations, and
species—allows hypothesis testing about the effects of landscape and resource
changes on ecological diversification over time.

(A) **Hypsodonty index** High tooth crowns (hypsodonty) in mammals represent evolved
responses to physical properties of diet, such as abrasive or tough plant matter, or
exogenous grit (dust) common in open, arid environments [17]. Herbivorous rodents
and open-habitat specialists typically display high-crowned teeth, reflecting relative
openness (or grass dominance) of habitats through time [87].

(B) **Dental microwear textures** Microscopic wear patterns on teeth result from
processing of foods consumed shortly before death [88]. Dental microwear texture
analysis differentiates between tough and hard-object consumption using scale-
sensitive fractal analysis [18]. While studies on how habitat change influences
terrestrial communities have often focused on large mammals, this approach can
potentially resolve small mammal dietary ecology, habitat, or local substrate.
(C) **2-D and 3-D tooth morphology** Shape analysis using geometric morphometrics relies on 2-D or 3-D Cartesian coordinates of morphological structures, independent from size variation or *a priori* chosen traits [37]. This approach has quantified dental shape change along environmental gradients and through the evolution of small-mammal lineages [18,89]. Digital indices of high-resolution 3-D tooth surfaces (e.g., orientation-patch count, relief index) present alternative ways to measure tooth shape and discriminate dietary categories (granivore, folivore, omnivore, insectivore) in extant and fossil small mammals [90].

(D) **Stable isotopes** Stable carbon isotopes of mammalian tooth enamel reflect the isotopic composition of the diet, with ~11‰ enrichment for small mammals [91]. Carbon isotopes record differences in vegetation composition (e.g., % C₄ plants in diet) and habitat structure (e.g., canopy height), while oxygen isotopes reflect temperature, precipitation, and water use [92]. Isotopic analyses of small-mammal teeth using laser-ablation and -fluorination sampling techniques help infer ecological interactions and document fine-scale habitat variation [93,94].

**Phytoliths (see Fig. 3, main text)** Phytoliths are microscopic silica bodies in plant tissues and often preserve in paleosols and fluvial sediments associated with mammalian fossils [71]. Phytolith assemblage analysis provides information about vegetation structure and grass community composition [72-74]. Often reflecting mainly local vegetation, phytoliths can inform spatial heterogeneity in vegetation relevant for small-mammal ecology and evolution.

Box 3, Figure 1 caption
Approaches for inferring species ecology. (A) Illustration of tooth-crown categories from left (low-crowned) to right (high-crowned): brachyodont, mesodont, hypsodont, and hypselodont (ever-growing). (B) Dental microwear texture analysis of a gopher (*Thomomys bottae*) incisor with relief on the enamel surface false colored to illustrate texture roughness and orientation. (C) 3-D image of rodent tooth morphology captured by high-resolution X-ray computed microtopography and quantified based on surface curvature. (D) Carbon isotopic composition and inferred percent $C_4$ vegetation in the diets of modern rodents from Nebraska (solid symbols, left panel) and fossil rodents from the Big Springs Gravel at ca. 2.4 Ma (open symbols, right panel). Different symbols refer to rodent families, including Cricetidae (diamonds), Heteromyidae (triangles), Sciuridae (inverted triangle), and Geomyidae (circles). Rodent isotopic values have been adjusted by the appropriate enrichment factor and according to changes in the isotopic composition of atmospheric $CO_2$ to be comparable to mean $C_3$ (small dash) and $C_4$ (long dash) vegetation values.

**Glossary**

**Basin extension**: Development of topography characterized by fault-bounded mountain ranges and intervening basins, through tectonic extension or stretching of Earth’s crust. Such regions have high relief across basins and mountains.

**Miocene Climatic Optimum**: An interval from 17 to 14 million years ago, when global climate was warmer around the world, supported by evidence from marine and continental data.
Neo-endemism: Species of recent divergence that have restricted geographic distributions. Many neo-endemic species occur in montane regions, often at high elevations.

Phylogeography: The integration of molecular phylogenetics, population genetics, and biogeography to understand the genetic structure, and thereby the patterns of gene flow (or lack thereof), among populations in the context of landscape history.

Tectonically active region: A region where tectonic plates are converging or diverging, resulting in substantial surface uplift, leading to the formation of mountain ranges, volcanoes, and large subsiding areas.

Topographically complex region: A region with high relief, resulting from tectonic uplift and erosion that create high-elevation mountains and plateaus and deep river valleys on land, and shallow platforms and deep trenches in the oceans. These regions maintain high elevations and relief over millions of years.

Topographic diversity gradient: Species diversity per unit area is high in areas of complex topography, such as entire mountain ranges and regions with mountains and small intervening basins (e.g., the Basin and Range of western North America).
Badgley et al., TREE

Highlights/Trends Box

1. Today topographically complex regions feature high taxonomic and ecological diversity.

2. Ancient topographic diversity gradients arose and declined over millions of years.

3. Ecological and evolutionary processes contribute to topographic diversity gradients.

4. Topographically complex regions have high conservation value.
Box 1: How complex topography is generated

Topography results from the interactions of tectonics, climate, and erosion. Tectonic processes in Earth’s crust and mantle produce high-elevation landscapes, and together erosion and surface uplift generate relief at large spatial scales ($\geq 10^2$ km) (e.g. [B1R1]). At convergent plate margins, the development of high surface elevations and relief result either from thickening of the crust, which increases elevation by isostasy [B1R2], or from changes in the density structure of the underlying mantle (e.g. [B1R3]). In extensional regimes (such as the Basin and Range province of western North America), vertical faulting can give rise to significant local relief independent of changes in regional elevation. Climatically driven erosional processes amplify large-scale elevation and relief to generate the complex topography observed in many mountainous regions. A network of river valleys provides a ‘skeleton’ on which such topography continually evolves in response to climatic and tectonic drivers. Adjacent to elevated regions, deposition of eroded material in basins generates relatively smooth landscapes. These different landscape regimes (erosional vs. depositional) provide different magnitudes of topographic complexity and relief (Fig. 1).

A major insight in recent decades is that climatic and tectonic processes interact through the evolution of topography. Essentially, changes in the distribution of mass on Earth’s surface resulting from climatically driven erosion can influence the tectonic forces causing mountain uplift and significant topographic adjustment of a region. Moreover, the building of mountainous topography by tectonics influences local, regional, and even global climate (e.g. [B1R4]). Therefore, understanding the topographic history of a region requires integrating records of mountain building, paleoclimate, and erosion rates.

Advances in quantifying topographic change have led to discoveries about Earth’s topographic history and rates of topographic change. Reconstructions of past elevations of a region, e.g., from stable isotope paleoaltimetry, are able to detect changes in elevation more precisely than absolute elevations [B1R5]. Estimating rates of erosion and topographic change with thermochronology [B1R6] or numerical landscape models [B1R7] provides ways to test ideas about the relative contributions of tectonics and climate as drivers of topographic change.
Advances in biological and geological inquiries provide an opportunity for a transformative recognition of the interactions of the atmosphere, geosphere, and biosphere. The richness of biosphere - landscape interactions, from biological influences on erosion to topographic influences on evolutionary processes, provides new insights into an integrated-systems view of Earth processes and history.

Figure 1. Landscape-evolution model (B1R8) for an 8-million-year simulation. In this model, half of the domain is undergoing active tectonic uplift (at 0.5 mm per yr), while the other half is subsiding at a rate significantly lower than the uplift. Output is shown for the initial model set-up (A), at 4 million years (B), and at 8 million years (C) of model simulation time. As part of the landscape becomes uplifted, climate-driven processes of erosion, sediment transport, and deposition are modeled with established geomorphic principles. Bedrock erosion dominates in the Active region as the landscape steepens from sustained uplift, leading to development of complex topography. Sediment deposition dominates in the Passive region, leading to a smoother landscape.

Box 1 References

Active tectonic uplift and erosion
Deposition and subsidence

Time = 0

Time = 4 My

Time = 8 My
Box 2. Diversification models

Combining data from extant and fossil taxa will be critical for evaluating diversification processes—speciation, extinction, and immigration—within the context of dynamic landscape histories. Diversification rates can be quantified from time-calibrated phylogenetic trees [1] or from fossil species-occurrence data [2]. The generation of large molecular, paleontological, and ecomorphological datasets and their integration with comparative methods makes understanding the history of diversity patterns such as the topographic diversity gradient a tractable prospect.

Here we present three theoretically plausible models for generating a topographic diversity gradient and describe tests from the present-day and fossil records to evaluate them. Extinction rate is constant over time or space in these models; however, variable extinction rates could be tested.

(A) Mountains as cradle Speciation rate is stochastically constant but elevated in the tectonically active region (AR) compared to the tectonically passive region (PR).

*Present-day (phylogenetic) test:* Instantaneous rates of speciation for extant taxa are higher in the AR than in the PR.

*Fossil (occurrence-based) test:* Speciation rates are consistently higher in the AR.

(B) Tectonic pulse Speciation rate is elevated during an interval of tectonic activity in the AR, but remains constant in the PR.
Present-day test: Increase in older branching events during the tectonic pulse. A speciation rate slow-down may appear for extant AR lineages, while rates remain low and time-invariant in the PR.

Fossil test: Speciation rates increase in the AR but not in the PR during the tectonic pulse.

(C) Climate-driven immigration During global warming, immigration into the AR increases.

Present-day test: In likelihood-based biogeographic methods (Lagrange, BioGeoBEARS), model comparison could be used to infer increased immigration rates during certain time periods using a time-stratified analysis.

Fossil test: Distinguishing immigration and speciation events in the fossil record is difficult. Fossil taxa can be integrated into BioGeoBEARS as tips or direct ancestors. Alternatively, fossil coverage over large geographic regions offers the potential to track the geographic distribution of lineages and resolve these distinctions.

Ecomorphological and geographic data can be mapped onto clade history to reconstruct evolutionary and biogeographic processes [3]. For example, state-dependent speciation/extinction (SSE) models offer potential for the comparative study of regional diversification. In SSE models, speciation or extinction rate can vary as a function of a character state (or geographic region) that itself is evolving on the tree [4]. The complexity and flexibility of SSE models also raise challenges [5], with some already being addressed [6-7].
Box 2, Figure 1 caption

Three theoretically plausible models (A-C) for generating the topographic diversity gradient of rodents in North America over the Cenozoic. Simulated phylogenies for the Active (blue) and Passive (red) regions for each model are shown in the upper panel, with corresponding lineage-through-time (LTT) plots in the lower panel. The timing of speciation (B) and immigration (C) rate shifts is indicated by gray bars. See box text for descriptions of each model and tests for evaluating model fit to the North American rodent record.
Box 3. Paleoecological information from the continental fossil record

North American rodents possess an array of dietary and locomotor specializations reflecting variation in diet, substrate use, and habitat selection (Samuels and Van Valkenburgh 2008, Samuels 2009). Below we summarize major paleoecological approaches to reconstruct mammalian diet and terrestrial vegetation. Integrating these data—from individuals, populations, and species—allows hypothesis testing about the effects of landscape and resource changes on ecological diversification over time.

(A) **Hypsodonty index**

High tooth crowns (hypsodonty) in mammals represent evolved responses to physical properties of diet, such as abrasive or tough plant matter and exogenous grit (dust) common in arid environments (Williams and Kay 2001, Damuth and Janis 2011). Herbivorous rodents and open-habitat specialists typically display high-crowned teeth, reflecting relative openness (or grass dominance) of habitats (Jardine et al. 2012).

(B) **Dental microwear textures**

Microscopic wear on teeth results from processing of foods consumed shortly before death (Walker et al. 1978). Dental microwear texture analysis differentiates between tough and hard-object consumption using scale-sensitive fractal analysis (Scott et al. 2005, DeSantis 2016). While studies of habitat change have often focused on large mammals, this approach can potentially resolve small mammal dietary ecology, habitat, or local substrate (Caporale and Ungar 2016).
(C) 2-D and 3-D tooth morphology

Shape analysis using geometric morphometrics relies on 2-D or 3-D Cartesian coordinates of morphological structures, independent from size variation or \textit{a priori} chosen traits (Zelditch et al. 2012). This approach has been used to quantify dental shape change along environmental gradients and through the evolution of small-mammal lineages (Polly 2003, McGuire 2010, Kimura et al. 2013). Digital indices of high-resolution 3-D tooth surfaces (e.g., orientation-patch count, relief index) present alternative ways to measure tooth shape and discriminate dietary categories (granivore, folivore, omnivore, insectivore) in extant and fossil small mammals (Evans et al. 2007, Wilson et al. 2012).

(D) Stable isotopes

Stable carbon isotopes of mammalian tooth enamel reflect the isotopic composition of the diet, with $\sim 11\%$ enrichment for small mammals (Podelsak et al. 2008). Carbon isotopes record differences in vegetation composition (e.g., $\% C_4$ plants in diet) and habitat structure (e.g., canopy height) (Koch 1998, Cerling et al. 2007). Oxygen isotopes reflect temperature, precipitation, and water use (Dansgaard 1964, Kohn 1996). Isotopic analyses of small-mammal teeth using laser-ablation and -fluorination sampling techniques help infer ecological interactions and document fine-scale habitat variation (Passey and Cerling 2006, Grimes et al. 2008).

Phytoliths (see Fig. 3)
Phytoliths are microscopic silica bodies in plant tissues and often preserve in paleosols and fluvial sediments associated with mammalian fossils (Piperno 2006, Strömberg 2002). Phytolith assemblage analysis provides information about vegetation structure and grass community composition (Fig. 3; Strömberg 2004, Dunn et al. 2015). Reflecting mainly local vegetation (Piperno 1988), phytolith assemblages indicate spatial heterogeneity in vegetation relevant for small-mammal ecology and evolution.

Box 3, Figure 1 caption
Approaches for inferring species ecology. (A) Illustration of tooth-crown categories from left (low-crowned) to right (high-crowned): brachyodont, mesodont, hypsodont, and hypselodont (ever-growing). (B) Image from dental microwear texture analysis, with relief on the enamel surface false colored to illustrate various microwear features. (C) 3-D image of rodent tooth shape captured by high-resolution X-ray computed microtopography and quantified based on surface curvature. (D) Carbon isotopic composition and inferred percent C₄ vegetation in the diets of modern rodents from Nebraska (solid symbols, left panel) and fossil rodents from the Big Springs Gravel (Nebraska) at ca. 2.4 Ma (open symbols, right panel). Symbols refer to rodent families, including Cricetidae (diamonds), Heteromyidae (triangles), Sciuridae (inverted triangle), and Geomyidae (circles). Rodent isotopic values have been adjusted by the appropriate enrichment factor and by changes in the isotopic composition of atmospheric CO₂ to be comparable to mean C₃ (small dash) and C₄ (long dash) vegetation values.
Box 4. Outstanding questions

Hotspots over geological time: Do biodiversity hotspots form around centers of active tectonism?

At continental and regional scales, mammal diversity hotspots are centered on relatively young mountains [4,24]. Greater geographic coverage and temporal resolution of both geological and paleontological data will facilitate understanding the shifting geography and magnitude of biodiversity hotspots in the past (e.g., [52]). In particular, we can begin to evaluate the relative contributions of geographic-range shifts versus in situ speciation to past diversity peaks.

Integrating fossils and molecular data: Do macroevolutionary processes inferred from the fossil record and extant taxa yield similar diversification histories in relation to the development of topographic complexity?

The geographic distribution and temporal range of fossil and extant lineages offers complementary information about the tempo and mode of diversification [40,44,58,80]. Integrating fossil taxa into phylogenies, not just as calibration points but as informative tip taxa with associated morphological, ecological and geographic data [81,89], has great potential to constrain biogeographic hypotheses about the origin and maintenance of diversity gradients.

Taxonomic and ecological diversity: How does the topographic diversity gradient correspond to gradients in ecological diversity?
Connecting diversification processes to phenotypic divergence and adaptive evolution in association with landscape history requires data from modern and fossil biotas [46,81]. Linking patterns of functional diversity and species diversity in tectonic, climatic, phylogenetic, and community contexts should reveal how landscape history influences adaptive and non-adaptive radiations [37].

Conservation in montane ecosystems: Which taxonomic and functional groups are most vulnerable to changes in climate and habitat connectivity in topographically complex regions today?

Paleontological analyses can help detect those species most at risk given impending climate change by demonstrating their vulnerability to environmental changes through time [25,61]. These insights will contribute to more informed strategies for protecting landscape diversity for the sake of biodiversity.