Published in final edited form as:
Trends Ecol Evol. 2017 March ; 32(3): 211–226. doi:10.1016/j.tree.2016.12.010.

Biodiversity and Topographic Complexity: Modern and Geohistorical Perspectives

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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

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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** (see Glossary), such as large mountain ranges and deeply dissected plateaus. Mammals, birds, and flowering plants 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 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, how processes interact, or whether different geographic and geohistorical manifestations of each kind of gradient emerge from a common cause.

In this review, we focus on changes in taxonomic and ecological diversity that accompany gradients in topographic complexity. These topographic diversity gradients result from interactions among biogeographic, geomorphological, and climatic processes [4,5]. Biogeographic processes (speciation, extinction, and immigration) generate the taxonomic and functional diversity of species and their dynamic patchwork of geographic ranges. Species traits, biotic interactions, and range distributions are influenced by topography, which in turn is shaped by geomorphological processes at local, regional, and plate-tectonic scales. The creation of topographic complexity (Box 1) steepens climatic gradients, while increasing habitat heterogeneity and surface area within montane regions [6,7]. Earth's dynamic climate system may enhance or reduce 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 include many of the world's diversity hotspots today, harboring a high proportion of species vulnerable to extinction [8]. Thus, these regions have high conservation value, especially in light of habitat conversion and climate change.

Integrating Landscape and Biogeographic History: Major Questions

Topographic diversity gradients can result from the generation of new species or the accumulation of species via dispersal into an environmentally complex region. Different rates of biogeographic processes can strengthen or weaken a topographic diversity gradient (Box 2). For example, over time, higher speciation rates in a tectonically active, montane region could generate more species in the montane region compared to lowlands (Box 2, Figure 1A), or a brief pulse of accelerated speciation in response to increasing topographic complexity could increase diversity within the montane region rapidly (Box 2, Figure 1B). Alternatively, climatic warming could stimulate geographic-range shifts to higher elevations, where immigrants and residents could speciate more rapidly than in adjacent lowlands (Box 2, Figure 1C).

Testing hypotheses about how topographic diversity gradients arise, persist, or diminish requires demonstrating precise coincidence and interaction in time and space between causal factors and biogeographic responses. Robust analyses are possible only with a synthesis of geological and biological data. Within our analytical framework, four kinds of modern and historical data are evaluated systematically to address pertinent questions associated with each.

(i) Landscape history: Tectonically driven uplift interacting with climatically driven erosion produces topography and relief (Box 1, [9,10]). The timing of changes in topographic complexity provides the spatiotemporal context for testing models of diversification within mountain ranges compared to adjacent lowlands. Although the broad outlines of Earth's tectonic and climatic history over the past ~200 Ma are well known, the determination of paleo-elevation, relief, and topographic complexity over spatial scales of 10–100 km lies at the frontiers of geological research (e.g., [11–13]). Pertinent questions are 'When did topographic complexity arise?' and 'How have changes in elevation and relief altered environmental gradients over time?'

(ii) Diversification history: The net outcome of speciation and extinction of lineages determines the diversification history of a group across regions of different topographic complexity. Changes in species composition along elevational gradients in different mountain ranges today permit us to evaluate the environmental factors and ecological interactions that maintain 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. Both fossil and modern data are crucial for reconstructing diversification history and identifying processes that generate diversity, since neither data set in isolation can fully reveal both pattern and process [14].

The fossil record documents taxonomic and morphological diversity in space and time, along with ecological traits in lineages and communities. A dense regional fossil record provides evidence for past geographic distributions, spatial turnover, and landscape barriers and connectivity. Phylogenetic patterns specify a historical sequence of trait acquisition, loss, or transformation and point to regions and clades with young and old endemic lineages. If montane uplift stimulates speciation, then phylogenies should record a pulse of branching events whose timing matches the onset of uplift. While phylogenies based on extant species might record such pulses (e.g., [15]), phylogenies that combine extant and fossil data, especially the latter for extinct lineages, provide more robust estimates of patterns and timing of major events. Pertinent questions include ‘Which species ranges were fragmented by barriers resulting from montane uplift or rifting?’, ‘Is the montane region a source of new species over long periods of time?’, and ‘Does topographic complexity leave a signature of divergence in phylogenies?’

(iii) Spatial dynamics: The current 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 into a geohistorical context is fundamentally important, however, since most species ranges have moved 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 again, neither modern nor geohistorical data alone can fully capture the role of spatial dynamics in generating and maintaining diversity gradients. However, when integrated, both data sources can significantly advance our understanding. For example, in the context of landscape history, the geography of fossil occurrences combined with the spatial dynamics of species can reveal the degree to which dispersal contributes to changes in diversity and provide evidence of environmental sorting of species ranges along elevational gradients [16]. Pertinent questions are ‘How much does dispersal contribute to diversity in topographically complex regions?’ and ‘How do rates of dispersal change in relation to climatic history?’

(iv) 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 [17–20]. Together, functional and taxonomic diversity reflects changes in community structure that accompany the speciation and extinction history of clades. Comparison of ecological traits in diversifying and disappearing lineages can reveal how environmental filters bias and structure diversity. Fossils contribute data about the timing and geography of trait changes (e.g., [21]). Pertinent questions include ‘Do particular ecological traits predispose a group to proliferate in montane regions?’ and ‘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]. Testing scenarios of different biogeographic processes acting separately and in combination (e.g., Box 2) can clarify the historical consequences of different processes and the phylogenetic and geographic diversity patterns that 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 is the stage on which the biogeographic processes of speciation, extinction, and immigration take place. Persistent landscape barriers and habitat heterogeneity across elevation gradients provide numerous opportunities for fragmenting ranges and isolating populations. Thus, rates of neutral or adaptive divergence among populations and allopatric speciation can be elevated in topographically complex regions. Strong environmental gradients with elevation also provide opportunities 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., [22–25]). A topographic diversity gradient resulting from higher speciation rates (other processes being equal) should feature many **neo-endemic** species and high spatial turnover (beta diversity) in the montane region [26,27]. There, phylogenies should reveal a distribution of species ages skewed toward recent originations. By contrast, adjacent lowlands should have few endemics and a greater proportion of older species.

A small geographic range increases the vulnerability of populations and species to extinction, and geographic ranges are typically smaller in montane regions than in adjacent lowlands [28]. However, complex topography also enhances metapopulation dynamics. Similar habitats in a weakly or sporadically connected patchwork can serve as sources for recolonization following extirpation [29]. Climate change should enhance 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 there and more short-lived species in adjacent lowlands.

Dispersal could also give rise to a topographic diversity gradient if the rate of immigration into the montane region exceeded the rate of emigration to lowlands. Greater habitat heterogeneity in montane regions could facilitate dispersal and colonization by ecologically diverse species, resulting in tighter species packing. With greater immigration, topographically complex regions would feature few endemics and moderate beta diversity in the montane region because of the influx of widespread species. Adjacent lowlands would have few endemics and low beta diversity. Climate changes 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 for plants and mammals [30,31].

Phylogeographic analyses have enabled evaluation of the influences of climate and topography on genetic variation for a wide range of animals and plants [32]. For example, when climatic conditions restrict distributions by limiting habitat availability or connectivity, gene flow among isolated populations should cease and genetic drift should lead to loss of ancestrally shared alleles. Population divergence via this mechanism can be amplified by ecological differences among isolated populations, and more pronounced changes in ecological attributes should occur during episodes of climate change. For Australian arid-region geckos [33] and Southwest Australian Floristic Region plants [34], topographic complexity has been postulated to influence initial population divergence through geographic isolation during Pliocene climate changes. 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 become a barrier or filter to gene flow at different times throughout the evolutionary history of individual taxa [35]. Temporally discordant but spatially concordant vicariant events have been identified for birds isolated by Neotropical mountains and rivers [36], trans-Beringian small mammals [37], and Central American fishes [38].

One frontier of research concerns how selection acts on ecological traits in topographically complex regions. For example, mammalian dietary and habitat generalists have larger geographic ranges [39], yet we do not know if those species exhibit higher speciation rates in topographically complex regions, resulting in multiple distinct species with similar dietary and habitat requirements occupying different regions (e.g., [40]). Tracking ecomorphological differences 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 feature the Cenozoic history of rodents in North America. We highlight rodents for several reasons. As the most species-rich order of mammals, the clade Rodentia exhibits 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 are prominent in the North American fossil record (e.g., Heteromyidae [15,41]; Sciuridae [42]; Mylagualidae [43]). 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, which has been tectonically active throughout the Cenozoic, compared to the Great Plains, which has been tectonically stable over the same period (Figure 1). For convenience, we denote these areas as the active and passive regions, respectively. Today, nearly twice as many rodent species per unit area occur in the active region (Figure 2A). The spatial turnover of species is greater there, and many range boundaries follow major physiographic features (Figure 2B). Using process-based diversification models that incorporate specific aspects of geologic history (e.g., [44,45]), we can evaluate whether the diversification history for clades and regional faunas changed during particular intervals of tectonic or climatic history (Box 2 and Figure 3).

Over the past 30 myr, a highland extending from British Columbia into northern Mexico [46] was pulled apart into fault-bounded mountain ranges and intervening basins (the Basin and Range province), expanding the area by over 200 km from east to west [47]. Uplift in the northern and central Rocky Mountains accentuated elevation gradients, and from the middle to late Miocene, volcanic activity formed the Cascade Range. By 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 climatic drying across North America over the past 30 myr (Figure 3). In the active region, forest indicators comprised over 30% of phytolith assemblages until approximately 17 Ma, then declined as C_4 grasses increased. In the passive region, forest indicators were dominant until about 25 Ma, and grasses dominated thereafter. Increasing proportions of grass (especially C_4 grass) phytoliths indicate that aridification 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 (Figure 3). Over the past 34 myr, rodent diversity fluctuated substantially in both the active and passive regions, with higher diversity in one or the other region at different times. Two diversity peaks coincided with warm intervals – the **Miocene Climatic Optimum** (MCO) from 17 to 14 Ma and the Pliocene warm period from 4.0 to 2.5 Ma.

In addition to changes in species diversity, some intervals showed substantial change in taxonomic composition of regional faunas [48]. Within the active region, the number and proportion of rodent species per family changed markedly during the MCO in the Pacific Northwest and the northern Rocky Mountains, and entire families appeared or disappeared. 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, faunas of individual tectonic provinces experienced increase in diversity and high spatial turnover during the middle Miocene. In the passive region, faunal composition had more taxonomic continuity over time despite high volatility. The proportion of species with different tooth-crown heights (Box 3) changed in parallel in the active and passive regions, tracking changes in vegetation composition (Figure 3).

In relation to the scenarios of Box 2, the North American rodent record does not match the mountains-as-cradle model (Box 2, Figure 1A), since diversity was lower in the active region than in the passive region for millions of years (Figure 3). Likewise, the record does not match a mountains-as-museum model (not pictured), since mean species durations in the active and passive regions did not differ [49]. North American rodent diversity does match the tectonic-pulse model (Box 2, Figure 1B) during the MCO, when high diversity in the active region coincided with an interval of increasing topographic complexity [48]. 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. In accord with the climatic-pulse model (Box 2, Figure 1C), more geographic-range shifts and expansions occurred between 16 and 14 Ma within the active region and between the passive and active regions than earlier or later in the Miocene [48]. The Pliocene peak in rodent diversity within the active and passive regions also fits this model, since warming should stimulate geographic-range shifts into both regions. More elaborate scenarios, such as speciation following range expansion along specific dispersal routes (e.g., [50]), can also be tested.

Complementing the fossil record, phylogenetic and phylogeographic analyses also document evolutionary responses of North American rodents to changes in topographic complexity.

Deep branching events among genus-level clades of heteromyids (kangaroo rats and pocket mice) occurred during the middle Miocene [15], 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 in southern Idaho [51]. Among chipmunks (Sciuridae), distinct phylogeographic lineages in the yellow-pine chipmunk, *Tamias amoenus*, with divergence ages estimated at several million years or more, occupy different mountain ranges in the Pacific Northwest and northern Rocky Mountains [52]. Across the passive region, the phylogeographic structure of the eastern chipmunk, *Tamias striatus*, indicates population expansion over much of eastern North America from glacial refugia south of the Wisconsinan ice sheet [53].

Topographic Complexity and High Diversity in Other Systems

Beyond North American rodents, neontological and paleontological insights illuminate the powerful influence of topographic complexity in other groups and contexts.

i. 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 intermontane west [54]. Large rivers, high fluvial connectivity, low stream gradients, warm temperatures, and high precipitation in Appalachian headwaters of the Mississippi Basin support the highest species diversity, whereas short, high-gradient rivers with low connectivity and seasonal discharge in the montane west support lower diversity by an order of magnitude. Speciation rates estimated for six family-level clades with good Cenozoic fossil records across North America did not differ between eastern and western lineages; however, extinction rates were higher for western lineages, associated with tectonic fragmentation of the landscape and numerous montane barriers to recolonization.

ii. Where the Pacific, Australian, and Eurasian tectonic plates meet, 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 [55]. Strong depth gradients, complex ocean currents, and large islands provide high habitat diversity and barriers to dispersal, even for many species with plankto-trophic larvae. The Cenozoic fossil record of corals, foraminifera, and mollusks documents increasing local and regional diversity between 25 and 23 Ma, as converging Australian, Eurasian, and Pacific plates constricted deep circulation between the Western Pacific and Indian oceans [56] 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 [57]. As plate collisions produced large expanses of shallow habitats fragmented by islands and peninsulas, topographic complexity increased and each diversity hotspot grew.

iii. Of the approximately 12 500 tree species in Amazonia today [58], the highest local diversity occurs in western Amazonia and the equatorial Andes [59,60]. Pollen and plant macrofossils [61] indicate that rainforest was present throughout the Cenozoic, although the exceptionally high local and regional diversity dates from the early Miocene. The rising Andes [62] promoted allopatric speciation in lowlands and ecological speciation along expanding orographic gradients [23]. Deep river valleys and steep gradients in slope, soils, and microclimates contributed to high endemism [59]. For most of the Miocene, an extensive wetland east of the rising Andes presented a barrier to lowland plant distributions. Fossils from this wetland document changes in floral and faunal diversity and composition over the Neogene [63]. Along the eastern Andes, 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 [64].

Implications for Conservation

Understanding the ecological and evolutionary drivers of diversity gradients in different landscapes can help guide conservation strategies. 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]. Using the geologic record, we can develop strategies for conserving such landscapes where diversity is actively generated on evolutionary timescales [27,66]. Likewise, the geohistorical approach adds to the growing body of literature characterizing potential climatic refugia under global warming [67,68]. A critical goal of landscape-scale conservation is to establish connectivity among natural areas, promoting dispersal across anthropogenically altered regions [69–71]. By identifying where turnover occurred when climates changed in the past, the record of past diversity and landscape history can reveal climatic gradients where species were prone to move and thereby identify these landscapes as conservation targets for the future. Together, neontological and paleontological analyses can also reveal individual species that are most vulnerable to environmental change [72,73] based on their ecological traits.

Concluding Remarks

To understand the biogeographic and geohistorical processes that shape topographic diversity gradients, four kinds of data must be integrated: landscape history, diversification history, the spatial dynamics of species and biotas, and ecological traits in relation to changing environmental gradients. The paleontological and modern records of species distributions, their ecology, and their phylogenetic relationships over space and time are fundamental to this research framework. Since topographically complex regions are experiencing rapid changes in climate and habitats today, there is unprecedented urgency to understand the processes that generate and maintain diversity in these regions (see Outstanding Questions).

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.

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 mya, when global climate was warmer, 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 today, 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, 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, or large subsiding areas (such as the East African rift system)

Topographic diversity gradient

a spatial gradient over tens to hundreds of kilometers in which species diversity per unit area is high in areas of complex topography, such as entire mountain ranges and regions with mountains and intervening basins, and low in adjacent lowlands or plains

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

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Box 1

Generation of Complex Topography

Topography results from the interactions among tectonics, climate, and erosion. Tectonic processes in Earth's crust and mantle produce high-elevation landscapes, and together with erosion and surface uplift generate relief at large spatial scales ($\geq 10^2$ km) (e.g., [9]). At convergent plate margins, high surface elevations and relief result either from thickening of the crust, which increases elevation by isostasy [81], or from changes in the density structure of the underlying mantle (e.g., [82]). 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 montane regions. A network of river valleys provides a 'skeleton' on which such topography evolves in response to climatic and tectonic drivers. Adjacent to elevated regions, deposition of eroded material in basins generates relatively smooth landscapes. Erosional and depositional landscape regimes provide different magnitudes of topographic complexity and relief (Figure I).

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., [83]). 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 its rates of change. Reconstructions of past elevations of a region, for example, 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 [84] provides ways to test ideas about the relative contributions of tectonics and climate as drivers of changing landscape topography.

Advances in biological and geological inquiries have initiated a transformative recognition of the interactions among 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.

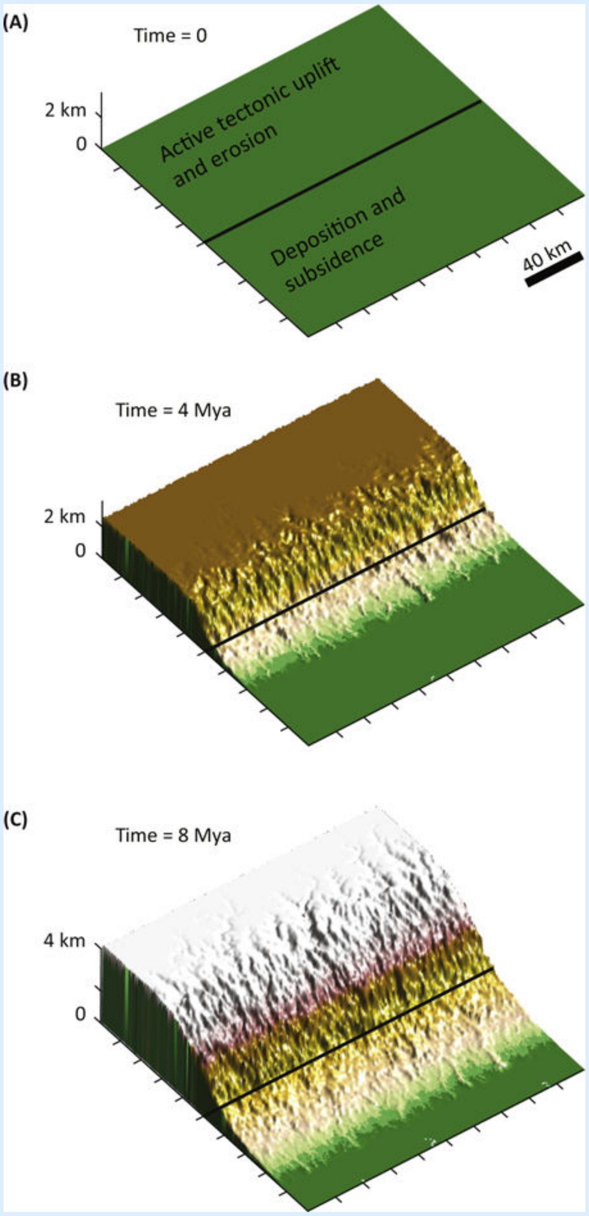

Figure I. Landscape-Evolution Model [85] for an 8-Million Year Simulation

In this model, half of the domain is underdoing active tectonic uplift (at 0.5 mm/year), while the other half is subsiding at a rate significantly lower than the uplift. Output is shown for (A) the initial model setup, (B) at 4 million years, and (C) at 8 million years of simulated 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 tectonically active region as the landscape steepens from sustained uplift, leading to development of complex topography. Sediment deposition dominates in the tectonically passive region, leading to a smoother landscape.

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 [86] or from fossil species-occurrence data [45,49]. The generation of large molecular, paleontological, and ecomorphological data sets 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 (Figure I) and describe tests from the present-day and fossil records to evaluate them. The extinction rate is constant over time or space in these models; variable extinction rates can also be tested.

(i) 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.

(ii) 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, whereas 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.

(iii) 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 evaluate 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 (Figure I).

Ecomorphological and geographic data can be mapped onto clade history to reconstruct evolutionary and biogeographic processes [87]. For example, state-dependent speciation/extinction (SSE) models enable the comparative analysis of regional diversification histories. 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 [88]. The complexity and flexibility of SSE models also raise challenges [89,90], with some already being addressed [50,91].

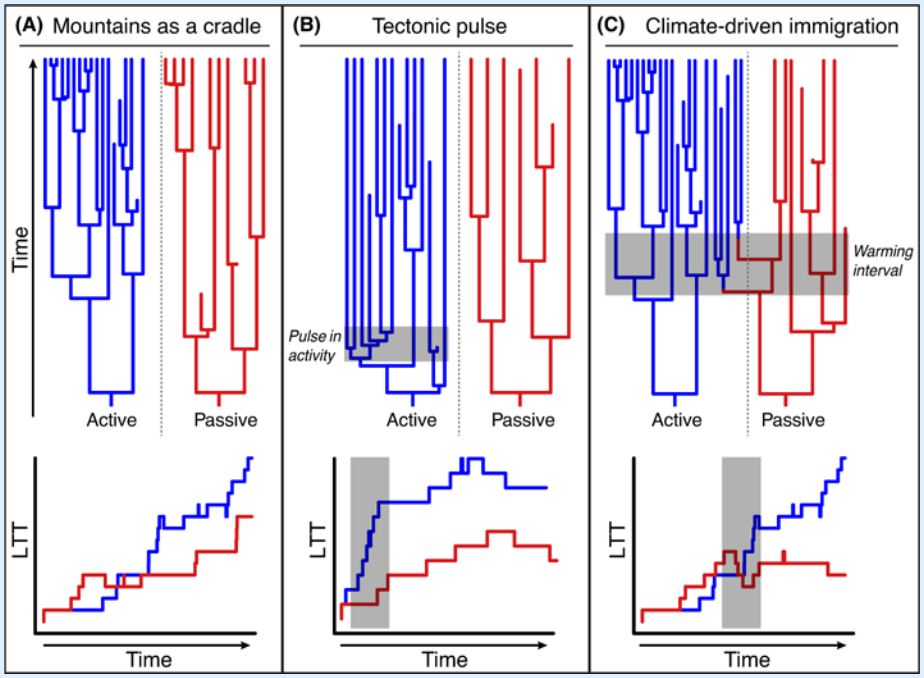

Figure I. Three Plausible Models (A–C) for Generating a Topographic Diversity Gradient

For each model, simulated phylogenies for the tectonically active (blue) and passive (red) regions 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.

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., [92]). Below we highlight major paleoecological approaches for reconstructing mammalian diet and terrestrial vegetation (Figure I). Integrating these data – from individuals, populations, and species – allows us to test hypotheses about the effects of landscape and resource changes on ecological diversification over time.

i. 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 [18]. Herbivorous rodents and open-habitat specialists typically display high-crowned teeth, reflecting relative openness (or grass dominance) of habitats through time [21].

ii. Dental microwear textures: Microscopic wear patterns on teeth result from processing of foods consumed shortly before death [93]. Dental microwear texture analysis differentiates between tough and hard-object consumption using scale-sensitive fractal analysis [94]. Although studies of mammalian responses to habitat changes have often focused on large mammals, this approach can potentially reveal small-mammal dietary ecology, habitat, or local substrate.

iii. 2D and 3D tooth morphology: Shape analysis using geometric morphometrics relies on 2D or 3D Cartesian coordinates of morphological structures, independent of size variation or *a priori* chosen traits [40]. This approach has been used to quantify dental shape change along environmental gradients and through the evolution of small-mammal lineages [19,95]. Digital indices of high-resolution 3D tooth surfaces (e.g., orientation-patch count, relief index) offer different ways to measure tooth shape and discriminate among dietary categories (e.g., granivore, folivore, omnivore, insectivore) in extant and fossil small mammals [96].

iv. Stable isotopes: Stable carbon isotopes of mammalian tooth enamel reflect the isotopic composition of the diet, with approximately 11m enrichment for small mammals [97]. Carbon isotopes record differences in vegetation composition (e.g., %C_4 plants in diet) and habitat structure (e.g., canopy height), while oxygen isotopes reflect temperature, precipitation, and water use [98]. Isotopic analyses of small-mammal teeth using laser-ablation and laser-fluorination sampling techniques are one means to infer ecological interactions and fine-scale habitat variation [99,100].

Phytoliths: Phytoliths (see Figure 3 in main text) are microscopic silica bodies in plant tissues and are often preserved in paleosols and fluvial sediments associated with mammalian fossils [77]. Phytolith assemblage analysis provides information about vegetation structure and grass composition [78–80]. Reflecting mainly local vegetation, phytoliths are indicative of spatial heterogeneity in vegetation relevant for small-mammal ecology and evolution.

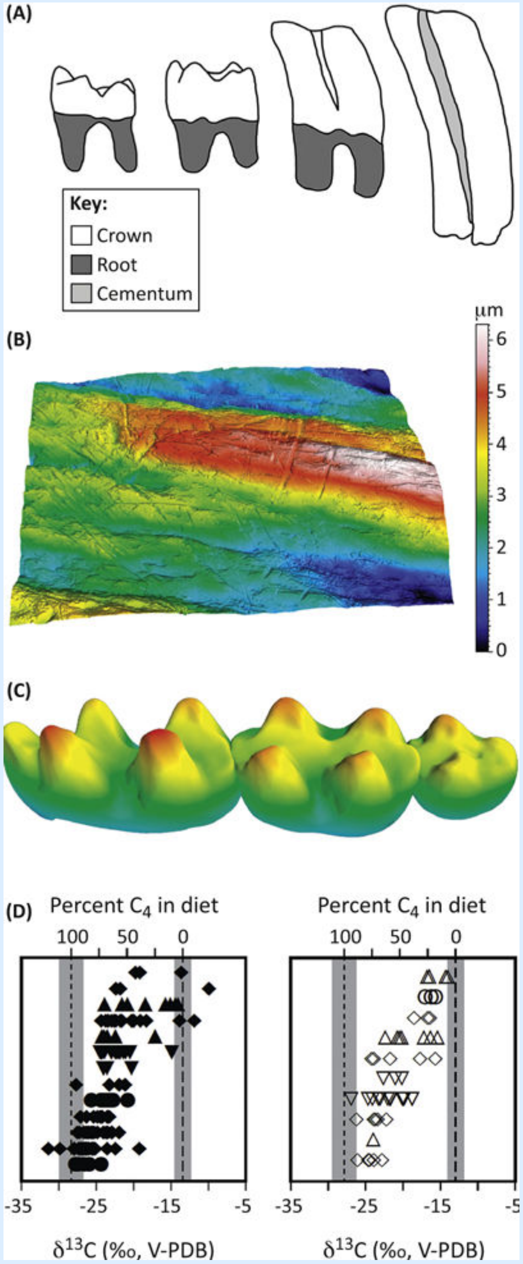

Figure I. Approaches for Inferring Species Diets

(A) Illustration of tooth-crown categories from left (low crowned) to right (high crowned): brachydont, mesodont, hypsodont, and hypselodont (ever growing). (B) Dental microwear texture analysis of a gopher (*Thomomys bottae*) incisor with false-colored relief on the enamel surface to illustrate texture roughness and orientation. (C) 3D 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 (filled symbols, left panel) and fossil rodents from the Big Springs Gravel locality at approximately 2.4 Ma (open symbols, right panel). Different symbols refer to rodent families: Cricetidae (diamonds), Heteromyidae (triangles), Sciuridae (inverted triangles), and Geomyidae (circles). Rodent isotopic values have been adjusted by the appropriate enrichment factor and by changes in the isotopic composition of atmospheric CO_2 to be comparable to mean C_3 (short dash) and C_4 (long dash) vegetation values.

Trends

Topographically complex regions today feature high taxonomic and ecological diversity.

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

Paleontological and modern data are crucial to understand topographic diversity gradients.

Topographically complex regions have high conservation value.

Outstanding Questions

Hotspots over geological time: Do biodiversity hotspots form around centers of active tectonism? At continental and regional scales, mammal diversity hot-spots are centered on geologically young mountain ranges [4,27]. Greater geographic coverage and temporal resolution of both geological and pale-ontological data will facilitate understanding of the shifting geography and magnitude of biodiversity hotspots in the past (e.g., [57]). 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 from 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 [42,45,49,63]. Integrating fossil taxa into phylogenies, not just as calibration points but as informative tip taxa with associated morphological, ecological, and geographic data [14,87,95], has great potential to test 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 [51,87]. Linking patterns of functional diversity and species diversity in tectonic, climatic, phylogenetic, and community contexts should reveal how landscape history influences adaptive and nonadaptive radiations [40].

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 identify those species most at risk, given impending climate change, by demonstrating their vulnerability to environmental changes over time [28,72]. These insights will inform strategies for protecting landscapes that support unique diversity as well as ecological and evolutionary processes.

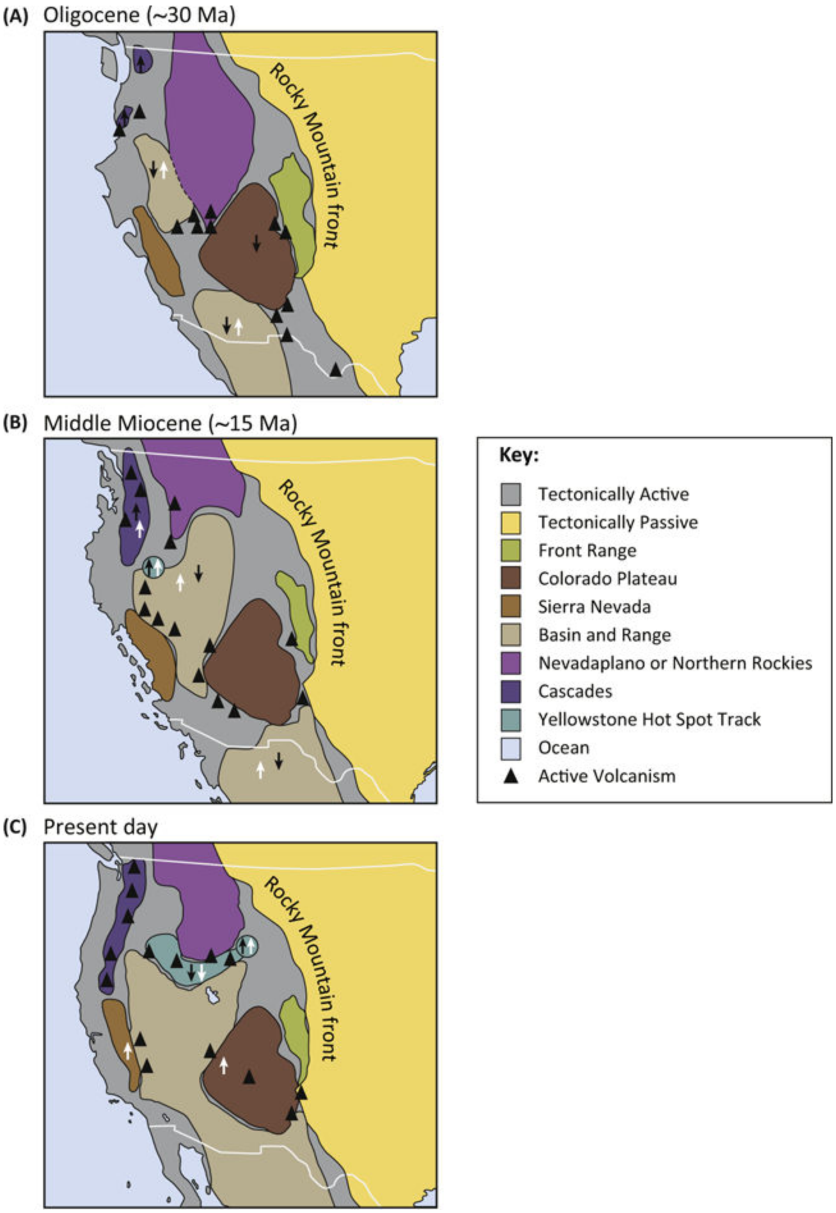

Figure 1. Geologic History of Western North America

Three representative time slices are based on information from [46,47,74]. The **tectonically active region** (gray shading) consists of several tectonic provinces that have changed in size, elevation, and relief over the past 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 breaking up into the Basin and Range. (B) At 15 Ma, in the Middle Miocene, the Basin and Range province was expanding rapidly and had greater relief than at 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.

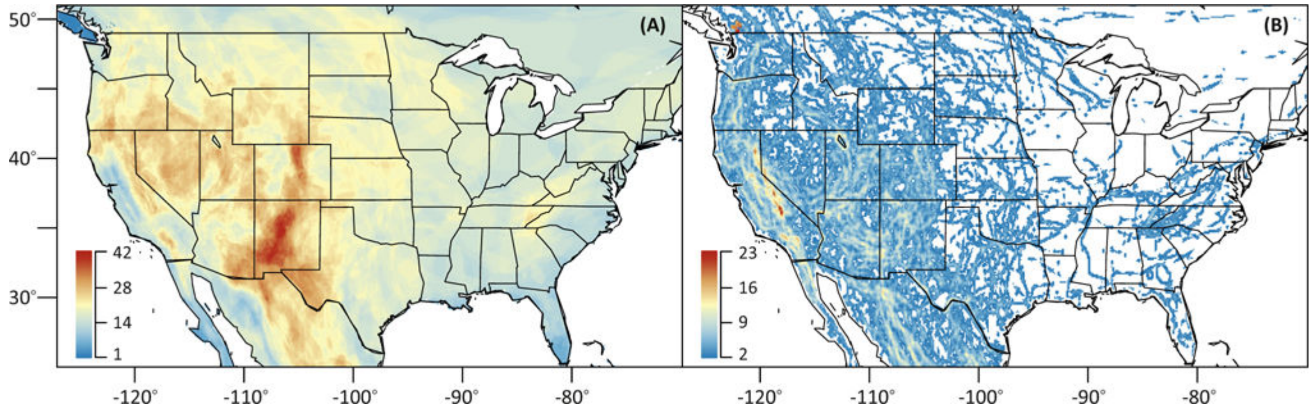

Figure 2. Present-Day Diversity of Rodents of North America at Midlatitudes

Diversity is based on species ranges in NatureServe [75], compiled at a resolution of 0.1°. (A) Species density of rodents. (B) Distribution of overlapping range boundaries for two or more species. Both species density and spatial turnover are greater in the tectonically active region than in the passive region today.

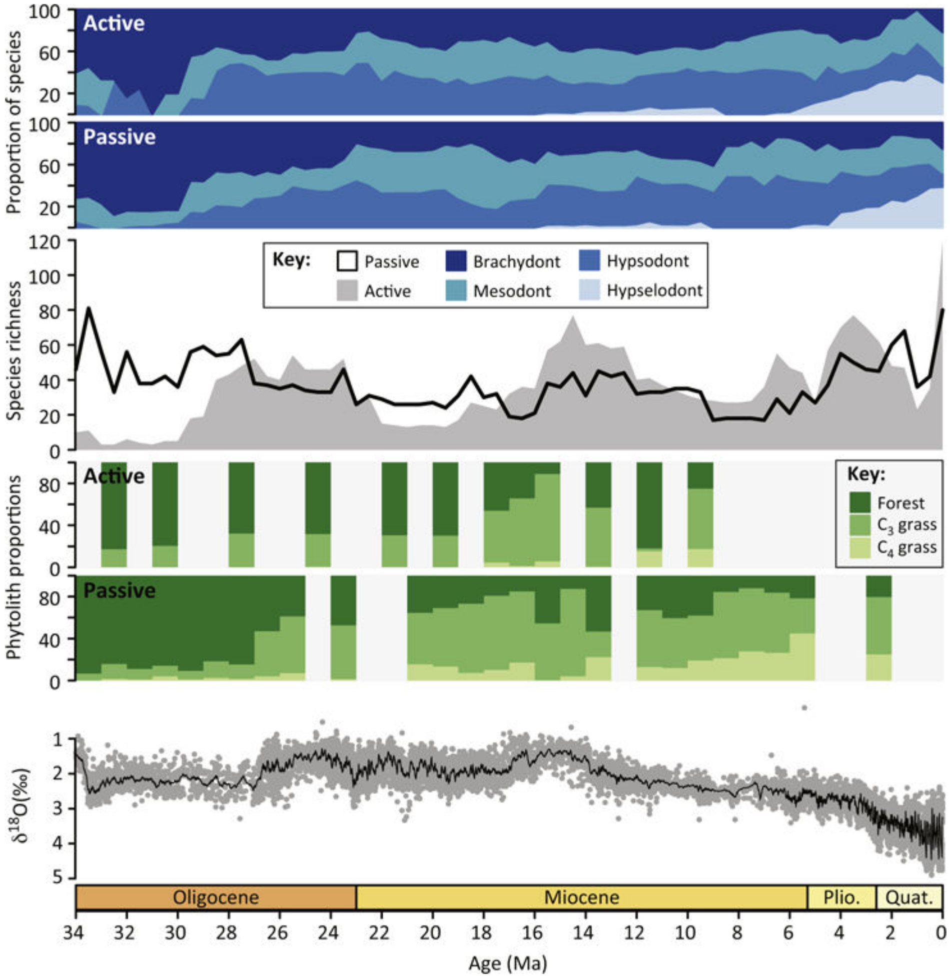

Figure 3. Climatic and Biotic Changes in North America over the Past 35 myr

The global temperature trend is from the benthic foraminiferal oxygen-isotope record (data from [76]). Notable warming during the Middle Miocene was followed by long-term cooling and Quaternary glacial 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 [77–80]). Although both regions exhibited a Neogene increase in grasses, the decline of forest ecosystems occurred earlier in the passive region. Between 34 and 28 Ma, 22 and 18 Ma, and 2 and 1 Ma, rodent diversity was higher in the passive than in the active region, whereas from 17 to 13 Ma, 7 to 5 Ma, and 5 to 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 coincided with changes in faunal composition [48,49]. Corresponding changes in dietary ecology are demonstrated by the increase in high-crowned species (hypsodont and hypselodont) toward the present day (data from J.X.S.). This increase preceded the expansion of grasslands in both regions, suggesting that adaptation to more abrasive diets was initially driven by volcanic ash in soils or grit on plants rather than increased consumption of grass.