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Mountains, Climate and MammalsCatherine Badgley¹, Tara M. Smiley^{2,3} and Rachel Cable¹¹ Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA² Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI, USA³ Integrative Biology, Oregon State University, Corvallis, OR, USA**Abstract**

More than half of present-day continental mammals occur in montane regions. This concentration of diversity in regions of high topographic complexity compared to adjacent lowlands and plains constitutes the topographic diversity gradient, one of the major biogeographic patterns across continents today. Several biogeographic processes have shaped the topographic diversity gradient for mammals. Strong elevational gradients of climate, soil and vegetation in montane regions provide diverse habitats from high to low elevations; these heterogeneous habitats can accommodate high mammal diversity, especially of small mammals. Montane regions also present strong barriers – in the form of deep valleys, steep climatic gradients and abrupt changes in topography – to the distribution of populations and species. Changes in these barriers over time due to tectonic activity and erosion lead to fragmentation or mixing of populations, circumstances that can increase speciation or extinction rates in montane regions. Global or regional climate changes cause geographic ranges to shift in elevation. Climatic warming during the current interglacial has caused mammalian range shifts to higher elevations since the Last Glacial Maximum, and this process is accelerating under current global warming. The mammalian fossil record indicates that the topographic diversity gradient is strong during some time intervals and weak during others. For a 20 million-year record of North American small mammals, the interval with the greatest intensity of tectonic activity and climate change coincided with the highest origination rates and the highest diversity in the topographically complex region. This pattern suggests that landscape history has a strong influence on past and future mammal diversification.

Keywords: *biogeography, diversification, diversity gradient, topographic complexity, fossil record*

14.1 Introduction

Today, montane regions harbor more species of mammals per unit of area than adjacent lowlands. This pattern occurs at the regional scale, such as in the Rocky Mountains compared to the Great Plains in North America or in the East African Rift System (EARS) compared to the Congo Basin in Africa. At least three biophysical properties of montane regions contribute to their high species richness. First, strong elevational gradients in topography and associated climatic conditions create a diversity of habitats in terms of area, slope, soil type and depth, vegetation and seasonal cycles of temperature and precipitation. Increased environmental heterogeneity can accommodate a high diversity of species with different environmental tolerances (Coblentz &

Riitters 2004). Second, the geographic ranges of species in montane regions are often fragmented across deep valleys and extensive crests above the snowline. Over thousands of generations, isolated populations may become genetically distinct, achieve reproductive isolation and form new species (Davis et al. 2008). Third, climatic changes over decades to millions of years affect the connectivity of habitats and stimulate geographic-range shifts within montane regions and between mountains and adjacent lowlands. These elevational shifts also move species ranges into and out of montane regions, resulting in periods of higher and lower species richness in entire tectonic provinces over geologic time (e.g., Finarelli & Badgley 2010). This combination of ecological and evolutionary processes unfolding over geologically dynamic landscapes implies that montane regions may serve as both a

source of new species and adaptations and a long-term refuge, especially during periods of global warming (Bush et al. 2004; Badgley 2010; Merckx et al. 2015).

In this chapter, we review the biogeography of present-day mammal diversity in areas of complex topography compared to adjacent lowlands, first across continents and then in selected regions. The fossil record offers a geohistorical perspective on diversity along topographic gradients, and we present one example from the fossil record of North American mammals over the last 25 My. We describe the kinds of mammals that are known to drive this pattern via rapid speciation and high spatial turnover, as well as several biogeographic processes that shape the modern pattern of high mammal diversity in montane regions. We distinguish between an elevational diversity gradient, which refers to changes in species richness along an elevational profile, and a topographic diversity gradient, which refers to changes in diversity between a region of high topographic complexity and a region of low relief. A region of high topographic complexity has high relief (the difference in elevation between the highest and lowest altitudes) over a large area (hundreds of square kilometers). Such regions include mountain ranges, incised plateaus and basins bordered by mountain ranges. An elevational diversity gradient may occur on individual mountains or across a mountain range (e.g., Rahbek 1995; McCain 2005); a topographic diversity gradient occurs between regions on the scale of tectonic provinces (e.g., Finarelli & Badgley 2010).

The diversity of mammals in montane regions appears to be as much a response to complex topography, including multiple mountain ranges and basins, as to high elevations per se (Simpson 1964; Davis 2005; Badgley 2010). Complex topography results from the interaction of tectonic processes – which increase elevation through rock uplift within compressional regimes, or increase land area and relief through extension (lateral stretching) or rifting (see Chapters 2 and 3) – with climatic processes that cause erosion (see Chapters 4 and 8). The formation

of mountain belts (orogeny) occurs over millions to tens of millions of years (Champagnac et al. 2012). High relief, steep slopes and deep valleys arise during early to middle stages of orogeny and accentuate bioclimatic zonation. In contrast, speciation of mammals occurs on time scales of hundreds of thousands to millions of years, and substantial geographic-range shifts may occur in a few thousand years. Later stages of mountain building correspond to basin infilling, slope smoothing and more gradual bioclimatic transitions over elevational gradients. The topographic profile of mountains at all orogenic stages can be strongly influenced by glacial processes, especially at higher latitudes (Egholm et al. 2009).

The regional climate and its effects on erosion, topographic roughness and vegetation are major influences on potential mammal habitation and diversity. The altitude of the snowline, the thermal lapse rate and the precipitation gradient across a montane region determine which parts of the region have sufficient quantities of vegetation and shelter to support persistent populations of mammals. The presence of rock shelters or friable soils for burrows is critical for small mammals (<1 kg in adult body weight). In cold regions, including high elevations at low latitudes, many small mammals must be able to hibernate or enter torpor to survive daily or seasonal cold periods (Merritt 2010). In regions of low-temperature seasonality (e.g., much of the tropics), narrow climatic zones and multiple vegetation assemblages along elevation gradients contribute to dispersal limitation and species turnover in montane regions (Janzen 1967; Ghalambor et al. 2006).

The biogeographic processes that result in high mammal diversity in montane regions are the same processes that occur in all environments – speciation, extinction and geographic-range shifts via dispersal (Lomolino et al. 2010). The interaction of these processes with Earth's tectonic and climatic history shapes diversity gradients over space and time. Figure 14.1 illustrates the influences of geologic history on mammal diversity in montane regions. Tectonic and climatic processes interact to generate landscapes of

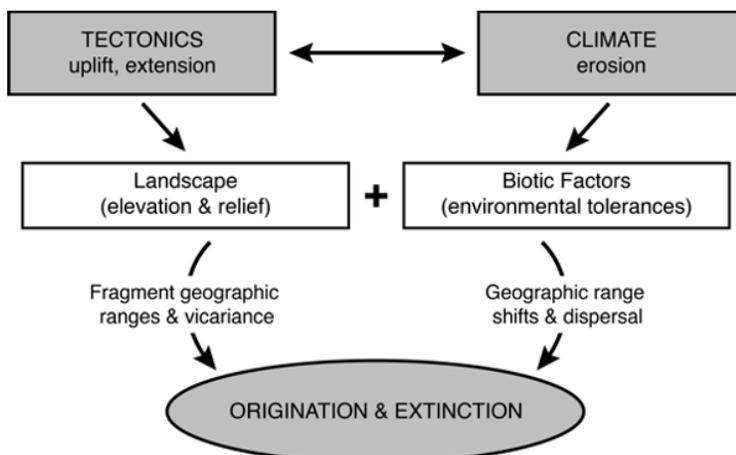


Figure 14.1 Conceptual diagram linking the tectonic and climate processes shaping regional landscapes, environmental conditions and species richness over geologic time scales. Within topographically and climatically complex regions, biogeographic processes include dispersal, geographic-range shifts and fragmentation of species ranges. These processes can promote origination and extinction, and geographic differences in origination and extinction rates in tectonically active versus passive regions can strengthen or weaken the topographic diversity gradient.

high elevation and relief. Areas of high relief feature climatically diverse habitats with a greater frequency of ecotones compared to foothills and lowlands (Coblentz & Riitters 2004). Species with environmental tolerances for montane climates and rocky slopes disperse into and colonize high elevations. Since such habitats are typically discontinuous, species occupying these regions have fragmented geographic ranges. Geologic intervals of global warming accentuate fragmentation as species ranges shift to higher elevations. Some populations may become new species as a consequence of sustained reproductive isolation. Geologic intervals of cooling cause species ranges to shift downslope, bringing fragmented populations into contact and providing opportunities for newly evolved species to disperse across the landscape. Some isolated populations at high elevations may disappear altogether, since alpine bioclimatic zones shrink during global warming and stochastic environmental or demographic factors heighten the risk of extinction for small populations (Williams & Jackson 2007; Sandel et al. 2011). With regard to diversification, the properties of mountains that distinguish them from lowlands include environmental heterogeneity resulting from high relief, numerous opportunities for fragmentation and isolation of microhabitats across complex topography and climatic changes over millions of years (Chapters 6, 12 and 13) (Brown 2001; Badgley 2010; Fjelds  et al. 2012).

14.2 Mammal Diversity Across Continents

At the continental scale, mammal diversity shows strong latitudinal and topographic gradients (Figures 14.2 and 14.3). In the New World (Figure 14.2a), the species

richness (documented as the number of species per grid cell) of mammals is greatest at low latitudes. Species richness declines sharply north and south of 20–25°. The lowest values occur at high latitudes, where continental ice sheets (North America) or extensive montane and valley glaciers (South America) have dominated these landscapes for over 2 million years (Simpson 1964; Badgley & Fox 2000; Tognelli & Kelt 2004). In addition to the latitudinal diversity gradient, mammals also show strong topographic gradients in diversity. At any particular latitude in North and South America, species richness is substantially greater in montane regions than in adjacent plains or river basins. This pattern is most striking in the equatorial region, where a band of high diversity follows the Andes Mountains (Figure 14.2a). In North America, species richness rises sharply from the Great Plains to the Rocky Mountains.

Topographic gradients in elevation and relief (Figure 14.2b) reflect the history of tectonic plate movements, as well as macroclimatic gradients (Figure 14.2c) that influence temperature and precipitation, glaciation, erosion rates and the distribution of vegetation. Climatic variables show contrasting spatial gradients (Figure 14.2c). Temperature variables typically vary with latitude in response to the latitudinal gradient in the intensity of solar radiation and convective atmospheric circulation (e.g., Hadley cells). Precipitation gradients follow the major mountain ranges as a consequence of orographic processes, resulting in strong longitudinal gradients in mean annual precipitation in North and South America. The interactions of temperature and precipitation determine the dominant vegetation present in different bioclimatic regions (Woodward 1987). Consequently, the distribution of biomes shows strong latitudinal and longitudinal boundaries.

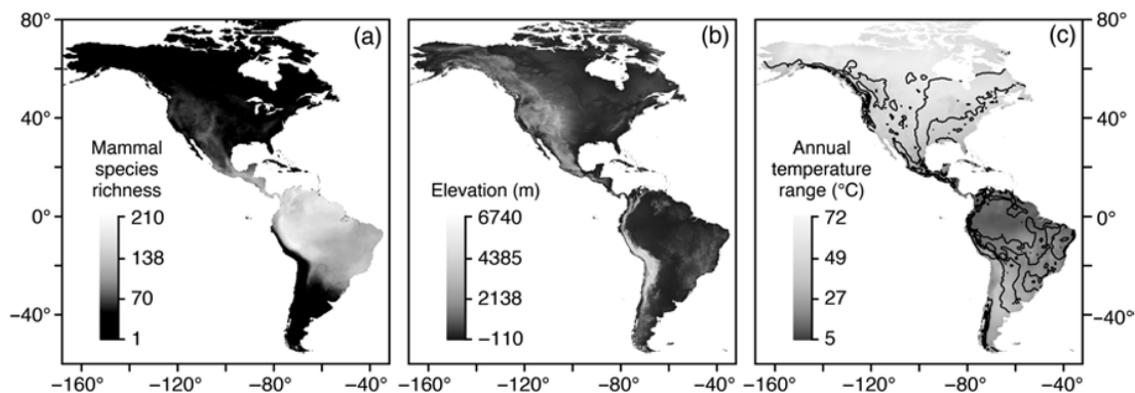


Figure 14.2 New World gradients of mammal richness, elevation and climatic variables. (a) Species richness of continental mammals, compiled at a spatial resolution of 10 km², in North and South America, based on species ranges from NatureServe. *Source:* Adapted from Patterson et al. (2007). (b) Mean elevation of grid cells at 1 km² resolution. Note that the species richness of mammals follows the topographic gradient as well as the latitudinal gradient. (c) Annual range of temperature (shading), a measure of climatic seasonality, shows a strong latitudinal gradient. Contours of mean annual precipitation follow the major mountain ranges in North and South America. The contour interval is 500 mm for precipitation. Climatic variables and elevation are both significant predictors of mammal diversity. *Source:* Adapted from Badgley & Fox (2000) and Hijmans et al. (2005).

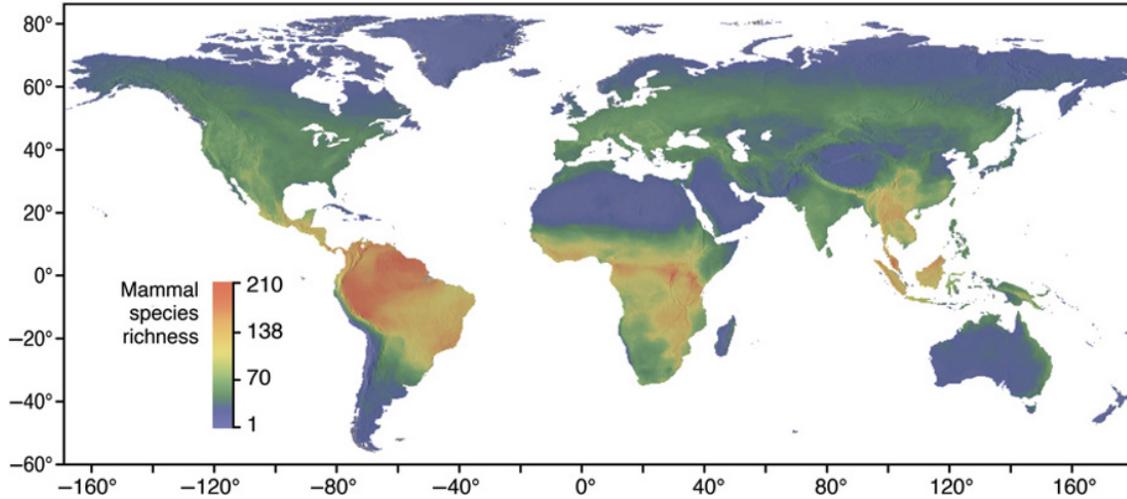


Figure 14.3 Richness of extant mammals, compiled for 10 km² grid cells. Overprinting the latitudinal diversity gradient is a strong topographic diversity gradient on all continents, excluding Antarctica. Mammalian species richness is elevated in the montane west of North America, along the Andes of South America, in the Alps of Europe, within the topographically complex East African Rift, over mountainous regions in India and south-eastern Asia and along the eastern coastal ranges of Australia. *Source:* Adapted from IUCN (2015). See also Plate 29 in color plate section.

Similar relationships among topography, climate and mammal diversity are found in Eurasia, Africa and Australia (Figure 14.3). In eastern Eurasia, the highest species richness of mammals occurs along the southern margin of the Himalayas, in montane Indochina and in the Malay Peninsula. In western Asia and Europe, high species richness occurs in the Caucasus Mountains, the Carpathian Mountains and the Alps. In Africa, a band of high species richness stretches across the Congo Basin and reaches its highest values along the western and eastern arms of the Rift Valley. In Australia, the highest species richness of mammals occurs in the mountain ranges and dissected plateaus that extend along the east coast (Strahan 1995). The topographic diversity gradient in mammals is most pronounced in regions of active tectonism, such as the Basin and Range Province of western North America, the Andes, the East African Rift and the southern edge of the Himalaya – regions where geologically recent topographic complexity and elevated species richness are evident. Montane regions also host high endemic diversity (number of small-range species) across the continents (Rosauer & Jetz 2015).

14.3 Topographic Diversity Gradients at the Regional Scale

A closer view of mammal diversity across topographic gradients is given in Figures 14.4–14.6, which depict transects across four present-day landscapes. Each transect spans an elevational gradient over several degrees of longitude along a single parallel. Based on detailed range

maps for each region, we plotted the longitudinal span of species ranges in 1° bins of longitude. Notable changes in the number of species per bin indicate places where many range boundaries occur. For each transect, the gradients in elevation, mean annual precipitation and seasonality of precipitation illustrate some of the important topographic and climatic changes across each region.

The US state of Colorado straddles the boundary between the extensive Great Plains to the east and the Rocky Mountains to the west; these mountains form the eastern edge of a topographically complex landscape that extends westward to the Pacific Ocean. Strong elevational, orographic and diversity gradients span the transect at 40° N through northern Colorado (Figure 14.4a,b). Elevation increases from about 1000 m on the plains of eastern Colorado to over 3000 m in the Rocky Mountains (Figure 14.4a). Changes in mean annual precipitation closely match the elevation gradient, with high values over the higher peaks and low values to the west and the east; seasonality of precipitation shows almost the mirror opposite (Figure 14.4b). Shortgrass prairie occupies the plains east of the Front Range; montane conifer forest, sagebrush steppe and arid grasslands and canyons characterize the mountains and western part of the state. Species richness rises from about 50 species in eastern Colorado to over 90 species at the Rocky Mountain front, dips to 70 species within the high mountains, then rises again to over 90 species to the west on the Colorado Plateau (Figure 14.4a) (Fitzgerald et al. 1994). The highest spatial turnover occurs at the junction of the plains and the Front Range. Turnover remains high across the western part of the state, whereas it is low in eastern

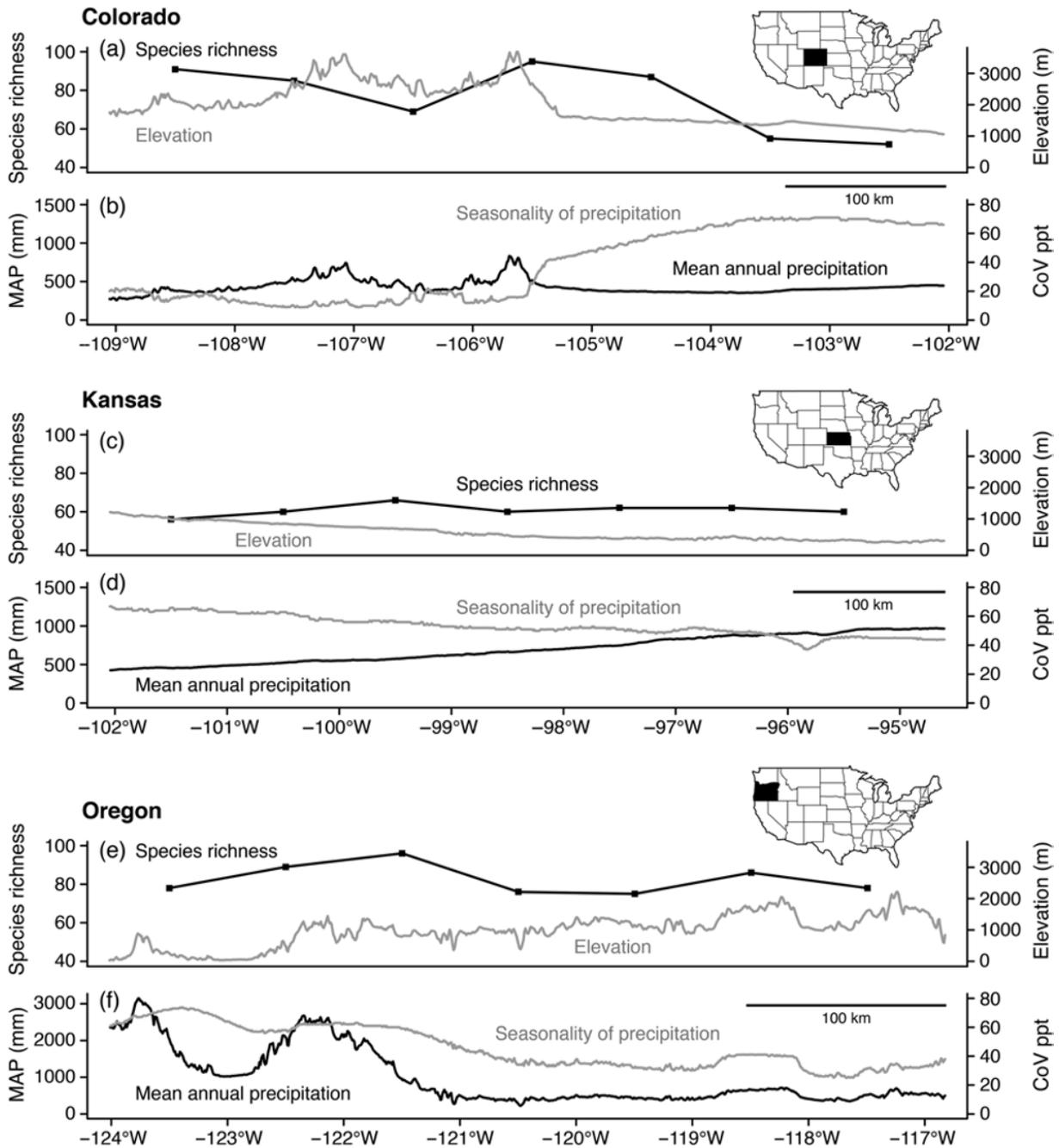


Figure 14.4 Transects illustrating topographic diversity gradients in relation to elevation and precipitation variables across three US states. Species richness is based on the distribution of species geographic ranges in 1° bins of longitude. Elevation is shown at a resolution of 1 km (lateral distance). Note that the vertical axis for mean annual precipitation changes from (b) and (d) to (f). *Source:* Data for elevation in each transect from US Geological Survey Center for Earth Resources Observation and Science (1996a). Data for mean annual precipitation (mm) and seasonality of precipitation (coefficient of variation of monthly precipitation) from the WorldClim database (Hijmans et al. 2005). (a) Transect across Colorado at 40°N. Species richness is low in eastern Colorado, where relief is low, then rises along the foothills and the front range of the Rocky Mountains around 105°W, dips slightly in the high mountains and rises again in western Colorado. *Source:* Species distributions from Fitzgerald et al. (1994). (b) Variation in mean annual precipitation (including snow) follows elevation closely, with the highest values in the high mountains. Seasonality of precipitation is almost the mirror image of precipitation, with low values in the mountains and high values over the plains of eastern Colorado. (c) Transect across Kansas at 39°N. Species richness fluctuates between 55 and 70 species per bin. Elevation increases from about 300m in eastern Kansas to about 1200m at the western border. *Source:* Species distributions from Bee (1981). (d) Mean annual precipitation steadily rises from west to east, the inverse of the trend in elevation; seasonality of precipitation varies little over eastern Kansas and increases slightly in the western half of the state. Gradients in species richness, elevation and precipitation variables provide a contrast with those from topographically complex regions in Colorado and Oregon. (e) Transect across Oregon at 45°N. Species richness ranges from 75 to 95 species per bin, with the highest values over the Cascade Mountains in western Oregon. The elevation profile captures the complex topography of the northern Basin and Range in the east and the Cascade Mountains, Willamette Valley and Pacific Coast Range in the west. *Source:* Species distributions from Verts & Carraway (1998). (f) Mean annual precipitation shows strong rain shadows from the Pacific coast and the Cascade Mountains in the west, with about 500 mm per year persisting over much of eastern Oregon. Seasonality of precipitation is higher in the west and declines across the eastern part of the state.

Colorado. This transect illustrates the topographic diversity gradient at the boundary between the tectonically active (western) and passive (eastern) regions of temperate North America (Badgley 2010).

The state of Kansas lies east of Colorado and is situated entirely within the Great Plains of central North America (Figure 14.4c,d). Although Kansas has the reputation of being “flatter than a pancake,” the elevation increases gradually but substantially from east to west, with a gain of about 1000 m (Figure 14.4c). Mean annual precipitation is inversely proportional to elevation, whereas seasonality of precipitation increases from east to west (Figure 14.4d). Tallgrass prairie characterizes the native vegetation of eastern Kansas, while shortgrass prairie characterizes the western edge, with mixed-grass prairie in between. Species richness ranges from 55 to 67 species per bin across the state, with low levels of spatial turnover (data from Bee 1981). This transect offers a contrast in topography and diversity to the three that feature strong topographic gradients.

The state of Oregon lies in the Pacific Northwest and features complex topography throughout (Figure 14.4e,f). The transect at 45° N passes through the western edge of the northern Rocky Mountains along the eastern border, then through the Blue Mountains and the Columbia Plateau in the central region of the state. The Cascade Range, which contains active volcanoes, lies in the western third of the state, and is bordered on the west by the broad Willamette Valley. The mountain peaks are generally lower than 2500 m in elevation, but relief is on the

order of several hundred meters over short lateral distances (Figure 14.4e). The coast and west side of the Cascade Range both receive high annual precipitation and form part of a temperate rainforest, where some of the largest trees in the world grow year round. The east side of the Cascades and the interior receive much less rainfall, with grassland and sagebrush scrub extending over much of central and eastern Oregon. In contrast to Colorado and Kansas, seasonality of precipitation tracks mean annual precipitation across Oregon (Figure 14.4f). Species richness ranges between ~75 and 95 species per degree longitude, with higher values in the Blue Mountains and the Cascade Range (data from Verts & Carraway 1998).

The transect across Ecuador depicts a tropical topographic gradient across a high mountain range (Figure 14.5). This striking gradient along the equator includes the western edge of the Amazon Basin at low elevation in eastern Ecuador, the eastern Andes with peaks that reach nearly 5000 m in elevation, a high plateau bordered by the western Andes at about 3000 m, then a gradual descent towards the Pacific Ocean (Figure 14.5a). Mean annual precipitation shows a peak along the eastern Andes and another along the western foothills. Although both peaks feature mean annual precipitation of nearly 4000 mm per year, the eastern peak is accompanied by low seasonality of precipitation, whereas the western peak is highly seasonal (Figure 14.5b). Evergreen rainforest is the dominant vegetation in the eastern lowlands, with areas of savannah and scrub near

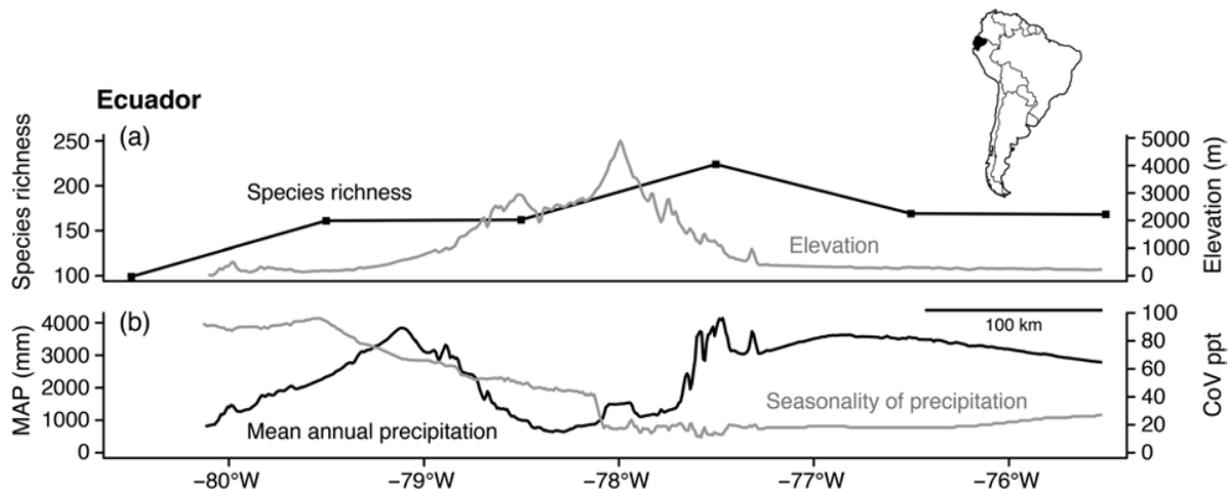


Figure 14.5 Transect across Ecuador at the equator. (a) Species richness for 1° bins of longitude, based on the distribution of geographic ranges that occur between 0 and 2° S. From east to west, species richness rises from ~160 species in the Ecuadorian Amazon Basin to ~225 along the eastern Andes, then declines towards the western Andes and the coast. Elevation, shown at a resolution of 1 km (lateral distance), is low east and west of the Andes and rises to nearly 5000 m in the eastern Andes. *Source:* Species richness adapted from Tirira (2007). Elevation data from US Geological Survey Center for Earth Resources Observation and Science (1996b). (b) The distribution of annual precipitation reflects moist air from Atlantic and Pacific sources, with peaks on the eastern and western flanks of the Andes. Mean annual precipitation is high throughout eastern Ecuador but declines steeply from the western Andes towards the Pacific coast. Seasonality of precipitation is highest in western Ecuador and declines across the mountains into the Amazon Basin. Note that the scale for all four variables differs from those in Figure 14.4. *Source:* Data for precipitation variables from the WorldClim database (Hijmans et al. 2005).

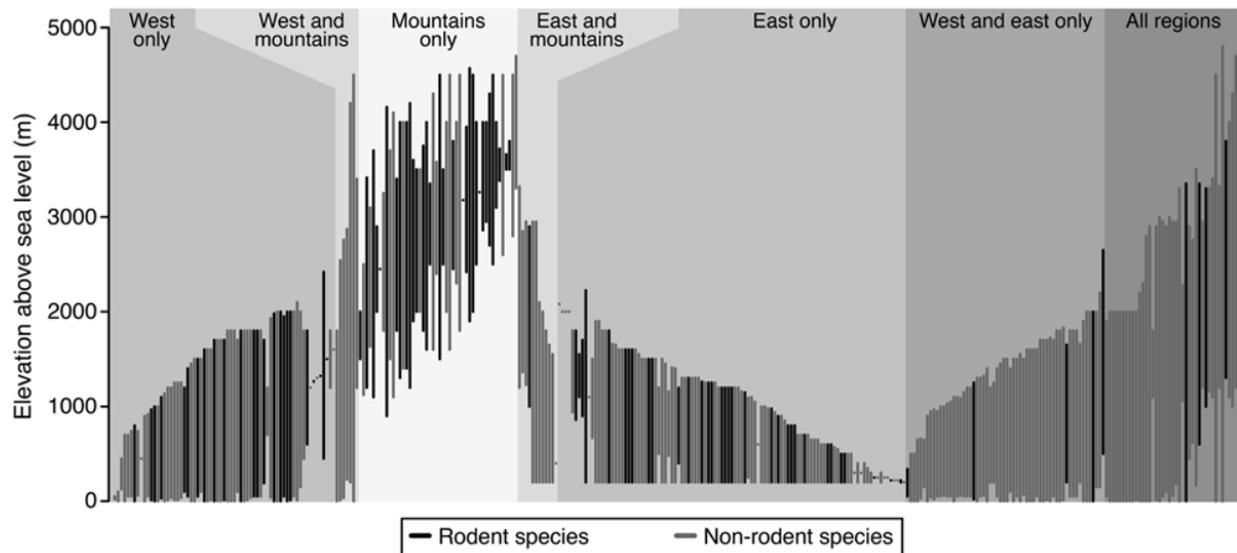


Figure 14.6 Elevational ranges for mammals in Ecuador, based on species from the transect in Figure 14.5. The range of each species is plotted as the lowest and highest reported elevational limits (Tirira 2007). Species are clustered geographically to illustrate the different geographic components of regional diversity. High regional richness is the consequence of species that uniquely occur at high elevations in combination with species that occur at lower elevations on either side of the Andes, as well as wide-ranging species.

the west coast. At higher elevations, a series of montane forest zones change to montane shrubland (*páramo*). The species richness of mammals ranges between 100 and 220 species per degree of longitude (data from Tirira 2007). From east to west, species richness rises from ~160 in the Amazon Basin to 220 on the eastern slopes of the Andes, then declines to ~160 in the western Andes and further to ~100 species along the west coast of Ecuador (Figure 14.5a).

The elevational ranges of Ecuadorian mammals illustrate several different geographic components of mammal diversity across topographic gradients (Figure 14.6). About 20% of Ecuadorian mammals occur west of the Andes, with elevational distributions mainly below 2000m. Another 20% of species occur only in the mountains, with elevational ranges between 1000 and 4500m. A few species' distributions are limited to the western side of the Andes at low to high elevations (west and mountains). About a dozen species occur only along the eastern slopes of the Andes from low to mid elevations (east and mountains). About 25% of species occur east of the Andes in the Amazon Basin. Nearly 20% of species occur both east and west of the Andes, but not at high elevations between these flanking regions. About 15% of species are found in all regions of Ecuador, some at lower elevations in river valleys and others with broad elevational ranges. The high regional diversity consists of species that occur uniquely on either side of the Andes at lower elevations, species that occur uniquely at high elevations and species with wide-ranging distributions. Notably, rodents make up more than half of the species that occur at only high elevations and about one-third of

the species that occur only west or only east of the mountains. In contrast, they make up around 10% of the species with more extensive longitudinal distributions. In addition to having more restricted geographic ranges, rodents often have lifestyles that are closely tied to properties of the substrate, which vary greatly over mountain slopes.

The four transects depicted in Figures 14.4–14.6 illustrate four general features of topographic diversity gradients for extant mammals: (i) the species richness of mammals rises sharply along major topographic boundaries between high and low elevation (Figures 14.4a and 14.5); (ii) regions of high topographic complexity show high diversity and high spatial turnover (Figures 14.4a,e, 14.5 and 14.6); (iii) regions of low topographic complexity show low diversity and low spatial turnover (Figure 14.4c); and (iv) the high diversity in montane regions consists of species restricted to high-elevation habitats (including many endemics), species that occur on either side of mountain ranges in heterogeneous habitats at lower elevations and wide-ranging species (Figure 14.6).

In contrast to transects across regions of high or low topographic complexity is a series of studies of mammal diversity in relation to elevation for individual mountains (Heaney 2001; Lomolino 2001; Rickart 2001; McCain 2004). The most common pattern is a peak in species richness at mid-elevations. The elevation at which diversity peaks is higher for taller mountains. Most of these elevational diversity gradients do not fit a mid-domain null model (the expectation that more species ranges overlap in the middle of a gradient due to spatial constraints at the end points) but correspond more closely

to area effects or climatic gradients (McCain 2005). The elevation of maximum diversity declines with increasing latitude, when controlling for base elevation and mountain height. This pattern reflects the overall decline in mountain and snowline height and the greater extent of Quaternary continental and montane glaciation at higher latitudes (Körner 2007; Egholm et al. 2009).

14.4 Topographic Diversity Gradients in Deep Time

If the topographic diversity gradient is such a fundamental feature of mammal distributions over Earth's topography today, then the fossil record should also contain evidence for this gradient. However, evaluating the geologic record of high elevations is problematic for continental landscapes, because high-elevation environments are erosional rather than depositional, and thus are rarely present in the long-term stratigraphic record. Although mountains and plateaus may exist for tens of millions of years, the fossil record is preserved primarily in basins at low elevations. Caves, montane lakes and high-elevation playas are an exception to this pattern; these settings may persist for a few million years, but diminish over the long-term record.

Although it is not possible to document changes in diversity across ancient mountain ranges per se, as in Figures 14.4–14.6, it is feasible to compare diversity at lower elevations in topographically complex landscapes with diversity in plains and lowlands. Even at lower elevations preserved in the fossil record, topographically complex regions exhibit elevated diversity as a consequence of high spatial turnover across heterogeneous habitats (Davis 2005; Badgley et al. 2014). This pattern can be seen in present-day North America by comparing the species richness of mammals in the transect across Oregon at 1000 m elevation (Figure 14.4e) with the diversity of mammals in the transect across Kansas at 1000 m (Figure 14.4c). Across Oregon, species richness is greater than 70 per bin at the lowest elevations, whereas in western Kansas it is below 60 per bin at the highest elevations. The continental fossil record contains little of the high-elevation component of mammal diversity, such as the species in Figure 14.6 that occur only in mountains. But sedimentary sequences of river systems and lake margins preserve a fossil record of some of the species that inhabited foothills along with basin inhabitants at low elevations.

The North American fossil record of continental environments includes numerous widely distributed Cenozoic sequences of fluvial, lacustrine and airfall deposits from contrasting topographic landscapes

(Woodburne 2004). A rich record of mammals occurs in fossil localities scattered across the tectonically active region from the Rocky Mountains to the Pacific Coast and from the tectonically quiescent Great Plains. This record allows us to contrast mammal diversity over millions of years in landscapes that were equivalent in topographic complexity to modern Oregon (Figure 14.4e) and modern Kansas (Figure 14.4c). Rodent diversity over time and space (Figure 14.7a) is especially informative, since rodents constitute over half of mammal diversity and their life habits are often closely tied to substrate properties, such as soil depth and texture (Merritt 2010). Figure 14.7b illustrates rodent diversity at the species level between 25 and 5 Ma (essentially over the Miocene) for the tectonically active and passive regions of North America. The areas sampled and the number of fossil localities in each region over time are commensurate, so these differences in diversity should not be an artifact of sampling (Finarelli & Badgley 2010).

The pattern of rodent diversity in tectonically active and passive regions of North America has three notable features (Figure 14.7b). First, diversity in the active region was lower than that in the passive region for about half of the 20 million-year record. Hence, if these records are accurate indicators of historical diversity, the topographic diversity gradient in North American mammals was absent for millions of years and present during extended time periods. Second, the strongest topographic diversity gradient occurred between 17 and 13 Ma, during an interval of global warming known as the Miocene Climatic Optimum (Zachos et al. 2001, 2008). During this interval, diversity in the active region greatly exceeded that in the passive region, reaching the highest diversity of the entire record. The highest per capita diversification rates also occurred during this middle Miocene interval (Finarelli & Badgley 2010). Using a Bayesian modeling approach, Silvestro and Schnitzler (Chapter 15) identified a peak in origination rates at this time for rodents in the active region but not in the passive region. Third, this interval featured widespread tectonic activity in the intermontane region, including eruptions of many of the Columbia Plateau flood basalts (Hooper et al. 2002), rapid extension and block faulting in the Basin and Range Province (McQuarrie & Wernicke 2005) and uplift in the northern Rocky Mountains (Fields et al. 1985).

This record offers two major insights into the topographic diversity gradient of mammals. First, this gradient is not a persistent feature over Earth history. Rather, high diversity in topographically complex regions is strongly expressed during certain periods and is absent in others. Second, the peak of diversity in the active region over the last 25 My, prior to today,

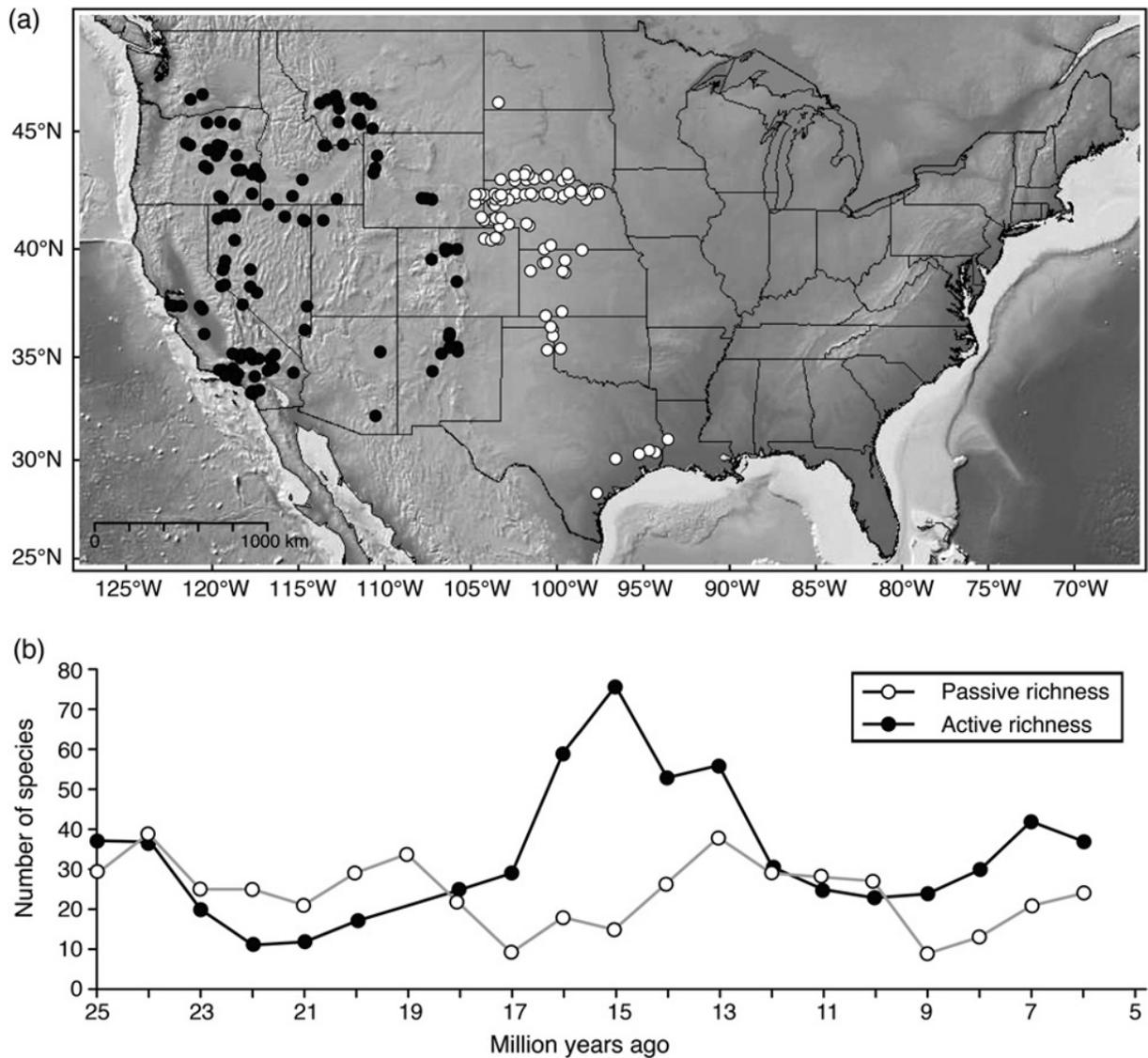


Figure 14.7 Fossil record of rodent richness from the tectonically active region of the western USA and the tectonically stable (passive) Great Plains. (a) Map of fossil localities from the western region (shaded circles) and the Great Plains (open circles) from 25 to 5 Ma. *Source:* Map made using GeoMapApp: www.geomapapp.org. (b) Rodent richness at the species level, compiled for 1 million-year intervals, from the western region (shaded circles) and the Great Plains (open circles). Rodent richness was much greater in the active region between 17 and 13 Ma, during an interval of global warming and widespread tectonic activity across western North America. *Source:* Adapted from Finarelli & Badgley (2010).

occurred when both climate change and tectonic activities were influencing the landscape – suggesting that the interaction of climate change and tectonic activity had a powerful influence on diversification (Finarelli & Badgley 2010). The modeling approach of Silvestro and Schnitzler (Chapter 15) confirmed this interpretation; in addition, they found that the rate of climate change had a greater impact on rodent diversification than did temperature per se. It is unclear how much of the diversity peak in Figure 14.7b resulted from speciation within the active region and how much resulted from

immigration into the active region from the passive region or from areas beyond the documented record. It is likely that both processes contributed to the middle Miocene peak in diversity in the tectonically active region of western North America. The divergence of major lineages of heteromyid and sciurid rodents in western North America dates to the middle Miocene, according to molecular phylogenies (Hafner et al. 2007; Zelditch et al. 2015), providing evidence that this period of tectonic and climatic change coincided with cladogenesis.

14.5 Mammals that Drive the Topographic Diversity Gradient

Among the ca. 5400 species of extant mammals, most are small, weighing less than 1 kg in adult weight (Wilson & Reeder 2005). The most species-rich orders are Rodentia (rodents), Chiroptera (bats) and Soricomorpha (shrews, moles); together, these clades of primarily small mammals make up more than 70% of living mammal species and dominate latitudinal and elevational diversity gradients for mammals (Simpson 1964; Pagel et al. 1991; Patterson et al. 1998; Badgley & Fox 2000; Heaney 2001; McCain 2005). In North America, for example, the latitudinal diversity gradient is dominated by bats, whereas the topographic diversity gradient is dominated by rodents (Badgley & Fox 2000). Both groups exhibit high spatial turnover along strong environmental gradients. Within mountains and topographically complex regions, spatial turnover in diversity and taxonomic composition is greater for rodents than for other mammalian orders (Patterson et al. 1998; Badgley et al. 2014).

Small mammals show strong responses to landscape history over geologic time as well. Western North America has a robust fossil record for both large and small mammals over the last 25 My (Barnosky & Carrasco 2002; Kohn & Fremd 2008; Badgley & Finarelli 2013; Riddle et al. 2014a). The Great Basin, a topographically complex region with nearly 200 mountain ranges and intervening basins, expanded by over 200 km in longitudinal width through the geological process of extension (stretching and faulting) from 25 Ma to the present time (McQuarrie & Wernicke 2005). The fossil record of the Great Basin shows that large and small mammals responded quite differently to these changes in the landscape (Badgley et al. 2014). The species richness of large mammals declined slowly, with regional extinction of several groups, including equids (horses), rhinocerotids (rhinos) and camelids (camels). In contrast, the diversity of small mammals, including Rodentia and Lagomorpha (hares and rabbits), increased from 16 Ma to the present. Consequently, the proportion of rodent species within the total mammalian fauna increased from ~0.20 at 12 Ma to ~0.50 by 2 Ma, approaching the modern proportion of 0.63 in the Great Basin.

The elevated diversification of small mammals during the middle Miocene in western North America is also supported by molecular phylogenies and phylogeographic patterns. For example, species in the Heteromyidae (kangaroo rats and pocket mice) occur across the western USA, Mexico and Central America today. Molecular phylogenies reveal deep branching events among extant genera and species of heteromyids that occurred during episodes of mountain building over the last 20 My (Riddle 1995; Hafner et al. 2007). Spatial

turnover in heteromyid species, as well as in other small-mammal clades, is high across the present-day North American landscape, with several species showing congruent patterns of geographic distribution linked to physiographic barriers (Riddle et al. 2014a). Likewise, in South America, rodents dominate high-elevation faunas and show high spatial turnover along elevational gradients (Figure 14.6). Radiations among several South American rodent groups coincided with the accelerated uplift of the Andes during the late Miocene (Hoorn et al. 2010).

Topographic, climatic and ecosystem changes influenced not only taxonomic diversity but also ecological diversity across space and time. North American rodents exhibit an impressive array of dietary and locomotor specializations that reflect adaptations to different food resources and substrates, as well as macro- and microhabitats found across topographically complex landscapes (Samuels & Van Valkenburgh 2008; Samuels 2009). The high diversity of rodents in the topographically complex region of western North America corresponds to a high frequency of small herbivores and granivores in regional and local faunas (Badgley & Fox 2000).

In contrast, some geographically and genetically distinct populations and species express little morphological or ecological divergence despite ranging across topographically complex regions. For example, a phylogenetic study of the heteromyid *Perognathus parvus* found deep divergences among populations lacking significant morphological differences, revealing the presence of a cryptic “species group” that resulted from geographic isolation among clades separated by physiographic barriers, including the Columbia Plateau and Snake River Plain (Riddle et al. 2014b). Likewise, in Sciuridae (squirrels), a decoupling of morphological disparity and taxonomic diversity among North American chipmunks and ground squirrels points to geographically mediated drivers of diversification during the tectonically active formation of western North America, rather than early rapid or steady phenotypic divergence (Zelditch et al. 2015). These examples indicate that regions of high topographic complexity can be sites of both adaptive and non-adaptive radiations in the evolutionary history of small mammals.

14.6 Biogeographic Processes in Topographically Complex Regions

The topographic diversity gradient results from the interaction of biogeographic and geomorphologic processes with Earth’s climate system. Biogeographic processes, including dispersal and geographic-range shifts,

speciation and extinction, have given rise to the taxonomic and ecological diversity of species whose geographic ranges are arrayed across Earth in a dynamic patchwork. The high diversity of mammals in topographically complex regions results from a high frequency of endemic species alongside a number of wide-ranging species, as in Ecuador (Figure 14.6). We present four examples in this section of biogeographic processes that contribute to the high diversity in montane regions, both in the present day and over Earth's history.

14.6.1 Geographic-Range Shifts

Species ranges expand or shift via dispersal. Dispersal is the movement of individual organisms out of their natal areas to colonize new areas (Lomolino et al. 2010). This process has contributed to changes in the topographic diversity gradient as species originating in lowland areas disperse into montane regions and species in montane regions expand into lowlands or cross drainage divides to colonize high-elevation habitats. Quaternary mammals experienced substantial shifts in their geographic ranges in response to glacial advances and retreats (Graham et al. 1996; Lyons 2003). For mammals from the contiguous 48 US states, the average shift in the centroid of the geographic range during the transitions from preglacial to glacial, glacial to Holocene and Holocene to modern time intervals was between 1200 and 1400 km (Lyons 2003), with shifts occurring along multiple geographic and climatic gradients. Species of larger adult size had larger range shifts than smaller species; however, both large and small species experienced significantly smaller range shifts in the topographically complex landscapes of the western USA than in the plains and lowlands of the eastern USA (Lyons et al. 2010). Montane species moved to lower elevations during glacial periods and to higher elevations during interglacials (Grayson 1987; Heaton 1990; Barnosky 2004).

Elevational range shifts have continued during the anthropogenic warming over the last few centuries. For example, a re-survey of small mammals (rodents, shrews and a pika) along an elevational gradient of 3000 m in Yosemite National Park, California between the early 20th and the early 21st century found that half of the species had shifted their elevational limits upward by 500 m (Moritz et al. 2008). During the 100 years of climate change between the first and second surveys, the average minimum temperature increased by $\sim 3^\circ\text{C}$.

14.6.2 Adaptations to High Elevation

High elevations differ in several physical properties that may require physiological or behavioral adaptations for sustained occupation. In addition to reduced land area at

higher elevation, temperature and atmospheric pressure decrease with altitude (Körner 2007). The American pika (*Ochotona princeps*), a small lagomorph that inhabits montane slopes in western North America, tolerates cool temperatures well and warm temperatures poorly (Smith & Weston 1990). Some mammals that live continuously at high elevations have the ability to enter torpor (some bats) or hibernation (marmots, mountain pygmy possum) where temperature seasonality is high. Some Andean mice (*Phyllotis andium* and *P. xanthopygus*) have a greater consumption of carbohydrates than fats, compared to relatives at low elevations; carbohydrate metabolism yields more oxygen than lipid metabolism and is considered a strategy for coping with the effects of elevations over 4000 m (Schippers et al. 2012). Most mammals that inhabit high elevations are small and utilize underground microhabitats or extensive rock piles for warmth and shelter from predation. Larger mammals, such as ungulates, may migrate between higher and lower elevations according to the availability of forage. Adaptations for montane habitats contribute high-elevation species to the topographic diversity gradient.

14.6.3 Allopatric Speciation and Neo-Endemism

Populations at high elevations often occupy habitats that are discontinuous because of steep slopes, deep valleys and heterogeneous microclimates. In some regions, individual mountains or small mountain ranges are “sky islands,” isolated by long distances separating high-elevation habitats. Thus, montane regions present numerous opportunities for the isolation of populations, in contrast to the distribution of the same species or sister taxa in nearby regions of low elevation and relief. Sustained isolation offers the opportunity for evolutionary divergence, which can result in genetic differentiation among populations, or in speciation. These processes contribute small-range endemic populations and species to topographic diversity gradients. For example, neo-endemism and polymorphic populations in Californian mammals are concentrated in the Sierra Nevada Mountains, the coastal ranges and the Transverse and Peninsular ranges of southern California (Davis et al. 2008). Other montane regions with endemic mammals include the Ethiopian Highlands (Yalden & Lagen 1992), the Trans-Mexican Volcanic Belt (Demastes et al. 2002) and the Andes (Tirira 2007). Recent divergence of species and populations in topographically complex regions is also the basis for recognizing many montane regions as areas of high conservation priority (Fjelds et al. 2012; Rosauer & Jetz 2015).

The genetic structure of mammal populations often has a distinctive landscape signature in topographically complex regions but not in adjacent lowlands or plains, reflecting

range shifts or range limits in response to topography. For example, geographic separation of distinct clades within two species of *Microdipodops* (kangaroo mice) predates Quaternary glacial cycles and instead aligns with complex topography in Nevada and increased aridification in the rain shadow of the Sierra Nevada Mountains (Hafner et al. 2008; Hafner & Upham 2011). A study of chipmunks (*Tamias*) found high phylogeographic structure and diversity in *T. amoenus* associated with specific mountain ranges from the north-western USA (Demboski & Sullivan 2003). In contrast, the phylogeographic structure of the eastern chipmunk (*T. striatus*) from the Great Plains and areas east of the Mississippi River reflects population expansion from glacial refugia in the south-eastern USA (Rowe et al. 2006).

For the American pika (*Ochotona princeps*) in western North America, Quaternary glacial cycles offered repeated opportunities for population fragmentation and coalescence. Range expansions during glacial intervals promoted genetic admixture, although montane glaciers and large pluvial lakes were barriers that enhanced isolation of populations during long glacial intervals (Galbreath et al. 2010). Phylogeographic structure in the American pika is congruent with patterns documented in co-distributed small mammals (Riddle 1996; Matocq 2002; Hafner et al. 2008; Neiswenter & Riddle 2010; Hafner & Upham 2011), suggesting that intermontane lineages share a common history of barriers to gene flow imposed by interactions between complex topography and climate.

14.6.4 Extinction of Montane Populations

Montane populations would seem to be more vulnerable to extinction than those of lowland regions because of their small areas of habitat and their isolation at high elevations. Many montane species may exist as metapopulations, with individual populations becoming extinct and dispersal leading to recolonization. Global warming should elevate extirpation rates of montane populations, as has been documented for the American pika in mountain ranges of the Great Basin (western USA) over the last century (Beever et al. 2003). Global cooling, in contrast, should reduce extinction rates in montane regions, as populations move downslope into larger areas and come into closer proximity with conspecific populations from other parts of the landscape (Brown & Kodric-Brown 1977).

For birds and plants, there is evidence that topographic complexity has buffered populations from extinction during Quaternary glacial cycles and earlier episodes of climate change (Bush et al. 2004; Fjeldså et al. 2012), due to the high heterogeneity of habitats and short distances among habitat refuges. If montane mammals have experi-

enced this influence, then reduced extinction rates would also contribute to high diversity in montane regions.

14.7 Effects of Modern Climate Change on Montane Diversity

Mammals in mountains are vulnerable to current and future climate changes. Like high latitudes, montane regions are predicted to experience some of the largest climate changes over the next 100 years, including the decline and loss of high-elevation alpine climates (Ackerly et al. 2010). Climatic warming impacts species individually as they shift their geographic ranges upward or poleward or adapt to new conditions, and alters biotic interactions under no-analog climates and during the formation of novel communities (Williams & Jackson 2007; Tylianakis et al. 2008; Gilman et al. 2010; Blois et al. 2013).

In western North America, upward shifts in mammalian ranges over the last century have been documented in three areas within the Sierra Nevada Mountains of California (Rowe et al. 2014) and in numerous mountain ranges of the Great Basin (Beever et al. 2003). Changes in small-mammal richness and associated changes in community abundance, structure and function in the intermontane west during anthropogenic climate warming and habitat transformation outpace natural variation and responses recorded over longer time scales in the fossil record (Grayson 2002; Blois et al. 2010; Terry et al. 2011; Terry & Rowe 2015). This combination of factors makes forecasting climate-change impacts within mountainous regions particularly challenging, yet it is critical for the protection of species, ecosystems and evolutionary processes in montane biodiversity hot spots.

14.8 Conclusion

Although mountains only cover about 10% of Earth's land surface, outside of Antarctica (Körner 2016), more than half of the world's continental mammals occur in montane regions today. This topographic diversity gradient is dominated by species of small mammals, which exhibit high spatial turnover in mountains and in topographically complex regions containing numerous mountain ranges and intervening basins. The fossil record suggests that this pattern has not characterized continental ecosystems throughout the Cenozoic. Instead, the topographic diversity gradient has been absent for millions of years and has been strongly expressed during intervals of climatic warming and tectonic activity.

A combination of ecological, evolutionary and historical processes has shaped the topographic diversity gradient of mammals. Evaluating the separate and combined influences of these processes presents an opportunity for integrating neontological and geohistorical data and perspectives (Badgley 2010; Graham et al. 2014). Protection of biodiversity in montane regions poses one of the major conservation challenges of the 21st century.

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