



PALEONTOLOGY

Tectonic extension and paleoelevation influence mammalian diversity dynamics in the Basin and Range Province of western North America

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Landscape properties have a profound influence on the diversity and distribution of biota, with present-day biodiversity hot spots occurring in topographically complex regions globally. Complex topography is created by tectonic processes and further shaped by interactions between climate and land-surface processes. These processes enrich diversity at the regional scale by promoting speciation and accommodating increased species richness along strong environmental gradients. Synthesis of the mammalian fossil record and a geophysical model of topographic evolution of the Basin and Range Province in western North America enable us to directly quantify relationships between mammal diversity and landscape dynamics over the past 30 million years. We analyze the covariation between tectonic history (extensional strain rates, paleotopography, and ruggedness), global temperature, and diversity dynamics. Mammal species richness and turnover exhibit stronger responses to rates of change in landscape properties than to the specific properties themselves, with peaks in diversity coinciding with high tectonic strain rates and large changes in elevation across spatial scales.

INTRODUCTION

Landscape history is crucial for exploring the drivers of biological diversity (1): Landscape properties provide the template over which species arise, adapt to spatiotemporal changes in their environment, shift their geographic ranges, and disappear. Mountain building, erosional processes, and climate feedbacks all contribute to the generation and maintenance of biodiversity hot spots in regions of high topographic complexity (2–4). Today, mountainous regions support elevated taxonomic, ecological, and phylogenetic richness for many clades and across all continents, yet the factors shaping what is known as the topographic diversity gradient (TDG) over deep time remain elusive (2, 5, 6). The fossil record and diversification history of clades in mountainous regions demonstrate the complex histories of these gradients in relation to uplift and climate (3, 7–11) and provide a key opportunity to investigate long-term landscape and biogeographic processes underlying the formation and persistence of the TDG. Disentangling the relative roles of tectonic activity, paleoelevation, and climate has been a great challenge, establishing the need for further integration of geologic and biotic records (12–14).

A promising region of study is the North American continent, with contrasting eastern and western regions of landscape history and topographic relief that parallel a marked east-to-west rise in mammal species richness (1, 5, 6). The complex landscape history of the Basin and Range Province is increasingly well studied (15, 16), including recent geodynamic models over the past 36 million years (Ma) (17–19). In these models, a large dataset of fault movement (16) and geophysical properties of the lithosphere form the basis for estimating horizontal crustal displacement rates within the region. Fitting these rates to the surface of a sphere provides estimates of

lithospheric strain rates as a function of position and time. Dilational strain rates are integrated to estimate changes in crustal thickness and elevation under the assumption of conservation of volume. These geophysical models thus provide estimates of extensional strain rates, crustal thickness, and paleoelevation that are smoothed over 50 to 100 km (17–19).

Continental basins in North America document an extensive but patchy record of mammal species richness, comprising large and small mammal taxa of diverse ecological roles, over the last 30 Ma (20). Prior work has contrasted diversity trends in the tectonically active western US versus the tectonically quiescent Great Plains region in relation to hypothesized landscape and climatic forcings (1, 7, 9, 21). A pronounced peak in species richness in the Basin and Range coincided with global warming and an increase in extensional faulting from 18 to 14 Ma ago (22). While Cenozoic climate change has been shown to contribute to continental-scale biodiversity patterns in North America (23, 24), lack of a corresponding richness increase in the tectonically quiescent eastern region suggests that increasing landscape complexity during this time exerted a first-order control on biodiversity patterns in the west. Furthermore, intervals of a weak or absent TDG in the North American fossil record suggest that the presence of topographic complexity alone is insufficient to result in a strong positive relationship between relief and species richness (9). By reconstructing geohistorical dynamics in the Basin and Range in relation to patterns from the fossil record, we build on this prior work and provide critical tests of the mechanisms promoting biodiversity in mountainous regions and a framework for understanding the TDG globally and over deep time.

Geophysical models of paleotopography provide elusive and critical estimates of the history of topographic barriers, ruggedness, and elevational gradients to test their potential influence on origination, extinction, and geographic-range shifts. Here, we couple novel quantitative estimates of area, extensional strain rate, paleoelevation, and topographic ruggedness for the Basin and Range with regional mammal richness and turnover over the last 30 Ma. Combined with records of global temperature and the regional sedimentary rock

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area, we evaluate the individual and joint effects of geohistorical variables as predictors of mammal diversity. Spatiotemporal variation in the timing and rate of tectonic extension and changing relief across the province (16, 17) influence the distribution of the sedimentary and fossil records (25). Therefore, we investigate these relationships within the Mojave region in the southern Basin and Range, testing the coupling between landscape history and species richness and composition across a hierarchy of spatial scales. As the longest subregional fossil record of the Basin and Range (26), evaluation of the Mojave region allows us to continuously sample at a subregional scale, reducing the potential for estimates of turnover to be confounded by spatial variation in the fossil record of the western US across temporal intervals (27, 28).

Here, we address three primary questions: (i) What are the primary landscape and climate predictors of species richness and turnover in mammals in the tectonically active western North America over the past 30 Ma? (ii) What is the relative importance of and interactions between predictors? (iii) What are the potential underlying mechanisms linking landscape, climate, and diversity change? Increased land area and ruggedness are known enhancers of biodiversity today and in the Plio-Pleistocene, including pronounced turnover and endemism in topographically complex regions (6, 8, 29, 30). Therefore, we expect to find a strong relationship between these landscape properties and fossil diversity. In contrast to analysis of modern-day species-richness-environment relationships, our geologic and paleontological datasets allow us to quantify the relative importance of rate of change variables compared to properties of the landscape themselves. We evaluate species richness and turnover in tandem, given that faunal turnover (e.g., changes in dominant mammalian families) can occur without changes in richness, thereby capturing a distinct biotic response. We expect the rate of change (landscape or climate) to be a key factor influencing variation in species richness and turnover over geologic time. We use horizontal extensional strain rate as a proxy for the rate of topographic change, which, in turn, acts as a control on erosional rates and geomorphic processes, the formation of orographic and temperature gradients, and the degree of habitat heterogeneity (31). Such landscape dynamics create novel habitats and ecological niches leading to species adaptation, facilitate geographic isolation of populations and speciation, and open corridors for species movement. We therefore expect strain rate to be a strong predictor of species richness and turnover patterns. We expect to see a decline in species richness as the transient and high relief generated during intervals of rapid uplift (e.g., period of high strain rate) reaches a steady-state landscape (e.g., erosion equals uplift) and persistent relief structure.

We expect interplay between climate change and topographic complexity to further shape diversity dynamics. Mountains alter regional climate conditions (32, 33), whereas periods of global climate change lead to different diversity outcomes in topographically complex versus low-relief regions, with elevational gradients often acting as refugia or dispersal corridors (34). Moderate rates of climate change may promote speciation and dispersal processes; however, high rates may lead to species loss if conditions change too rapidly for species to adapt or track their preferred climate (35). Given the changing configuration of topographic complexity of the Basin and Range over the Cenozoic (15, 17, 18), we further expect the opening of low-elevation corridors and climate conditions to facilitate movement into the province. To provide a control and isolate the specific influences of tectonic activity and topographic complexity (versus

climate change alone), results from western US are compared with the adjacent, low-relief, and tectonically quiescent Great Plains region. If climate, and warming in particular, exerts a first-order control on diversity, we expect to see parallel rises in diversity in both regions during the middle Miocene followed by declines with cooling, independent of regional changes in landscape. In contrast, if the two regions are decoupled, a global-scale driver, such as warming, is unlikely to be the dominant control on diversity patterns, necessitating an assessment of regional scale factors, such as landscape change. We note that a lack of correspondence in diversity records between the tectonically active western and quiescent eastern regions has been found in previous studies on specific mammalian clades (7–9, 21). Integration of geological, climatic, and biotic history is critical for unraveling the underlying ecological and evolutionary processes causing elevated biodiversity in topographically complex regions.

RESULTS

Trends in landscape, climate, and mammal diversity

Models of topography and ruggedness derived from geodynamic models (17, 18) demonstrate a marked reconfiguration of the Basin and Range landscape at model resolutions of $0.25^\circ \times 0.25^\circ$ (including formal errors) over the last 30 Ma (Fig. 1 and movies S1 and S2). Once dominated by continuous north-south running highlands (Nevadaplano, Mogollon Highlands) west of what are today the Rocky Mountains (Fig. 1A, 28 Ma ago), the region experienced lowering of mean elevation and increasing ruggedness during tectonic extension (Fig. 1, 21 to 0 Ma ago; Fig. 2F). Given the relatively coarse spatial scale of the tectonic model and topographic estimates, the roughness metric presented herein resolves broad-scale features (e.g., long-wave-length surface relief) rather than fine-scale features, like steep valleys and river drainages adjacent to neighboring peaks. Although we are unable to resolve fine-scale geomorphic features, we expect the two scales of roughness to be correlated, with increases in roughness from the modeled paleotopography capturing what is likely even higher localized relief as tectonic faulting leads to steep gradient formation and the rearrangement of physiographic barriers. Monotonic increase in surface area contrasts with variable strain rate over time, with the highest extensional strain rate occurring during the middle Miocene (Fig. 2, D and E). Global temperature declined and became more seasonal throughout this history (36, 37) except during the mid-Miocene Climatic Optimum (MMCO), when continental temperatures increased by 4° to 8°C from 18 to 14 Ma ago (Fig. 2C) (38). The rate (slope) of temperature change within 1-Ma bins is variable through the record, with higher rates of change at the Oligo-Miocene boundary, following the MMCO (e.g., during rapid cooling), and near the Plio-Pleistocene boundary (Fig. 2C).

Species richness in the tectonically active western US ranged from 51 to more than 200 species over the 30-Ma record, compared to the less variable record of the tectonically quiescent eastern region (species richness ranged from 90 to 189; Fig. 2A and figs. S1 to S3). Details and comparison of evaluated species richness estimators (range-through using Bayesian adaptive credible intervals versus shareholder quorum subsampling) can be found in Materials and Methods and the Supplementary Materials (Supplementary Results and figs. S4 and S11). In the tectonically active region, low species richness persisted through the late Oligocene and early Miocene, followed by a steep increase starting around 19 Ma ago, a peak in species richness at 16 Ma ago, and a subsequent decline toward the present. The decline

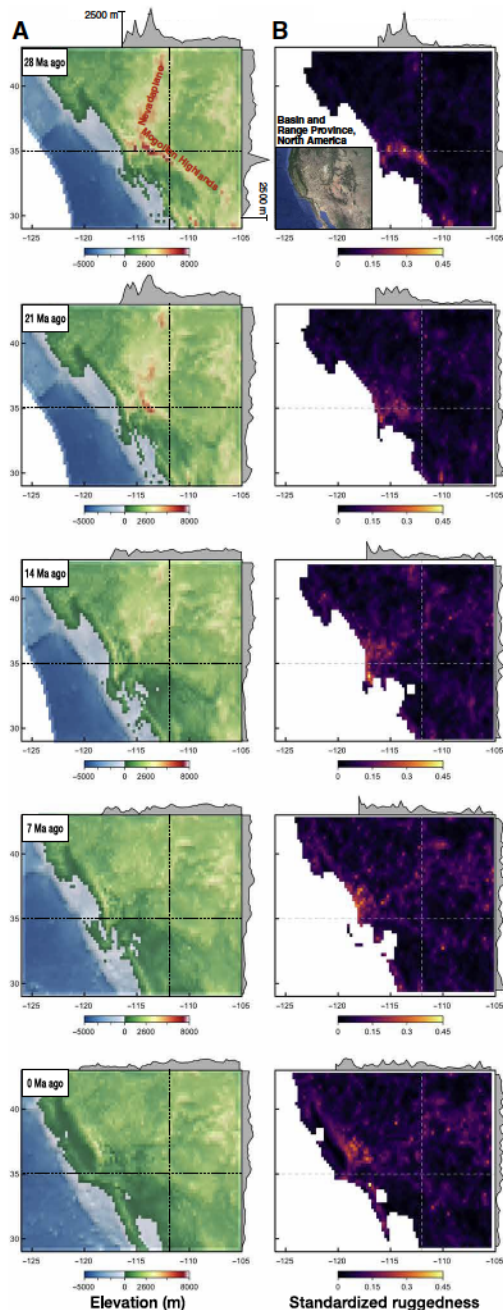


Fig. 1. Models of paleoelevation and standardized ruggedness of southwestern North America for four representative time intervals from the past 30 Ma and the present time. (A) Paleoelevation models represent topography estimates generated by geodynamic models, plotted at 0.25° resolution (17, 18) for time intervals 28 Ma ago, 21 Ma ago, 14 Ma ago, 7 Ma ago, and present (0 Ma ago). **(B)** Ruggedness is the mean of absolute differences between the paleoelevation of a 0.25° grid cell and the paleoelevations of its eight surrounding cells, standardized across all time intervals to better reflect the distribution of barriers and corridors through time independent of changes in the absolute values of elevation. Dashed gray lines show the position of the longitudinal and latitudinal transects presented along the top x axis and the right y axis, respectively, for each map. The elevational (A) and ruggedness (B) transects demonstrate the relief structure of the Basin and Range through time, including the presence of dispersal barriers and corridors. The inset map in the top right panel shows the present-day topography and location of the Basin and Range in western North America.

was greatest from 15 to 10 Ma ago, following the MMCO. Although richness patterns in the eastern quiescent and western active regions are moderately correlated [Fig. 2A; correlation coefficient (r) = 0.41; P = 0.02], the western diversity peak during the MMCO is distinct and marked, supporting a unique role for tectonic activity influencing regional diversity patterns. We evaluated changes in faunal composition following multinomial likelihood methods (9). Turnover patterns at the family level (increase or decrease of species within 48 mammalian families) in the western US are highest during the middle Miocene, further indicating biological response to landscape changes (Fig. 2B and figs. S5 to S7).

Relationships among landscape, climate, and mammal diversity

In the tectonically active western US, species richness is strongly correlated with the rate of tectonic extension (r = 0.85; P < 0.01) but uncorrelated with temperature (r = 0.10; P = 0.62) or temperature change (r = -0.08; P = 0.68). The strong relationship between species richness and strain rate remains after removing the effect of autocorrelation from our time series data (table S1). Richness is moderately correlated with area of the Basin and Range, topographic ruggedness, and outcrop area of the sedimentary rock record; however, these trends are weaker through time (Fig. 2 and fig. S8), and correlations are nonsignificant when data are time-series-transformed (table S1). Elevated rates of tectonic extension, leading to increasing land area and topographic ruggedness (Fig. 1) from 21 to 15 Ma ago coincide with the rapid rise in regional species richness (Fig. 2). Log-likelihood values expressing change in the proportional contribution of each family to total diversity is also highest during the middle Miocene (Fig. 2B and figs. S5 and S6). Turnover values are marginally significantly (P < 0.05) correlated with extensional strain rate (r = 0.40), standardized ruggedness (r = 0.37), area of the Basin and Range (r = 0.41), and temperature change (r = -0.40), but not with temperature or outcrop area (table S1 and fig. S9). In contrast to the tectonically active western US, the tectonically quiescent eastern US exhibits a significant correlation between species richness and $\delta^{18}\text{O}$ values (r = -0.50; P < 0.01), indicating a positive relationship between the number of species and global temperature (table S2).

Although neither global temperature nor rate of temperature change appears to influence patterns in mammal species richness in the western US during the Neogene, interactions between the generation of complex topography and climate change may still contribute to diversity patterns. To test for multiple drivers of species richness and turnover through time, we assessed the influence of different combinations of geohistorical variables on species richness and turnover with generalized least squares (GLS) regression and compared models in an Akaike information criterion (AIC) testing framework. The top models explaining variation in species richness (ΔAICc < 4, P < 0.05) all included strain rate (Fig. 3A), with the sum of the Akaike weights across all candidate models that included strain rate > 0.999. All but one model included at least one additional variable, with area, topographic ruggedness, temperature change, and outcrop area exhibiting low and roughly equal variable importance. Although not a significant correlate with species richness by itself, $\delta^{18}\text{O}$ values as a proxy for temperature were found in five of the top eight models, including the best fit model, suggesting that interactions between temperature and the rate of topographic change via tectonic extension play an important role in determining species richness patterns.

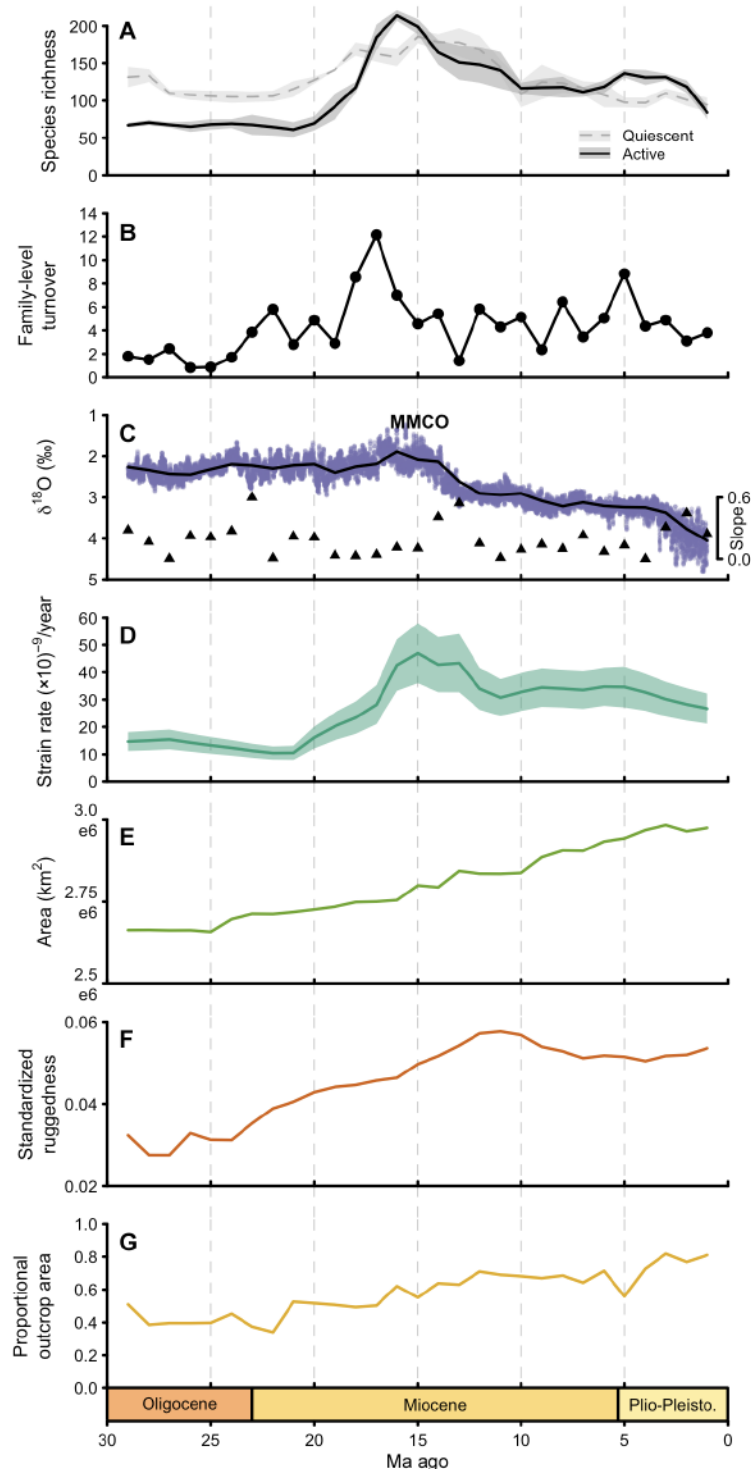


Fig. 2. Trends in species richness and family-level turnover from 30 to 1 Ma ago in relation to geohistorical variables. (A) Species richness and (B) family-level turnover are compared to (C) oxygen isotopic composition of benthic foraminifera [data from (36)] as a proxy for global temperature (1-Ma running average shown in black line) and rate of global temperature change (absolute value of the slope of oxygen isotopic composition within 1-Ma analytical bins shown in black triangles, refer to the right-hand axis for slope values); (D) strain rate as a measure of tectonic extension, (E) total area, and (F) median standardized ruggedness (higher values indicating higher relative ruggedness) of the Basin and Range; and (G) the proportional outcrop area of the rock record in the tectonically active region of western North America. Species richness in the tectonically active western region is contrasted against species richness in the tectonically quiescent eastern region in (A), with shading illustrating variation in species richness estimates based on age uncertainty for fossil localities. Shaded region in (C) represents uncertainty in strain rate estimates. Data for (D) to (F) are derived from models produced by Bahadori *et al.* (17) and data for (G) are derived from the Macrostrat database (50) as presented by Smiley (44).

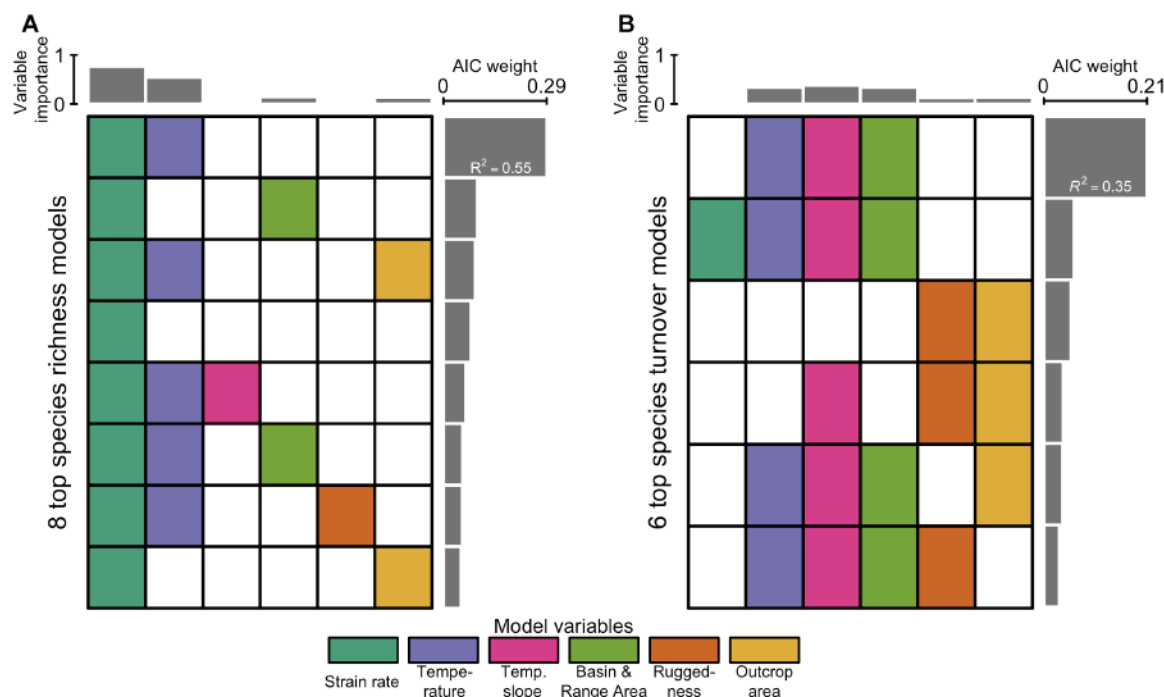


Fig. 3. Across a suite of candidate models, variation in species richness is consistently explained by tectonic strain rate, whereas family-level turnover is weakly explained by a combination of factors. Aggregated corrected Akaike information criterion (AICc) based support for top multiple regression models fitted using generalized least squares (GLS; delta AICc < 4 and $P < 0.05$) for (A) species richness and (B) family-level turnover. Each row represents a candidate model, with colored boxes indicating the abiotic variables present within that model. The top histogram shows the relative importance of each variable, with 1 indicating that the variable is found in all models and lower values indicating the proportion of models featuring that variable, weighted by each model's AIC weight. The side histogram reflects model support, with bar height indicating the proportional support for each model (out of 1). Nagelkerke (39) pseudo- R^2 values are shown for the top GLS model in each group. The dominant variables explaining variation in species richness and turnover are strain rate and temperature change, respectively.

Our results show a more complex relationship between landscape and climate variables and faunal turnover. Temperature, the within-bin rate of temperature change, and the area of the Basin and Range are found in the top model and share somewhat higher variable importance (Fig. 3B), with additional contributions from topographic ruggedness and outcrop area. Counter to expectations, tectonic extension (e.g., strain rate) does not appear to influence faunal turnover when evaluated in combination with other abiotic factors. GLS multiple regression models for turnover had poorer fit than for species richness [Nagelkerke (39) pseudo-coefficient of determination (R^2) = 0.35 versus 0.55 for top models, respectively], and correlation coefficients between turnover and landscape variables were weaker (table S1). Likewise, it would be reasonable to expect a positive relationship between turnover and rate of climate change, given that both often contribute to our designation of epochal boundaries. However, we find the opposite relationship, with elevated turnover sometimes occurring during high rates of climate change (e.g., Oligo-Miocene boundary), but not elsewhere in the record (e.g., turnover is low during rapid post-MMCO cooling). While the highest turnover values (Fig. 2B) occur at the onset of the MMCO and high rates of tectonic extension, suggesting an strong influence of these combined factors, a long-term association between landscape, climate, and turnover throughout the Cenozoic is not recovered. Given the variable spatial distribution of fossil localities through the Neogene, regional- to global-scale drivers may provide a poor fit to temporal turnover data if spatial turnover is

also high; therefore, study of topographic and climatic features within the Basin and Range will be necessary to further characterize the causes of faunal turnover.

Results at finer spatial scales within the Mojave region reflect broader regional patterns. The Mojave region experienced westward translation, rotation, and changes in area, mean elevation, and ruggedness through the Miocene (16, 17, 40). Fossil-rich formations in the Mojave, including the well-known Barstow and Dove Spring formations, present the longest subregional record in the Basin and Range (41–43), with peak mammal richness also occurring during the MMCO (Fig. 4A and fig. S10). Peak turnover in faunal composition within the Mojave occurred from 19 to 15 Ma ago (Fig. 4C and fig. S7). Changes in species richness correspond strongly with absolute changes in the mean elevation of the Mojave ($R^2 = 0.41$, $P < 0.01$; Fig. 4D). The magnitude of elevation change matters to a greater degree than the direction of change, with large increases in species richness and turnover occurring when landscape change is greatest for both elevation increase and decrease (Fig. 4, B to D). At the relatively coarse resolution of our geophysical model, large changes in elevation, either positive or negative, likely reflect increased topographic relief along local faults within the subregion. These rapidly generated topographic and associated climate barriers could then influence immigration and speciation processes (see Discussion), elevating species richness, contributing to faunal turnover across the landscape, and strengthening the TDG during this time.

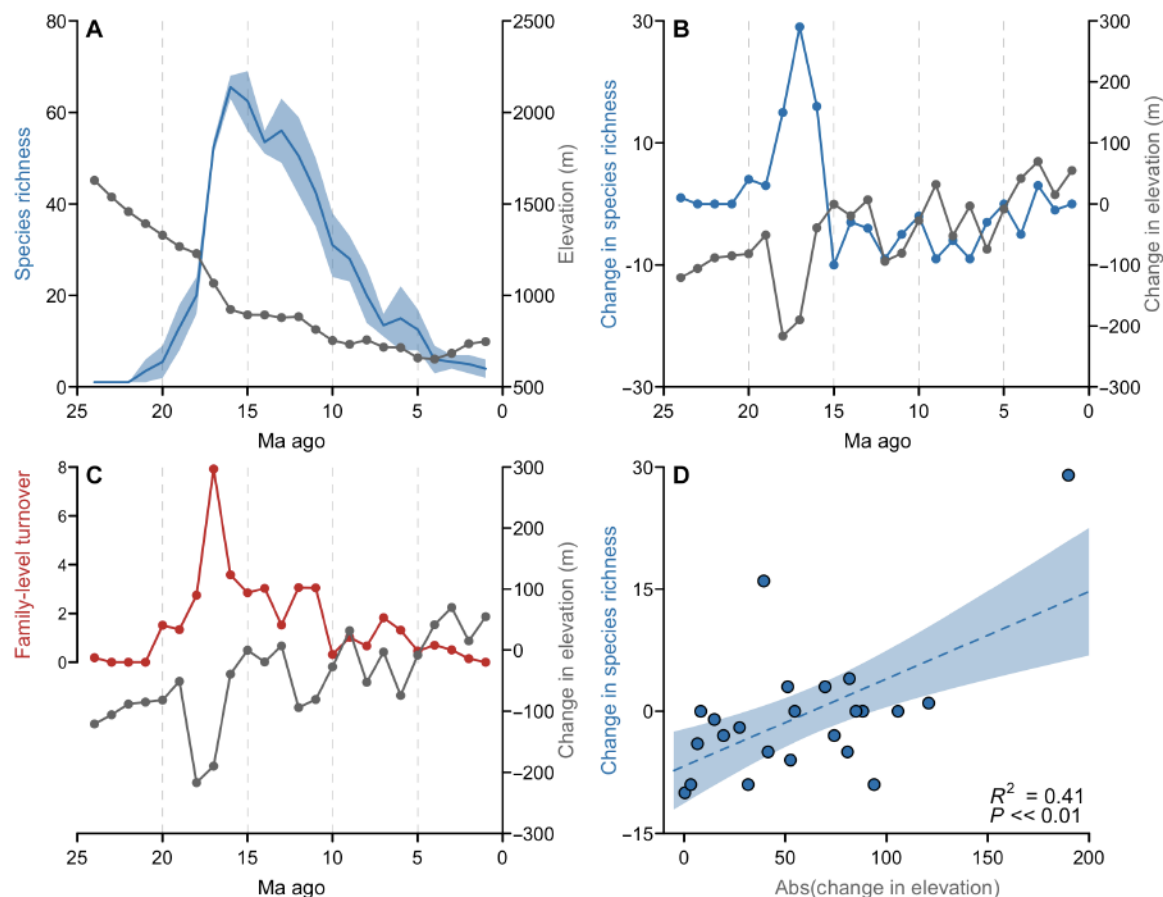


Fig. 4. Patterns of species richness, turnover, and elevation in the Mojave region of the Basin and Range Province. (A) Species richness (shaded region illustrates variation in species-richness estimates based on age uncertainty for fossil localities) in blue compared to mean regional elevation (gray symbols), (B) change in species richness in blue, and (C) family-level turnover in red compared to change in elevation from 25 to 1 Ma ago. (D) Change in species richness is significantly correlated with absolute changes in mean elevation, indicating a greater role for the magnitude of elevation change than for the absolute elevation in driving changes in species richness.

We find significant correlations between sediment outcrop area and strain rate ($r = 0.63$, $P < 0.01$) and species richness ($r = 0.55$, $P < 0.01$; table S1). However, poor linear model fits (fig. S8) suggest fundamentally different patterns of correlation among these variables, and correlations are not significant once data are transformed using first and generalized differences for time series data (table S1). Because regional species richness did not tightly track changes in province area or sediment outcrop area, we do not find support for strong species-area effects or preservation dominating the record. Although sampling bias may have contributed to low species richness before 19 Ma ago, the Middle Miocene peak richness remains a feature that cannot be explained by outcrop area or the number of fossil localities (22, 44).

DISCUSSION

Phases of diversity change in relation to climate and landscape

Our results support a clear relationship between mountain-building processes and the generation of the TDG. The integration of geophysical and fossil data through the Neogene extends this strong association through deep time. We find that the rate of landscape

change is the strongest and most consistent predictor of species richness across spatial scales. On the basis of our analyses, we recognize three phases in the history of mammalian diversity in the western US from 30 to 1 Ma ago and propose a set of underlying mechanisms for those phases.

(Phase 1) From 30 to 20 Ma ago, species richness was low and steady with low to moderate faunal turnover (Fig. 2, A and B). The collapsing Nevadaplano and Mogollon highlands were likely still a topographic barrier to immigration from the east and south, respectively, whereas large areas of low relief meant few opportunities for geographic speciation within the province (Fig. 1, 28 Ma ago). The comparatively smaller area of the tectonic province and outcrop area of basin sediments would have dampened fossil preservation, potentially leading to underestimates of species richness, especially of poorly preserved high-elevation fauna, across the region.

(Phase 2) From 19 to 14 Ma ago, elevated rates of tectonic extension and widespread fault activation, leading to increasing land area and topographic ruggedness (Fig. 1, 21 to 14 Ma ago), coincided with the rapid rise in regional species richness (Fig. 2). Landscape reorganization, in combination with MMCO warming, created circumstances for geographic and ecological speciation, elevational range shifts, and immigration into the province. In the

Mojave region, species richness and turnover increased markedly when localized changes in elevation were large and rapid (Fig. 4). These results imply a nonlinear response to landscape change, whereby biodiversity response is concentrated during intervals of rapid and large elevation change. Findings across spatial scales suggest that regional landscape processes serve as a primary regulator of species richness and that richness responds to the rate of landscape change more than to the specific properties themselves. While extensional processes leading to the formation and filling of basins allow for a more persistent fossil record, preservation is not the primary process contributing to elevated species richness or turnover patterns during this time.

(Phase 3) Following the MMCO, from 13 to 1 Ma ago, species richness declined with low to moderate faunal turnover. After the middle Miocene peak, strain rate declined and remained steady from 11 to 1 Ma ago; with a lag of 2 to 3 Ma, ruggedness followed a similar pattern as the land surface reached a dynamic steady-state phase (Fig. 2, D and F). Although ruggedness remained high during this period (Fig. 1B, 7 to 0 Ma ago), our results suggest that processes generating diversity are subdued without marked changes to the relief structure or climate warming. Global cooling and increasing area and ruggedness may represent balancing negative and positive effects, respectively, maintaining constant, moderate mammalian species richness.

Proposed mechanisms for diversity changes

Immigration and in situ speciation may promote increases in regional species richness and changes in turnover over geologic time. Although quantifying the relative roles of these processes on diversity patterns remains a challenge outside the scope of this paper, both processes likely played a role in generating the MMCO diversity peak in the western US and the strongest expression of the TDG over the Neogene. Here, we first discuss immigration, followed by speciation processes in relation to landscape and climate change, concluding with discussion of turnover patterns.

Immigration

During the Neogene formation of the Basin and Range, the collapse of large-scale barriers and subsequent opening of connective corridors between geologic provinces would have influenced immigration processes into and within the region. The late Oligocene and early Miocene extensional collapse of the Mogollon Highlands and Nevadaplano, respectively, removed a major high-elevation barrier, facilitating immigration into the Basin and Range. High-elevation faunas may have tracked that extensional collapse, dispersing to newly emerging and isolated mountain ranges (potentially followed by subsequent allopatric speciation). Following this collapse and the westward expansion of the landscape, major dispersal corridors formed between the Mojave region, the central and northern Basin and Range, and the southern Basin and Range. The expansion of low-elevation habitats combined with global warming (MMCO) likely led to the northward range shifts of southern species. Inclusion of the Mexican fossil record as well as coupled topographic-climate-landscape models are needed to identify the spatial configuration and timing of effective corridor formation in the past.

Species movement from the topographically complex and high-elevation western landscapes into the Great Plains following the MMCO may have precipitated the later decline in species richness in the western US. Although it is difficult to track species movement and ranges through the fossil record (45), there is evidence

for dispersal from tectonically active regions of western North American into the low-relief Great Plains during Miocene cooling (10). Mountains as sources of biodiversity for adjacent low-relief regions during cooling has been documented for other taxonomic groups and regions (46).

Speciation

In addition, the development of topographic relief within the dynamic Basin and Range landscape over the Cenozoic likely facilitated geographic isolation of populations and thus speciation, while the increased elevational gradients and habitat heterogeneity would have provided variable habitats for species to adapt to and undergo ecological speciation processes (1, 2). The interplay of climate change on a dynamic landscape (e.g., the development of orographic gradients in precipitation and rain shadow effects) would have served to further isolate populations, limit species ranges, and lead to high spatial turnover across the province and elevated regional diversity. During the MMCO in particular, warming coincided with increasing relief from high strain rates, influencing climatic gradients and habitat heterogeneity along newly formed elevational gradients. Stronger elevational zonation, and thus barriers to dispersal, in mountainous regions with warm and stable climates today has been implicated in elevating species richness through speciation processes (47); therefore, it is reasonable to expect that periods with warmer, more stable climates might also see higher species richness across a topographically complex landscape. At smaller spatial scales, mammals in the Mojave subregion likely underwent in situ speciation during the middle Miocene period of rapidly changing elevational gradients and climate warming. High turnover in small-mammal species composition at the basin scale within the Mojave region potentially reflects locally elevated rates of speciation and endemism on a rapidly changing landscape (43, 48). Alternatively, the diversity peak (as well as subsequent decline) apparent at smaller spatial scales could also be the result of interactions between the diversity of the regional species pool, dispersal, and local community assembly processes (49).

The rate of physiographic landscape change is shaped by tectonic processes leading to surface uplift and by geomorphological processes such as erosion. We expect isolation and adaptation to occur in response to broadscale tectonic processes that shape paleotopography at long wavelengths (hundreds of kilometers) and over millions of years, as captured by our current geophysical models. However, we also expect speciation processes to be further amplified by geomorphic processes that alter drainage patterns and local relief over shorter spatial and temporal scales. Displacement along small- to large-scale faults during this interval of rapid extension would have led to steep gradient formation, the rearrangement of physiographic and climatic barriers, and higher localized relief than is captured by the smoothed paleotopography from geophysical modeling (16–18). Although mechanistic landscape evolution models are needed to fully characterize diversity responses to the combined influence of uplift and geomorphological processes, the temporal and spatial distribution of sediment accumulation provides some indication of how basin formation and filling occurred in the past (19, 25, 50). These records suggest that tectonic activity, especially during the initiation of the rapid extension phase (18 to 15 Ma ago), stimulated the geomorphic engine and that rapid and fine-scale landscape response provided a strong stimulus to the processes of speciation and extinction that shape regional and local diversity.

Turnover

While changes in species richness demonstrate a strong coupling with the rate of landscape change, the underlying mechanisms contributing to turnover patterns are less clear. One may expect high turnover during periods of rapid landscape and climate change (e.g., initiation of Basin and Range faulting), due to increased rates of both speciation and extinction. However, we find low support for any of our tested variables as a persistent first-order control on faunal turnover. Instead, turnover in species composition in the western US and Mojave subregion is highly punctuated during the middle Miocene and tightly linked with rapid paleoelevational changes in the Mojave. At both spatial scales, this event is characterized by complex turnover in the composition of rodent families and the rise and fall of dominant families of carnivores and large-bodied ungulates (figs. S5 to S7). Turnover (and richness) patterns may also track changes in vegetation structure, such as the Miocene spread of grasslands, in ways that both reflect underlying climate drivers of vegetation change and the independent influence of regional variation in vegetation itself (1, 23, 51). Inclusion of regional vegetation variables will likely improve the ability of our models to explain long-term patterns in turnover.

Complex interactions between landscape, climate, and vegetation change may be more pronounced in the turnover patterns of groups like rodents and other small-bodied mammals. With small home-range sizes, limited dispersal capabilities, and often small geographic ranges, small mammals are more susceptible than large mobile and migratory mammals to landscape changes that fragment and isolate populations (52, 53). Warming climate in a region of high topographic and habitat heterogeneity can lead to further isolation of populations, especially in small-bodied and nonmigratory taxa. Therefore, these taxa may exhibit earlier and stronger eco-evolutionary responses to landscape change. Evidence for increased hypsodonty earlier in the rodent record than in the ungulate record (54, 55) indicates high sensitivity to changes in local- to regional-scale environments, including the expansion of grasslands. Evidence from clades originating in North America shows deep branching and regional speciation events to have proliferated during the middle Miocene [e.g., Heteromyidae; (56)]. The signature of topographic barriers persists in phylogeographic population structure and spatial distribution patterns of many small-mammal species today (57, 58). Future evaluation of individual clade dynamics, including differences in ecology, taphonomy, and sampling, in a comparative framework would help distinguish the complex processes and interactions between species biology and landscape change that underlie the observed patterns of species richness and turnover.

Study limitations

Factors such as vegetation, primary productivity, precipitation, and climatic seasonality have been shown to influence mammalian diversity dynamics across spatial scales (23, 59, 60) and need future consideration as potential influences on mammal richness and faunal composition in the topographically complex western US. In addition, a greater number of regional proxies are needed to identify the linkages between topographic change, regional climate, geomorphological process, and resulting relief structure. Continuous Cenozoic regional climate data are not currently available for North America, although recent climate model results for key intervals over the Neogene (19) may be used in future evaluation of spatial

and temporal diversity patterns. Likewise, an increasing number of studies in the western US will help address the spatial and temporal gaps in existing compilations of regional vegetation (1, 61). Data from phytolith and paleobotanical studies will be valuable to distinguish the distinct role of grassland expansion that has been demonstrated in other systems (23), and we expect to influence mammalian diversity and turnover in the late Miocene.

Variation in preservation across time, space, and taxonomic groups remains a challenge in paleontological studies (25, 62, 63). Outcrop area does not capture the full suite of factors that cause variation in preservation and sampling (64) and is likely also related to tectonic processes [e.g., rapid sedimentation during basin extension could lead to a higher rate of fossil preservation (25)]. Further work is needed to fully evaluate taphonomic influences on this record, as well as common cause hypotheses (50); however, prior simulation studies have found that the fossil record is a reliable recorder of shifts in diversification rates across a range of preservation histories (44). In our analysis, the low relative importance of outcrop area and the correspondence of species richness patterns using different diversity estimators suggests that our findings present a robust biological pattern. The relative contributions of speciation, extinction, and immigration processes need further examination to fully understand the mechanistic underpinnings of the observed diversity and turnover patterns (65, 66). The use of process-based models to jointly infer preservation, speciation, and extinction rates from fossil occurrence data and proposed biotic and abiotic predictors (12, 67) as well as phylogenetic approaches to quantify macroevolutionary dynamics (68) represent the next steps of analysis. Spatially explicit analyses tracking the movement or turnover of lineages within and between the tectonically active and quiescent regions (8, 10) will further illuminate how landscape and climate change influence species range dynamics and speciation over complex topography. Last, the incorporation of species ecology (e.g., body size and diet) into such analyses will help us determine the direct and indirect influences of broad-scale climate and landscape change and local-scale habitat change (13).

Implications for the TDG globally and over deep time

In contrast to prior work at the continental and global scales (23, 24), we do not find a strong relationship between species richness and temperature or rate of temperature change at the regional scale. Distinct species richness patterns for the tectonically active and quiescent regions (Fig. 2A) indicate different regional impacts of global climate change. While temperature may have had a stronger influence on diversity dynamics in the Great Plains (table S2), tectonic extension, as well as interactions between the development of topographic complexity and climate change, likely drove diversification and immigration in the intermontane western US. The Great Plains record demonstrates a temporally broader and more muted peak in diversity through the middle Miocene than that observed in the western US, indicating fundamentally different processes contributing to diversity patterns in regions of low versus high topographic complexity. Persistently elevated species richness in the Great Plains following the MMCO warm period until ~12 Ma ago suggest complex climate-related dynamics during both warming and cooling phases in the region. Prior research has indicated that immigration from higher elevation regions of the western US into the Great Plains region during post-MMCO global cooling may have contributed to higher species richness during this time (10).

Beyond the Basin and Range and the western US, tectonic activity and mountain building have been found to play a role in shaping biodiversity patterns in the fossil record in other mountainous regions, including the Andes, Anatolia, and Europe (3, 11, 69). These tectonically active mountain ranges represent both extensional tectonic regimes, like the Basin and Range Province, as well as convergent margins. Our primary finding that the rate of landscape change is the dominant influence on species richness change is meaningful and generalizable to a diversity of geophysical and tectonic settings. While modern patterns of biodiversity provide compelling rationale for expecting a relationship between mountain building processes and biodiversity, identifying the proximal drivers of the processes that generate patterns such as the TDG requires deep-time information from the fossil record and elsewhere (1, 7, 12, 13). Furthermore, the co-occurrence of warming and a concentration of tectonic events leading to mountain building in many regions of the globe during the middle Miocene (70) likely interacted to shape the long-observed global peak in diversity during the Middle Miocene (23). Similar interplay between topographic and climatic change has been proposed to influence biodiversity patterns during both older and younger intervals of mountain building (28, 71), providing multiple windows of opportunity to further test hypotheses about the TDG across tectonic settings and global climate conditions.

Temporal information from the fossil record and recent approaches like geogenomics (72) will help determine the relative contribution of relief generation and climate change to the initial generation and long-term maintenance or shifting nature of the TDG. Likewise, these approaches can advance our understanding of the distinct roles immigration, and in situ speciation may play over the history of a regional TDG. Our findings, combined with a growing body of evidence across mountain ranges globally and over time, emphasize the need to integrate regional geologic and climate dynamics with investigations of diversity patterns; continental-scale biotic analyses and global-scale proxies may obscure the mechanisms underlying biodiversity change over deep time.

In summary, we find strong evidence for tectonic and topographic controls on mammalian species richness and faunal turnover from 30 to 1 Ma ago in western US. Neither increasing area of the entire Basin and Range Province during extension nor increasing sediment-outcrop area and thus fossil preservation explain variation in species richness, although both appear to contribute to the changing nature of mammal richness and composition over time. While global temperature change does not directly predict species richness trends, interactions between the changing landscape and major changes in global temperature may have driven geographic-range shifts into and out of the Basin and Range Province during and following the MMCO, respectively, contributing to the strong expression of the TDG during the warm MMCO (1, 7). The integration of landscape history and biogeographic processes is critical to our understanding of modern-day biodiversity gradients. Similar expressions of the TDG across global mountain ranges today, including the Andes, East African Rift Zone, Himalaya, and Alps—all regions of recent tectonic activity—can be evaluated using a similar integrative approach. Further efforts to estimate rates of tectonic activity, paleotopography, and ruggedness, as presented herein, as well as regional climate models that use regional paleotopography reconstructions as boundary conditions, will make this work possible. A comparative framework will be key for determining the generality of landscape controls on diversity. In parallel with increasing

resolution of regional tectonic, topographic, and climate models, implementation of macroevolutionary and biogeographic modeling and inclusion of ecomorphological traits will further illuminate the controls on diversity over deep time.

MATERIALS AND METHODS

Tectonics, climate, and outcrop area

Our study uses quantitative estimates of strain rate and paleotopography from geodynamic models for the Basin and Range from 36 Ma ago to the present (17, 18). The temporal scale varies over the model run with time steps of 6 Ma (36 to 18 Ma ago) to 2 Ma (18 to 0 Ma ago); estimated strain rates in this study represent the mean 1-Ma rate over each time step of the model, where strain rates between time steps are temporally smoothed while preserving total offset estimates (16, 17). The geodynamic model provides crustal thickness and surface paleoelevation estimates, including formal errors, within grid cells of $0.25^\circ \times 0.25^\circ$ dimension, which corresponds to the dimension used for the averaging of fault offset data for crustal strain rates for each 1-Ma interval. From these results, we calculated the geographic area as well as surface area inclusive of topography of the Basin and Range during the primarily east-west extension (stretching of the crust) and the median ruggedness of the regional paleotopography. Geographic area and surface area of the Basin and Range Province were highly correlated ($r > 0.99$); therefore, geographic area is reported herein. To accentuate the overall relief structure, rather than extremes in absolute ruggedness, we standardized paleoelevation data to a common maximum of one before calculating the ruggedness metric. The terrain ruggedness index is the mean of the absolute elevational differences between the value of a cell and the value of its eight surrounding cells (73) and was calculated at a resolution of $\sim 770 \text{ km}^2$ (0.25°) per grid cell. Paleoelevation data for the Mojave region were geographically constrained based on a convex hull around the spatial extent of Mojave fossil localities; the paleo-coordinates of localities were determined by the geophysical model of lithospheric evolution. Mean elevation was calculated for the subregion as a measure of topography and difference in mean elevation between adjacent intervals calculated as a measure of topographic change.

Global temperature was approximated by the oxygen isotopic composition of deep-sea benthic foraminifera from Westerhold *et al.* (36). We calculated the 1-Ma mean $\delta^{18}\text{O}$ value for correlation and multiple regression analyses. To capture the rate of temperature change, we additionally calculated the slope of the oxygen isotopic values within each analytical bin (absolute value plotted), with higher slopes indicating faster rates of temperature change within a given 1-Ma interval. We used proportional outcrop area of the tectonically active region of western North America from Smiley (44); data were originally compiled from the Macrostrat database (macrostrat.org; version 0.3; accessed April 2016). Calculations for landscape and climate variables were performed in the R open-source programming environment (74), using the raster (75), sp (76), and scales (77) packages.

Richness and turnover

We extracted mammal fossil data from the MioMap and FaunMap databases [(78); accessed November 2019] for regional species richness and turnover estimates. Fossil occurrence data included any species-level record within the tectonically active region (west of the

Rocky Mountain Front Range; $n = 8021$ specimen-level records) or the tectonically quiescent region (Great Plains and east; $n = 7159$ specimen-level records) from 30 to 1 Ma ago (fig. S1). Geographic designation was based on the physiographic divisions of the conterminous US (79). Although the tectonic data are restricted to the Basin and Range Province, we chose to analyze diversity patterns for the topographically complex region west of the Rocky Mountain Front Range for the following reasons: (i) much of the western US is tectonically active over the same period of time and/or is influenced by Basin and Range tectonics (15, 17–19); (ii) although this tectonic activity does not lead to extensive increases in area during extension as experienced in the Basin and Range Province, it does build topographic complexity, the main proposed mechanism for promoting speciation processes; (iii) fossil data from the Basin and Range Province are ~75% of the western dataset and exhibit strong correlation with western species richness as a whole ($r = 0.75$, $P < 0.001$); (iv) we expect spillover effects from the Basin and Range Province into adjacent areas with connected dynamics as the entire region undergoes changes in topographic complexity; and (v) the broader spatial scope enables us to use a larger dataset that is more comparable to the record of paleodiversity in the tectonically quiescent eastern US.

Here, we present a species richness estimate, whereby first and last occurrence data are estimated on the basis of observed species occurrence data and a Bayesian adaptive Beta method (80) for estimating the true stratigraphic range of a taxon based on fossil occurrences and recovery potential models. Species ranges are based on the 90% credible interval of the posterior distribution of first or last occurrence dates, which are then used as estimates of origination (by in situ speciation or immigration) and extinction (or regional extirpation) dates, respectively (fig. S2). At the spatial scale of analysis (within region or subregion), we assume that species range-through or are found in all intervening intervals between the 90% credible intervals. For each fossil occurrence, three estimates were generated to reflect uncertainty in age based on the maximum, minimum, and mid-point age estimate for each fossil locality. Species richness was tallied for each 1-Ma interval, with singleton taxa (those occurring in only one time bin) excluded from the analysis. Species richness measures derived from the mid-point locality-age estimates were used for subsequent correlation and multiple regression analyses. The same methods were used to generate richness estimates for the tectonically quiescent and Mojave regions. To test the robustness of our approach using Bayesian credible intervals and the range-through assumption, we compared richness results with the shareholder quorum subsampling diversity estimator (62, 81, 82; see Supplementary Methods).

We evaluated changes in faunal composition following multinomial likelihood methods presented in Finarelli and Badgley (9). For each 1-Ma time interval, we calculated compositional similarity using the multinomial likelihood of the proportional contribution (fraction of species) of each family-level group to total mammalian richness. The log-likelihood (LnL) of the multinomial distribution is given by

$$(83) \quad \text{LnL}(i) = \sum_j a_j \ln(p_j)$$

where a_j is the count of species in family j and p_j is the proportion of total species in interval i assigned to family j . Summing over j families gives the LnL for interval i ; this value is then compared with the LnL calculated for interval $i - 1$ (i.e., the previous time interval). The

difference in likelihood estimates between adjacent 1-Ma time intervals reflects the amount of faunal turnover in the record, with differences in LnL greater than 2.0 considered to represent significant faunal change (83).

Statistical analysis

We use global climate and regional tectonic (Basin and Range Province) and sedimentary-rock outcrop (western US) variables as predictors of temporal variation in mammal species diversity within the tectonically active western region. We assessed correlations between abiotic variables and species richness and turnover metrics using a rank-based correlation test statistic, Spearman's rho. Because our temporal data are trending (e.g., exhibit non-stationarity), we additionally implemented two approaches—first differences (FD) and generalized differences (GD)—for nonindependence that may be present in time-series data with either long-term trends or short-term autocorrelation. Both approaches have been implemented for paleontological time-series data (63, 84), with R code for calculating GD provided (www.graemetlloyd.com/methgd.html). The same methods were used to test for richness-climate correlations in the tectonically quiescent east.

We used GLS multiple regression models to assess variation in richness and turnover as a function of different combinations of six predictor variables: land surface area, tectonic strain rate, standardized topographic ruggedness, $\delta^{18}\text{O}$ value as proxy for global temperature, $\delta^{18}\text{O}$ slope as proxy for rate of global temperature change, and outcrop area as proxy for preservation potential. GLS is appropriate for time series and nonindependent data because it does not assume independence of data series or points within a data series and allows one to account for autocorrelation with an underlying autoregressive model. We tested a range of autocorrelation structures using AIC, implementing a second-order autoregressive-moving average [corARMA(2)] correlation structure across our candidate models. GLS is further advantageous because it allows multiple explanatory variables to be tested. From all candidate models, we evaluated model support using AICc, accepting models with a delta AICc < 4 relative to the best-fitting model and a P value of < 0.05 , using Nagelkerke (39) pseudo- R^2 values, as our top models. Calculations were performed in R (74), using the MuMIn (85), nlme (86), and rcompanion (87) packages; supplementary figures were produced using the ggplot2 package (88).

Supplementary Materials

This PDF file includes:

Supplementary Methods and Results

Figs. S1 to S11

Tables S1 and S2

Legends for movies S1 and S2

Legend for data S1

Other Supplementary Material for this manuscript includes the following:

Movies S1 and S2

Data S1

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