

Tectonics, topography, and mammalian diversity

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Terrestrial vertebrates show striking changes in species richness across topographic gradients. For mammals, nearly twice as many species per unit area occur in topographically complex regions as in adjacent lowlands. The geological context of this pervasive biogeographic pattern suggests that tectonic processes have a first-order impact on regional diversity.

I evaluate ecological, evolutionary, and historical influences of tectonics and topography on the regional diversity of terrestrial mammals, focusing on the hypothesis that diversification rates are higher in active versus passive tectonic settings. Ten predictions follow from this hypothesis. 1) The timing of peaks in speciation should be congruent with the timescale for tectonic episodes. 2) The rates of speciation and genetic differentiation of populations should be greater for species inhabiting topographically complex regions than spatially continuous landscapes. 3) If topographic complexity per se promotes diversification, then a cluster of young divergences should occur for montane species compared to lowland relatives. 4) Endemism in tectonically active regions should reflect origination within the region rather than range reduction from larger areas. 5) Extinction rates should differ for lineages in tectonically active regions compared to adjacent lowlands. 6) The relationship between local and regional species richness should differ between topographic settings because of higher beta diversity in topographically complex regions. 7) Species originating in topographically complex regions should colonize adjacent lowlands more often than the reverse pattern. 8) North-south mountain ranges should have higher regional species richness than east-west mountain ranges. 9) Areas with multiple mountain ranges should have higher regional species richness than comparable areas with single mountain ranges. 10) Global climate changes should affect diversification in tectonically active regions. Research addressing these topics places elevational diversity gradients into a geohistorical context and integrates data from modern biotas and the fossil record.

One of the most striking patterns in biogeography is the high species richness of terrestrial vertebrates in topographically complex regions compared to adjacent regions of low relief. The pattern involves both the accumulation and spatial turnover of species along steep elevational and environmental gradients, resulting in high regional species richness. The association between complex topography and high species richness has been documented for many groups of terrestrial vertebrates (mammals, birds, amphibians) and vascular plants, as well as for different continental regions (Qian and Ricklefs 2008). The geological context of this diversity pattern suggests that tectonic and associated erosional processes, which create gradients in topographic complexity, have a first-order impact on regional diversity.

In this paper, I evaluate the potential causes of elevated richness of terrestrial mammals in areas of high versus low topographic complexity resulting from different tectonic histories, with data from modern and fossil mammalian faunas and lineages. I review ecological, evolutionary, and historical processes that could determine the major features of the general pattern. In particular, I focus on the hypothesis that evolutionary processes affecting speciation, extinction, dispersal, and adaptation differ in active versus

passive tectonic settings. Several predictions that follow from this hypothesis are evaluated in light of current data and suggest directions for new research.

Background

Mountainous regions are well known to harbor greater species richness than adjacent lowland areas for many groups and regions, resulting in spectacular diversity hotspots for terrestrial vertebrates (Humboldt 1805, Simpson 1964, Rahbek and Graves 2001, Sechrest et al. 2002, Grenyer et al. 2006, Wiens et al. 2007, Thomas et al. 2008). Increasing topographic complexity creates new habitat, enlarges environmental gradients, establishes barriers to dispersal, and isolates populations, potentially contributing to adaptation to new environmental conditions and speciation in excess of extinction for terrestrial organisms. For freshwater fishes, topographic complexity reduces habitat area and connectedness and results in elevated extinction rates (Smith et al. pers. comm.). Although this idea has old roots (Simpson 1964, Cracraft 1985, Moritz et al. 2000, Brown 2001), it has received far

less attention than latitude and the associated environmental and historical correlates in relation to taxonomic and ecological diversity; and predictions associated with the influence of topography remain to be adequately tested.

For mammals, the association of high species richness with regions of complex topography has been documented on several continents. In the first continent-wide analysis of mammalian biogeography, Simpson (1964) highlighted latitudinal and longitudinal gradients in species density of extant North American mammals. The longitudinal gradient follows topographic complexity (Fig. 1). Simpson (1964, p. 69) noted that “where there are latitudinal gradients, these are additive with topographic gradients, the two accounting for most of the pattern”. Kerr and Packer (1997) documented the predictive power of topography, interpreted as a surrogate for habitat heterogeneity,

on species density of North American mammals. Badgley and Fox (2000) showed that climatic and topographic variables predict most of the variation in both species density and ecological structure of North American mammals. South American mammals also show a strong longitudinal gradient: species density across the Andes is twice as great as in the Amazon Basin at the same latitude (Patterson et al. 2005, InfoNatura 2007). In Europe, spatial clustering of mammalian species density and ecological structure reflects climate and physiography (Heikinheimo et al. 2007). In equatorial Africa, mammalian faunas (excluding bats) of the East African Rift system harbor 106–122 species, whereas faunas from the Congo Basin contain 56–78 species (Badgley unpubl.). Most Australian mammal species inhabit the coastal mountains and dissected plateaus of eastern and northeastern Australia compared to the vast lowland desert interior (data from Strahan 1995). Although the documentation of Asian mammals is uneven, regional compilations show exceptionally high species richness and extinction risk in the eastern Himalayas and mountainous peninsulas of southeastern Asia compared to adjacent lowlands or high plateaus (Sechrest et al. 2002, Schipper et al. 2008).

Where the mammalian fossil record permits comparison of coeval assemblages from nearby lowlands and uplands, species richness is greater in the upland assemblage. In an early Cenozoic example, Gunnell and Bartels (2001) compared well sampled, Middle Eocene mammalian faunas from basin-center and basin-margin areas of the Green River Basin in Wyoming, USA. The basin-margin site at the edge of actively rising mountains contained substantially greater species richness of mammals and other vertebrate groups than did coeval assemblages from the basin center. Presumably, the higher richness reflected the ecotone between lowland and upland habitats. Several groups of mammals showed evidence of speciation in situ (ancestor-descendant pairs or sister species with an ancestral species in an older interval). A late Cenozoic example contrasts fossil assemblages from the Miocene of Pakistan and southwestern China. In floodplain sediments from the Himalayan foreland basin of Pakistan, the greatest species richness of mammalian assemblages over a 12-million yr period was 70 species documented at 10 Ma (million years ago, unpubl., Barry et al. 2002). In contrast, a late Miocene fossil locality at the same latitude from a montane valley in Yunnan Province (southwestern China) preserved ca 120 species (Badgley et al. 1988, Z. Qiu pers. comm.). Both localities have mammals indicative of mesic forests and are documented by >1000 fossil specimens. Even more compelling are increases in species richness following tectonic episodes that altered topographic gradients or geographic barriers. Barnosky and Carrasco (2002) and Kohn and Fremd (2008) documented increases in regional species or generic richness of mammals from the montane western United States in step with Middle Miocene tectonic extension, volcanism, and rifting. These modern and historical examples document high mammal richness in tectonically active regions compared to nearby lowland environments and motivate this inquiry into the different processes that have shaped this widespread pattern.

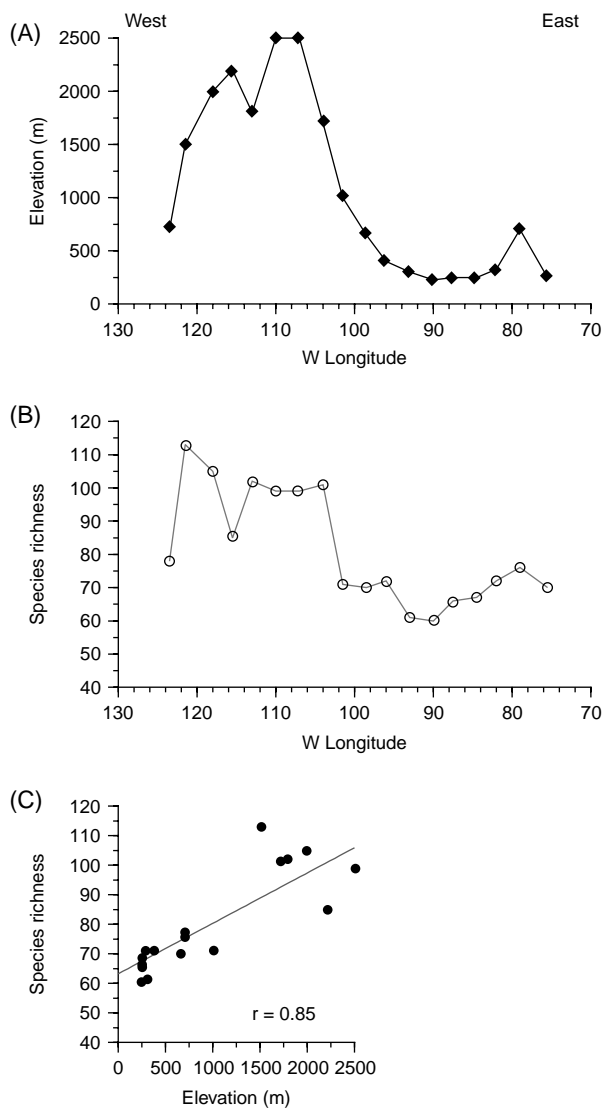


Figure 1. A transect across North America at 40°N demonstrates the strong correlation between elevation and mammalian species density. Data from equal-area quadrats in Badgley and Fox (2000). (A) Average elevation of quadrat in meters above sea level. (B) Species density (including bats) per quadrat. (C) Scatterplot and Pearson correlation coefficient between elevation and species density.

Evolutionary consequences of different tectonic regimes

The focus of this paper is the hypothesis that tectonically active areas, such as active mountain belts and rift valleys, are engines of mammalian diversity by increasing diversification rates relative to those in tectonically quiescent regions. I am not concerned with species richness or turnover within elevational gradients of individual mountains or mountain ranges *per se*, but with processes that generated differences in species richness, taxonomic composition, and ecological diversity between major geologic provinces. The spatial scale of mammalian geographic ranges, ecoregions, and life zones is the scale over which the evolutionary component of diversity gradients is most evident (Ricklefs and Schluter 1993). Tectonic activity converts landscapes of low elevation, low relief, and spatially continuous climate and vegetation into landscapes of high relief with steep climatic gradients and fragmented vegetation zones. These transformations occur over thousands to millions of years and are driven by plate subduction, rifting, and mantle hotspots (Windley 1995). Complex topography may result from deformation at convergent (e.g. Andes, Himalayas) or divergent (e.g. East African Rift, Rio Grande Rift) plate boundaries. Changes in elevation and relief alter climatic and atmospheric conditions, habitat area, and connectivity among habitats. For terrestrial mammals, the operational properties are continuity and area of habitats, proximity and connectivity among areas of similar habitat, strength of environmental and resource gradients, and topographic stability of habitats (Coblentz and Riitters 2004).

Topography interacts with climate at many spatial scales, from the microhabitats of hillsides to entire mountain ranges and massive plateaus. Changes in temperature, atmospheric pressure, and humidity with elevation mimic latitudinal climatic changes, such that alpine tundra and high-elevation deserts have climatic, edaphic, and floral parallels with arctic tundra and polar deserts (Barbour and Billings 1999). The altitudinal temperature gradient changes with latitude and global temperature. Today, for example, the snowline occurs at 4500 m at the equator, rises toward the Tropics of Cancer and Capricorn, then falls with increasing latitude, reaching sea level near the poles. Snowlines fell during the last glaciation, by up to 1000 m in the tropics (Porter 2001), rose during the current interglacial, and are rising further from modern global warming (IPCC 2007). Both climate and physiography influence the effectiveness of high mountains or plateaus as barriers to dispersal. Janzen's (1967) assertion that mountain passes are higher in the tropics refers to the higher extension of habitable life zones in tropical versus temperate regions, lower seasonal temperature variations throughout the tropics, and different thermal tolerances of tropical versus temperate and boreal organisms. The predictions about thermal tolerances have been borne out better for ectotherms than for endotherms (Ghalambor et al. 2006). Nonetheless, for birds (Rahbek and Graves 2001) and mammals (McCain 2005), climatic conditions effectively sort species along elevational gradients. Thus, topography cannot be fully separated from climate and climatic history in its ecological or evolutionary influences on diversity.

The processes that increase regional (and local) species richness are intensified in montane regions. The environmental gradients have the potential to accommodate many kinds of species in superjacent life zones (Merriam 1894, Lomolino et al. 2006). Immigration occurs from adjacent life zones as well as within zones. During Quaternary glacial cycles, areas of montane vegetation expanded during cool intervals, creating low-elevation connections for dispersal (Brown 1978, Grayson 1993, Thompson and Anderson 2000). Geographic isolation of habitats on individual mountains or mountain ranges increases opportunities for genetic differentiation and speciation, as well as extinction (Cracraft 1985, Brown 2001). Steep environmental gradients present strong selection gradients, creating circumstances for disruptive selection to act on contiguous populations (Endler 1977, Moritz et al. 2000). These conditions should affect small mammals more than large ones, because of size-related differences in home-range area and resource requirements in relation to habitat area and barriers. Surveys show that small mammals indeed drive the major gradients in species richness (Patterson et al. 1998, Badgley and Fox 2000, Lomolino 2001, McCain 2005).

In contrast, tectonically quiescent areas, such as the ancient shields and passive margins of continents, slowly lose habitats through erosion. Such areas exhibit spatially continuous habitats and low climatic heterogeneity that promote geographically extensive populations with high gene flow. Although such areas can potentially accommodate many species, immigrants from different habitats are far away. The low frequency of strong barriers facilitates high gene flow over large areas, with less opportunity for lineage differentiation or speciation in mammals. Selection gradients related to environmental conditions are weak. During Quaternary glacial cycles, bioclimatic zones were latitudinally compressed during glacial advances and expanded during interglacials (Wright et al. 1993, Williams et al. 2004). Compression of climatic zones during glacial periods would have further enhanced gene flow within and among habitats. This contrast in physiography and Quaternary history should lead to differences in the phylogeographic structure of sister taxa occupying regions of high versus low topographic complexity.

The elevational gradient in North America

A North American example highlights the contrast in taxonomic and ecological diversity from different tectonic contexts. North America (including Central America) consists of tectonically active western and southern regions and a tectonically passive eastern region. The mountain ranges, basins, and plateaus of the tectonically active region have been created over the last 100 myr (million years), with current tectonic activity concentrated along the western margin of North America and under mantle hotspots, such as the Yellowstone Hotspot (Burchfiel et al. 1992, Pierce and Morgan 1992). For a given latitude, species richness per unit area is twice as great in most areas of the tectonically active west as in the tectonically quiescent east (Fig. 1A–B), and richness is strongly correlated with elevation (Fig. 1C). (Active and passive regions occupy comparable areas.) Likewise, certain trophic groups, such as

herbivores and granivores, show high montane species richness, whereas others, notably carnivores and omnivores, do not (Badgley and Fox 2000). Taxonomically, rodents and bats dominate the latitudinal richness gradient, whereas rodents dominate the longitudinal gradient.

Rodents constitute just over half of extant North American mammal species (Hall 1981, Wilson and Reeder 2005). Sixty-two percent of rodent geographic ranges lie within the active region compared to 12% within the passive region, while 26% have ranges overlapping both regions (Table 1). Four families – cricetids (muroids including voles, deermice, and packrats), geomyids (pocket gophers), heteromyids (pocket and kangaroo mice), and sciurids (squirrels) – dominate North American rodent diversity. All four families have more than twice as many species occurring only in the active region compared to the passive region, with about one-fourth or fewer species occurring in both regions. This consistent geographic pattern suggests a difference in macroevolutionary processes between the active and passive regions.

At a finer scale, the mammals of Colorado illustrate species richness and turnover along the boundary between active and passive regions (Fig. 2). A strong elevational gradient spans this boundary. Based on detailed documentation of species ranges throughout the state (Fitzgerald et al. 1994), I recorded the eastern and western range limits of all species within 1-degree bands of longitude (ca 100 km wide) for mammals inhabiting the northern half of Colorado (Fig. 2A). Since the Rocky Mountains run north-south, the longitudinal range boundary is also an elevational boundary. Twenty-six species have ranges principally in the Great Plains (eastern Colorado), with some ranges extending into the Rocky Mountain front (central Colorado); 69 species have ranges within the Rocky Mountains and the plateaus of western Colorado, with some ranges extending further west; 30 species occur throughout Colorado (Fig. 2A). Species richness rises from the Great Plains, peaks at the Rocky Mountain front, and declines slightly further west (Fig. 2B–C). The number of range boundaries, a measure of spatial turnover, shows a unimodal pattern, with the highest value at the Rocky Mountain front (Fig. 2D). Notably, the number of range boundaries west of the mountain front is not significantly greater than the number

east of the mountain front, signifying that the sustained increase in species richness across western Colorado results from the accumulation of species (mainly from the west) more than from spatial turnover.

These patterns as well as the high beta diversity of mammals (also, birds and amphibians) in mountainous areas of North and South America (McKnight et al. 2007, Melo et al. 2009, Qian et al. 2009) provide strong evidence for a general macroecological pattern. But it is necessary to evaluate evolutionary processes in the context of tectonic and environmental history for a more fundamental understanding of the origins of this gradient.

Predictions and preliminary tests

A number of predictions pertaining to evolutionary and ecological processes follow from the hypothesis that tectonic history is a driver of mammalian diversification. Ten of these are given below with representative data from the neontological and paleontological literature, when available. When neither data nor literature are available, I provide suggestions for appropriate tests.

Timing of speciation

The timescale for peaks in mammalian speciation should be consistent with the timescale for tectonic changes in topography. Peaks in origination should correspond to peaks of tectonic activity if the increase in topographic complexity forms barriers, fragments populations, and strengthens selection gradients. Alternatively, if montane regions are simply accommodating species that have immigrated from lowland as well as montane regions, then no correspondence between tectonic history and origination rates should occur, thereby falsifying the prediction. Data required to test this prediction include well resolved phylogenies with robust estimates of divergence times for the lineages under consideration, fossils of the focal lineage to document the timing of origination, and geochronological data about the timing of tectonism. Since small mammals drive the major features of the diversity trends, the ideal analyses would involve fossil rodents or insectivores from paired tectonically active and passive regions (Finarelli and Badgley 2010). (Fossil bats are too scarce for such comparisons.) Two studies of mid-Cenozoic mammals demonstrate the potential for comparing origination rates in different tectonic settings (Barnosky and Carrasco 2002, Kohn and Fremd 2008), although the latter analyzed changes in generic richness.

Speciation and genetic differentiation

The speciation rate should be greater for mammals in topographically complex regions than for sister taxa in spatially continuous landscapes. Speciation rates that are either systematically higher or statistically similar in spatially continuous landscapes relative to topographically complex regions would falsify the prediction. Fragmentation and isolation of habitats by physiographic barriers and strong resource gradients should promote speciation in

Table 1. Number of extant North American rodent species with geographic range entirely within the tectonically active region, the passive region, or overlapping both regions. Geographic-range data from Hall (1981), Patterson et al. (2005), Wilson and Reeder (2005), and InfoNatura (2007).

	Active region	Passive region	Both regions
All rodents (n = 387)	241	47	99
Aplodontidae (n = 1)	1	–	–
Castoridae (n = 1)	–	–	1
Caviidae (n = 1)	–	–	1
Cricetidae (n = 191)	117	21	53
Dasyproctidae (n = 2)	–	1	1
Dipodidae (n = 4)	1	1	2
Echimyidae (n = 3)	1	–	2
Erethizontidae (n = 3)	1	–	2
Geomyidae (n = 37)	21	10	6
Heteromyidae (n = 56)	39	5	12
Sciuridae (n = 87)	60	9	18

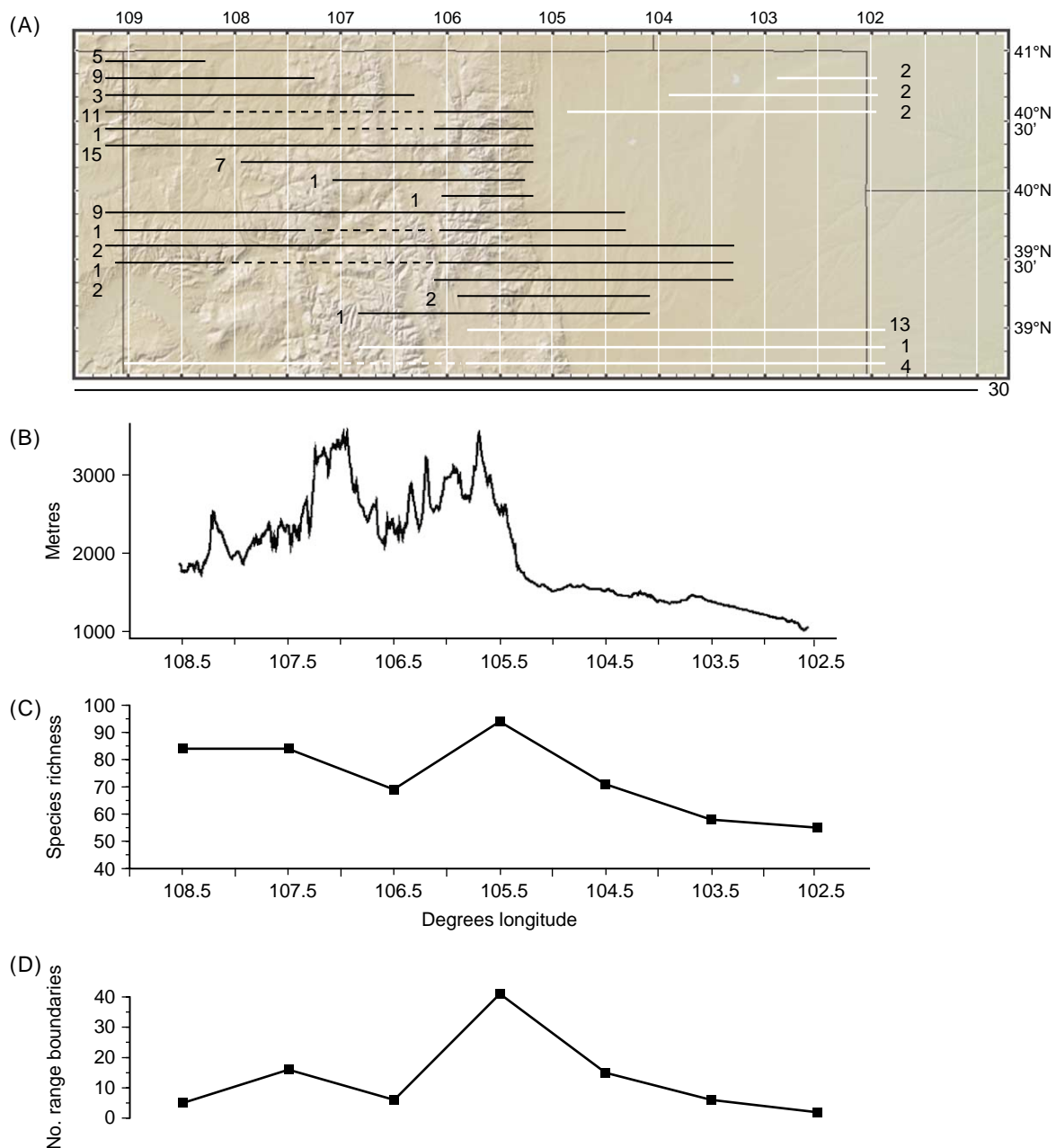


Figure 2. Transect across the northern half of Colorado (USA), spanning the boundary between tectonically active and passive regions of North America. (A) The longitudinal extent of mammal species ranges is indicated by horizontal lines across a topographic base map (from GeoMapApp, <www.geomapapp.org/>). Numbers next to lines signify the number of species with that longitudinal range distribution. Dark lines indicate geographic ranges that are entirely within the mountainous region or extend further west; light lines indicate ranges on the high plains or extending to the east. (B) Topographic profile across northern Colorado at ca 40°N (from GeoMapApp). (C) Species richness of mammals based on presence of geographic ranges across 1-degree bands of longitude (ca 100 km wide). (D) Number of range boundaries in each 1-degree band of longitude as a measure of spatial turnover. Geographic-range data from Fitzgerald et al. (1994).

topographically complex regions, especially for species with small home range sizes or stenotopic habitat preferences. Sister species in continuous landscapes should experience higher rates of dispersal and gene flow as well as weak resource gradients, thereby lowering the likelihood of reproductive isolation and allopatric speciation. Data relevant for testing this prediction include phylogenetic and phylogeographic studies of mammals with sister taxa in both montane and lowland landscapes.

Two examples involving North American rodents support this prediction. Demastes et al. (2002) conducted a phylogenetic analysis of pocket gophers (Geomyidae) from the Mexican Plateau and the Trans-Mexican Volcanic Belt (TMVB). The authors sampled mtDNA from 38 localities across the geographic ranges of *Cratogeomys* and *Pappogeomys*. Their maximum-likelihood tree based on cytochrome *b* showed a different pattern of cladogenesis on the broad, stable Mexican Plateau compared to the young mountains

and deep valleys of the TMVB. From divergence estimated at 3.2 Ma into two lineages of *Cratogeomys*, one branch gave rise to two species now occupying the northern part of the Mexican Plateau and one occupying the southeastern part of the Mexican Plateau. The other branch split into five clades (that do not correspond neatly to currently recognized species) that live above 2000 m in the TMVB; the distribution of these clades corresponds to geographic subdivisions of the TMVB by volcanic plateaus and rivers. Estimated divergence times imply that since 2.6 Ma, two clades arose in the northern Mexican Plateau and five clades arose in the TMVB, during an interval of volcanic activity in the TMVB and glacial-interglacial climatic changes. Based on extant species, cladogenesis was about twice as great in the volcanically active TMVB as in the stable Mexican Plateau.

The second example involves *Tamias amoenus* (yellow-pine chipmunk), which occupies montane conifer forests in northwestern North America, and *T. striatus* (eastern chipmunk) from eastern North America. Phylogeographic analysis based on sequence variation in cytochrome *b* revealed 12 clades in *T. amoenus* (Demboski and Sullivan 2003). The distribution of haplotypes corresponds closely with different mountain ranges in several distinct geological provinces. The degree of sequence divergence (4.5–7.4%) implies differentiation before the mid-Quaternary. In contrast, the phylogeographic structure of *Tamias striatus* has no concordance with landscape features but indicates population expansion since the last glacial maximum from multiple refugia in the eastern United States (Rowe et al. 2006). Thus, the geographic structure and temporal depth of mtDNA variation differ in congeners that occupy topographically complex versus simple landscapes.

Species ages

Two scenarios need evaluation. First, if montane regions continuously promote speciation, then higher diversification rates should result in a cluster of young divergences compared to lowland relatives. Alternatively, if tectonic activity per se stimulates speciation, then peaks in origination should coincide with the timing of tectonism, irrespective of age. These alternatives could be evaluated with a high-quality fossil record that spans intervals of tectonism. Geographic differences in the timing of divergence of extant species could also test these scenarios. Moritz et al. (2000) document younger species-level divergence ages for Andean small mammals compared to their Amazonian relatives. For example, in murid rodents, the mean genetic distance between sister taxa in the Amazon is twice as large as the mean genetic distance between sister taxa in the Andes, implying that Andean rodent faunas contain younger species. This example supports the first scenario in which montane regions systematically promote speciation, since divergences occurred over millions of years in both regions. If younger species consistently occur in tectonically quiescent versus active areas, or if speciation rate does not change in response to an episode of tectonic activity, then the general hypothesis is falsified.

Endemism

Endemism in tectonically active regions should reflect cladogenesis within the montane region rather than contraction of geographic range(s) from a much larger region. Endemism can result from alternate historical trajectories – origination in a region and persistence in that geographic region alone, origination in one region and relocation to an entirely different area, or reduction of geographic range to produce a relict distribution (Lomolino et al. 2006). Endemism resulting from the second or third processes would not support the hypothesis. The geographic isolation of the areas under consideration has a substantial impact on geographic-range expansion, immigration, and endemism. In their comparison of vertebrate faunas from two montane ecosystems of comparable area, Yellowstone National Park in the northern Rocky Mountains and two national parks in northern Patagonia, Barnosky et al. (2001) noted lower mammalian species richness and higher levels of endemism due to origination in situ in Patagonia compared to Yellowstone. They attributed both properties to the isolation of Patagonia from other temperate sources. Well resolved phylogenies can demonstrate whether geographically clustered endemics are also closest relatives, supporting the scenario of endemism reflecting origination and persistence. In addition, data from the fossil record documenting mammalian faunal composition from both montane and adjacent lowland areas over time, as well as indicators of paleoenvironmental history, are needed to evaluate the patterns of endemism in tectonically active regions. Areas with a fossil record of montane and adjacent lowland species include the western U.S. (Carrasco et al. 2005, Janis et al. 2008) and Ethiopia (Yalden and Lagen 1992), each with many endemic mammals today.

Extinction rates

How mammalian extinction rates compare between topographically complex regions and lowlands is an open question, since topographically complex regions have opposing influences on extinction rates. Three scenarios are possible. First, extinction rates could be higher in topographically complex regions than in lowlands. Diversification could be still higher in the former if per-lineage speciation rates exceed extinction rates. This scenario implies that the average persistence time of mammalian lineages would be shorter and faunal turnover higher in montane regions than in lowlands. The smaller, often fragmented geographic ranges and large distances between areas of suitable habitat in topographically complex regions should elevate extinction risk for non-volant mammal populations (Brown 2001). Isolation of low- to mid-elevation vegetation zones by high elevation or barren stretches in extensive, linear mountain ranges or of alpine regions on smaller, separated mountain ranges (such as in the Great Basin) should reduce dispersal and increase extinction risk, as is presently occurring for *Ochotona princeps* (pikas) of the western United States (Grayson 2005). Second, mammalian extinction rates could be similar between topographically complex regions and their adjacent lowlands. Under this scenario, montane

diversification would be driven by speciation and immigration. Third, extinction rates could be lower in topographically complex regions than in lowlands, despite differences in the size and fragmentation of geographic ranges. Under this scenario, species persistence times would be greater and faunal turnover lower in topographically complex regions. Areas of complex topography feature steep environmental gradients with many life zones in close geographic proximity, which may facilitate dispersal among suitable microhabitats. In their analysis of Quaternary vegetation change on the Andean flank, Bush et al. (2004) noted that the rate of change in forest composition was similar during intervals of substantial climatic change and climatically stable periods. They postulated (p. 828) “that the ease with which species can migrate and avoid extinction in response to climate change may be a major factor promoting diversity in these [montane] systems”, suggesting that extinction risk is reduced in topographically complex regions.

Extinction rates in topographically complex regions should also differ between cooling and warming periods. During intervals of global cooling, extinction rates should decline as ranges expand, isolation is reduced, and dispersal increases (Brown and Kodric-Brown 1977, Brown 1978). During periods of warming, extinction rates should increase as high-elevation habitats shrink and vanish. The North American mammal record has numerous fossil localities across the tectonically active montane regions and tectonically quiescent plains over much of the Cenozoic (Janis et al. 1998, 2008, Carrasco et al. 2005) with high taxonomic and temporal resolution suitable for testing these scenarios.

Local versus regional species richness

If tectonics drives diversification, then regional mammalian richness in tectonically active regions should comprise a set of distinctive local faunas. Beta diversity should be high across topographically complex regions because of vicariance and strong environmental gradients. In contrast, lowlands should feature low beta diversity as a consequence of low speciation rates and large geographic ranges. Local and regional richness should have a strong positive correlation, and local richness and species composition (per unit area) should vary little across the landscape.

These principles also apply to mammals of different body size and dispersal ability inhabiting each region. For large-bodied species with large home ranges and high mobility, local and regional species richness should be similar. For small-bodied species with small home ranges and short dispersal distances, local species richness should represent a small fraction of regional species richness. This relationship remains to be tested empirically. On the other hand, the close proximity of many life zones and moderate dispersal capabilities of most mammals lead to higher local species density in topographically complex regions than in topographically continuous ones (Lomolino 2001). Dispersal into adjacent life zones should also enrich lowland faunas close to montane source areas, an effect evident for mammals of Colorado (Fig. 2A) from the montane front into the Great Plains.

Export of diversity

Topographically complex regions should export species to adjacent lowlands. This pattern could arise when a species originates in the tectonically active region and then expands or shifts its geographic range to the passive region. Higher species richness in topographically complex regions could reduce the likelihood of immigrations from adjacent regions with higher richness serving as a barrier to immigrants (Shea and Chesson 2002). Likewise, species from regions of high diversity could be more successful immigrants to other regions because they experience more biotic interactions in the area of origin, as proposed for reef biodiversity in topographically complex marine habitats (Kiessling et al. 2010).

For mammals of northern Colorado (Fig. 2), I assessed the proportion of species whose geographic ranges lie predominantly in the topographically complex region but extend onto the high plains, and vice versa (Fitzgerald et al. 1994). For the montane region (largely west of 105°W), 18 species have extended their geographic range eastward to lower elevations. For the plains region (largely east of 105°W), 18 species have extended their range westward, with three species occurring only at lower elevations (below 2000 m) and 15 species expanding into higher elevations. This example does not support the prediction that higher species richness is a barrier to immigration. The prediction could also be addressed with high-resolution fossil records to assess expansion of geographic ranges over geologic time.

The evolutionary counterpart to this ecological pattern involves species from montane regions expanding into lowland regions and the lowland populations then evolving into new species. The question is whether montane regions contribute to the diversity of lowland regions through speciation (even if origination rates occur at a higher frequency within the montane members of the clade) to a greater degree than lowland regions contribute to the diversity of montane regions. Well-resolved phylogenies of clades with broad geographic coverage permit comparison of branching patterns in relation to tectonic context. For pocket gophers (Geomyidae, Spradling et al. 2004), pocket mice in the genus *Liomys* (Heteromyidae, Rogers and Vance 2005), the major heteromyid lineages (Hafner et al. 2007), and deer mice in the genus *Peromyscus* (Cricetidae, Bradley et al. 2007), there was considerable concordance between branching patterns and tectonic context, based on data from Table 1. For *Liomys*, older lineages inhabit the tectonically active area more often than both areas, and species inhabiting both areas occur on young branches (Fig. 3). This pattern suggests that colonization proceeded from the active to the passive region, if modern distributions provide accurate information about area of origination. The opposite pattern occurs for geomyines: older lineages include a higher frequency of species occupying passive regions or both regions today, and species on younger branches occur more frequently in tectonically active areas (Fig. 4), suggesting colonization of the active region from the passive region. These patterns are merely suggestive. Since many species origins are estimated to date to the Miocene or Pliocene, and geographic ranges may shift substantially over time, high-resolution fossil records in

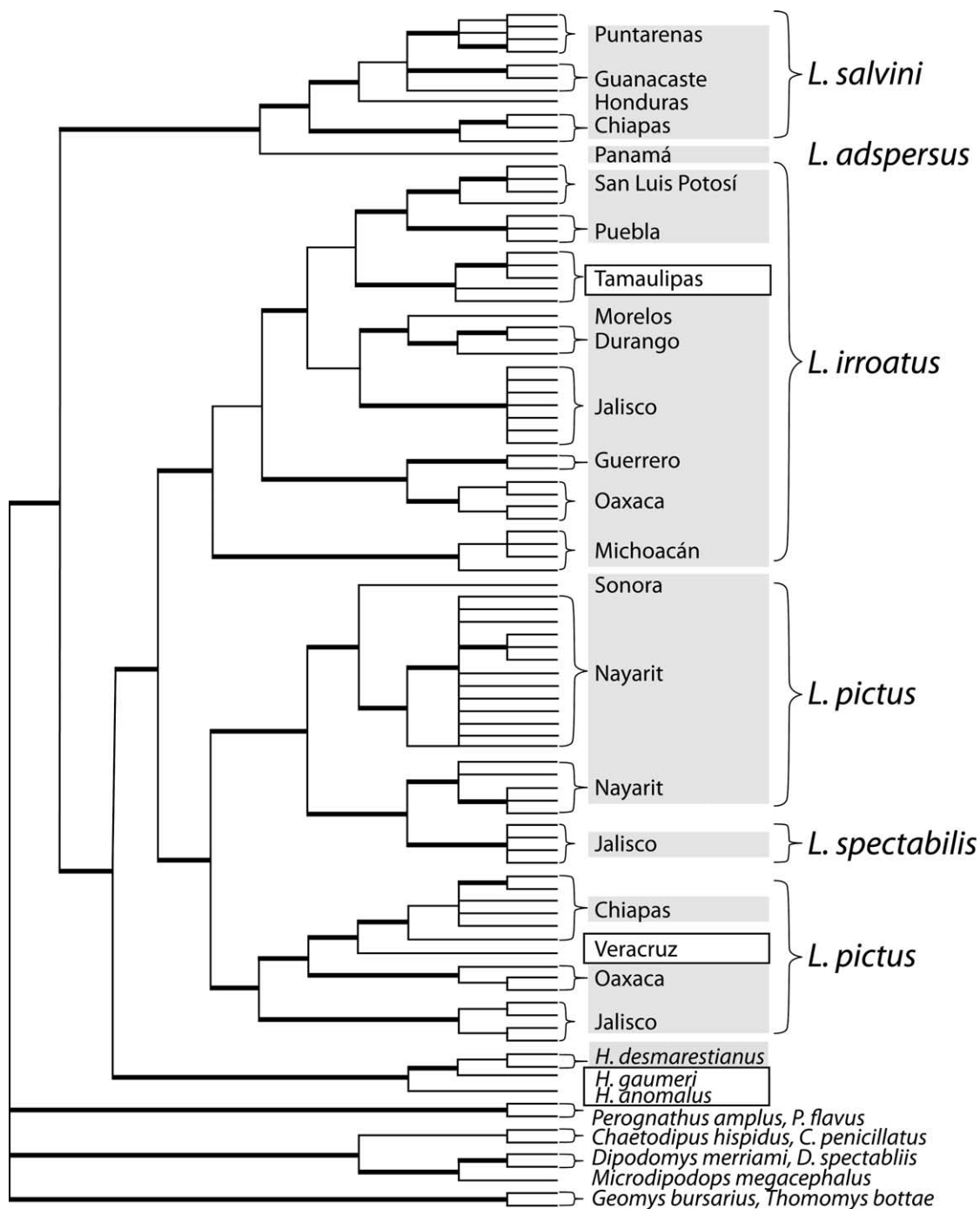


Figure 3. Phylogenetic tree of heteromyid species in the genus *Liomys* from Rogers and Vance (2005). Tree results from a Bayesian analysis of mitochondrial cytochrome *b* sequence data. Nodes in bold are supported by Bayesian posterior probabilities >95%; values for other nodes are >50%. Shading indicates whether each population occurs in the tectonically active region or both active and passive regions of Mexico. Gray shading = active region, white box = both active and passive regions. Most lineages occur in the tectonically active region, and those in both active and passive regions are on younger branches, suggesting that colonization proceeded from the active to passive region. Modified from Fig. 2 in Rogers and Vance (2005).

conjunction with well resolved phylogenies are needed to assess these geographic histories.

Orientation of mountain ranges

Regions with north-south mountain ranges should feature higher regional species richness than areas with east-west

ranges. A north-south orientation facilitates latitudinal range shifts of species in response to global temperature changes, as species move along north-south corridors, and lowers extinction risk (Coblentz and Riitters 2004). In contrast, an east-west orientation of mountain ranges inhibits movement of species north and south during global cooling or warming episodes. This prediction can be evaluated by comparing regional species richness of

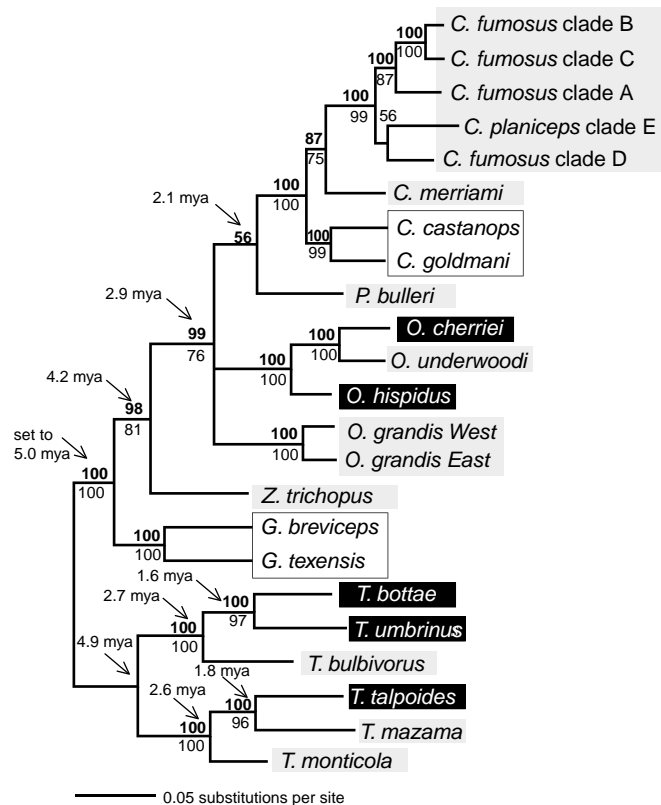


Figure 4. Bayesian phylogeny of geomyids from Spradling et al. (2004), based on analysis of mitochondrial and nuclear genes. Estimated divergence dates are shown for some nodes. Shading indicates whether the species or phylogroup occurs in the tectonically active region, the passive region, or both regions. Gray shading = active region, white lettering on black = passive region, white box = both regions. Species in the outgroup (*Thomomys*, or “*T*” species) and older branches occur more often in the passive region or both regions, and younger branches occur mostly in the active region, suggesting that colonizations proceeded from the passive to active regions. Modified from Fig. 4 in Spradling et al. (2004).

European mammals north and south of the Alps with North American mammals at similar latitudes, and also the regional species pools of the east-west trending Uinta Mountains with the contiguous north-south trending Wasatch Mountains in Wyoming and Utah, USA. Brown and Maurer (1989) made a related point in demonstrating that the geographic orientation of small ranges runs north-south, whereas large ranges are oriented east-west for North American mammals, and predicted that European mammals would show few ranges oriented north-south but many east-west orientations. The comparison remains to be done. A finding of similar or lower regional richness in north-south compared to east-west mountain ranges would falsify this prediction.

Multiple versus single mountain ranges

Areas with multiple mountain ranges should have higher regional species richness than areas with single mountain ranges. The expectation is that areas with multiple mountain ranges would generate and exchange species, resulting in higher regional species richness than areas with single mountain ranges (standardized for latitude and area). This prediction can be addressed by comparing species richness from regions (of equal area) with several small ranges in the Great Basin to single large ranges of the

eastern Rocky Mountains (e.g. Wind River Range, Wyoming) or to outlying ranges (e.g. Guadalupe Mountains of western Texas). The Ethiopian highlands, a single mountainous complex, compared to the extensive eastern and western African Rift valleys and highlands offer another example.

Global climate change and diversification

Global warming or cooling should cause geographic ranges to shift in elevation, but do these changes affect diversification? Global warming causes species ranges to shift to higher elevations, thereby increasing the regional species richness within topographically complex regions. Warming also reduces the area and increases the isolation of habitat zones at higher elevations. Fragmentation and isolation of such habitats could promote speciation in mammals if sustained over geologic time. However, it could also promote extinction on mountaintops, as has occurred since the last glacial maximum (Brown 1978) and continues today (Grayson 2005). Global cooling causes species ranges to shift to lower elevations, reducing regional species richness within topographically complex regions and increasing richness in adjacent lowlands. This process may explain why mammalian richness was more similar in the eastern and western US following the last glacial maximum

than it is today (Cannon 2004). If global warming influences diversification in topographically complex regions, then fossil records from such regions should show a pulse of originations during episodes of global warming, with only a modest increase in species richness (from poleward range shifts) in adjacent lowlands. This process should also cause a clustering of divergences corresponding to the warming interval in the phylogeny of clades from tectonically active regions. Absence of diversification during intervals of global warming would falsify this prediction.

Conclusion

I have presented a general hypothesis that tectonic activities on the continents create topographic and climatic heterogeneity that directly affects the magnitude of resource gradients and the connectivity versus isolation among habitats. In turn, these environmental properties promote diversification in tectonically active regions and suppress diversification in tectonically quiescent regions. This hypothesis pertains to terrestrial clades (mammals, plants, birds), whereas aquatic clades (freshwater fishes) experience high extinction rates in tectonically active regions and low extinction rates in passive regions (Smith et al. pers. comm.).

The evidence presented here, while preliminary, largely supports the hypothesis of tectonics as a driver of mammalian evolution while highlighting the need for more investigation. Three research questions stand out for refinement and testing of this macroevolutionary hypothesis. First, does topographic complexity per se or active tectonism (increase in topographic complexity and elevational gradients) stimulate diversification? Second, do extinction rates differ significantly between tectonically active and passive regions, or is the contrast in species richness driven primarily by speciation? Third, how does global climate change interact with tectonic history to influence diversification? Well-resolved phylogenies and fossil records are needed to address these questions rigorously.

This hypothesis and its recommended tests have several implications for the assessment of diversity gradients in extant mammals (and other groups). Most recent analyses have focused on environmental properties as predictors of alpha diversity, ecological structure, beta diversity, and for evaluation of null models of species distribution at local to regional scales (Currie 1991, Badgley and Fox 2000, McCain 2005, McKnight et al. 2007, Qian et al. 2009). Such analyses quantify the sorting of extant species along environmental gradients but consistently reveal diversity anomalies that are not merely a function of the scale of analysis. Topographic variables (elevation, relief, topographic heterogeneity) are consistently strong predictors of species richness; their significance is interpreted as a surrogate for habitat heterogeneity (Kerr and Packer 1997, Coblenz and Riitters 2004, McKnight et al. 2007). This interpretation highlights ecological mechanisms: greater habitat heterogeneity generates increased species packing. The analysis of diversity gradients also needs to address the geographic and temporal origins of modern diversity. The major hypotheses for explaining the

evolutionary dimensions of diversity gradients (Mittelbach et al. 2007) involve area, time, and climatic stability in relation to diversification rates. The significance of these factors changes when placed into a geologic context at the continental scale. Biome or realm area has a different effect on diversification rate if the biome is fragmented or continuous. Duration of a biome or realm as a site of species accumulation depends on regional rates of speciation and extinction, which should differ according to physiographic properties. Climatic stability was rare at all latitudes over the Cenozoic, which witnessed long-term cooling, short-term warming intervals, and Milankovitch cycles throughout (Zachos et al. 2001, Lyle et al. 2008).

This idea also has implications for the relevance of the fossil record, which can make fundamental contributions to the assessment of macroevolutionary differences between different tectonic settings. Most of the continental fossil record prior to the Cenozoic is from depositional environments at low elevations in topographically homogeneous landscapes, such as river basins and coastal plains. Cenozoic fossil sites, however, occur in a range of intermontane and low-elevation settings. Comparison of origination rates, extinction rates, and taxonomic richness in adjacent tectonically active and quiescent settings will provide critical tests of this hypothesis (Finarelli and Badgley 2010). Also, this hypothesis offers a plausible explanation for why the earliest representatives of higher taxa of mammals are so often missing from the fossil record. If these early representatives arose at higher elevation in topographically complex areas in the early Cenozoic or late Cretaceous, they would be unlikely to leave a fossil record. Finally, the long durations of lineages and faunas characteristic of some continental vertebrate records (e.g. Miocene of Pakistan, Permian of Texas, USA) may reflect the tectonic setting rather than characterizing mammalian evolution more generally.

In conclusion, this hypothesis links a macroecological pattern in modern mammalian faunas to macroevolutionary processes that responded to the tectonic history of the continents. The predictions suggest a research program focusing on biogeographic processes that determine the regional diversity of mammals across different tectonic settings. This research will place the modern biodiversity hotspots for mammals into an evolutionary and geohistorical context – which should increase our appreciation of their uniqueness and elevate the imperative for their conservation.

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