PALEONTOLOGY

Tectonic influence on Cenozoic mammal richness and sedimentation history of the Basin and Range, western North America

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Tectonic activity can drive speciation and sedimentation, potentially causing the fossil and rock records to share common patterns through time. The Basin and Range of western North America arose through widespread extension and collapse of topographic highlands in the Miocene, creating numerous basins with rich mammalian fossil records. We analyzed patterns of mammalian species richness from 36 to 0 million years ago in relation to the history of sediment accumulation to test whether intervals of high species richness corresponded with elevated sediment accumulation and fossil burial in response to tectonic deformation. We found that the sedimentary record of the Basin and Range tracks the tectonic evolution of landscapes, whereas species-richness trends reflect actual increased richness in the Miocene rather than increased fossil burial. The sedimentary record of the region broadly determines the preservation of the fossil record but does not drive the Miocene peak in mammalian species richness.

INTRODUCTION

The fossil record is fundamentally linked to the sedimentary record and the processes of sediment accumulation. At regional scales, uplift and subsidence histories can determine the likelihood of fossil preservation by directing where sediment accumulates. The characteristics of landscapes that govern sediment dispersal and accumulation also affect species distributions, with elevation and relief among the most important landscape features (1). When substantial changes in the fossil and sedimentary records coincide, their patterns may be attributed to a common influence, such as tectonics or climate. Intervals of tectonically driven landscape change can alter sediment dispersal patterns through drainage development and the creation of basins; changing landscapes can also promote speciation and turnover, which may be pronounced in topographically complex regions (2). Tectonically driven landscape processes can then produce conditions that promote speciation and create accommodation—leading to increased species richness and sediment accumulation, as well as conditions that promote species turnover and destroy accommodation—leading to low species richness and little or no sediment accumulation.

Assessing the influence of landscape evolution on the preservation of the fossil and rock records requires an extensive fossil record and well-constrained estimates of topographic change through time. The Basin and Range (BR) Province of western North America has both a well-documented fossil record and a history of considerable landscape evolution through the Cenozoic (3, 4). We investigated how the fossil and rock records of the BR track its history of tectonically driven landscape change. We focus on the mammalian fossil record because it is well documented over much of North America through the Cenozoic.

The BR region of western North America (Fig. 1) began forming in the Late Eocene (4, 5). Widespread extension during and following the topographic collapse of montane highlands, the Nevadaplano and Mogollon highlands (5, 6), formed the numerous fault-bounded basins and ranges that characterize the region today (4, 7). This interval of elevated tectonic activity coincided with high mammalian species richness in western North America, particularly during the Middle Miocene (8). Similar trends in the rate of area change and
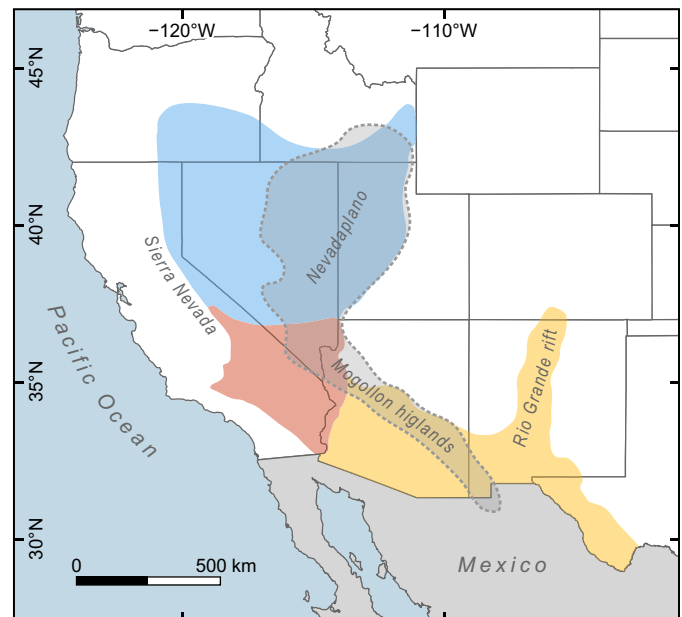

Fig. 1. Map of the subregions of the Basin and Range in the United States. The Northern (blue), Central (red), and Southern (yellow) subregions of the Basin and Range in relation to modern geography and paleohighlands (gray dashed lines). Subregion boundaries are based on tectonic history and modern topography following (4, 5, 7). The footprint of the Nevadaplano and Mogollon paleohighlands follow reconstructions from (6, 14).

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mammalian species richness through BR extension suggest that species richness was linked to increasing topographic complexity, basin development, and landscape evolution (9, 10). Along with basin development, sediment accumulation over the expanding BR should have increased as basins formed and highlands eroded. Observed patterns of species richness may have resulted from increased sediment and fossil accumulation over broad areas of high accommodation due to regional extension (11).

Here, we test how the sedimentary and mammalian fossil records of the BR compare to its history of landscape evolution. We compiled mammal occurrences from MioMap (12) and sediment records from Macrostrat (13) and the literature (gap-bound "packages" and fossiliferous units, respectively; see Materials and Methods) to analyze species richness in relation to sediment thickness and accumulation rates, tectonic deformation rates, and area-change rates since 36 million years (Ma) ago in 0.5-Ma time bins (5, 6). Because we are interested in the influence of sedimentation on fossil preservation, we focus on species richness from occurrences rather than on origination or other diversity metrics. We used change-point analysis to detect significant changes in means through time. We evaluate these records for the entire BR region as well as for the northern, central, and southern subregions (Fig. 1), as determined by modern physiography and tectonic history (4, 7). We expect that high rates of extension led to increased sediment accumulation and thick stratigraphic sequences. Species richness may have changed directly in response to tectonic activity or indirectly through changes in sediment accumulation and fossil burial. If patterns of species richness are directly related to tectonic activity, we expect that changes in richness and deformation will be synchronous. If thick stratigraphic sequences led to increased fossil burial, then we expect that species richness and sediment accumulation histories will be synchronous through time. If changes in species richness do not track either

deformation or sedimentation histories, then they must be controlled by other processes.

RESULTS

Species richness and rates of landscape processes increased during the Middle Miocene

Across the BR, a pronounced increase in mammalian species richness, sediment-accumulation rates (SARs), deformation rates, and area-change rates occurred between 17 and 14 Ma ago (Fig. 2). The overall trend in species richness was significantly correlated with trends in these landscape variables (table S1), with strong positive correlations between species richness and area-change rate, SAR of all sediment packages from Macrostrat (13), and SAR of fossiliferous sedimentary units. Trends in species richness were moderately correlated with deformation rate. First differences of species richness versus deformation rate and area-change rate were not significantly correlated, and the number of species slightly lagged area-change rate ($r = 0.72$) and led deformation rate ($r = 0.59$) by 0.5 Ma (table S2), indicating small offsets in these time series. First differences of species richness with SAR of all sedimentary packages and SAR of fossiliferous units were strongly ($r = 0.87$) and moderately ($r = 0.48$) correlated, respectively, indicating no differences in timing (tables S1 and S2). Species richness was also correlated with number of fossil localities and number of fossiliferous units (Fig. 3), with some offsets in timing between richness and number of fossiliferous units (table S2).

For the entire BR region, single–change-point analysis identified significant changes in means for mammalian species richness and most of the landscape variables in the Early and late Early Miocene. Significant shifts in mean species richness occurred at 17.5 Ma ago, in mean deformation rates at 23.0 Ma ago, in mean rate of area change
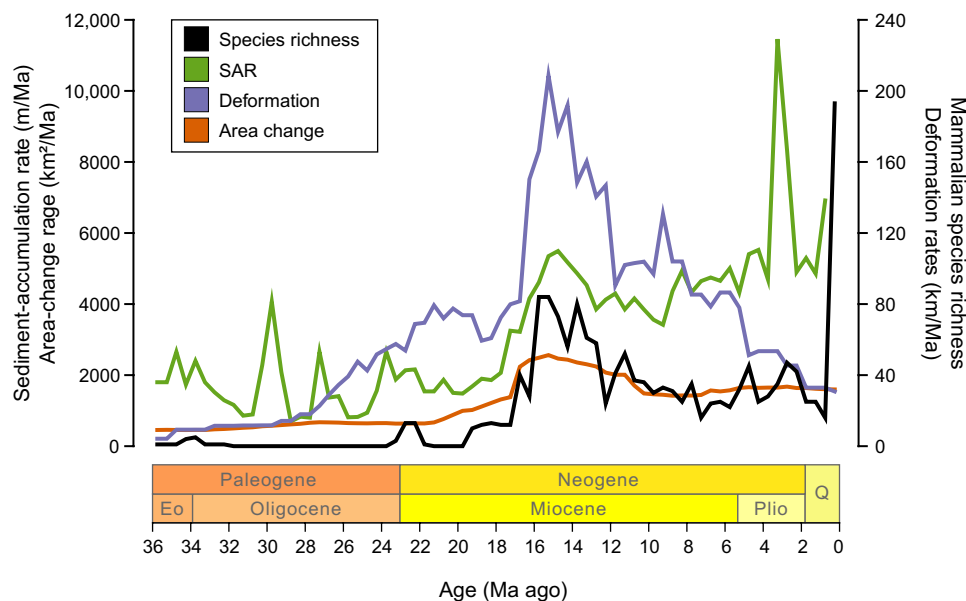

Fig. 2. Changes in mammalian species richness and landscape evolution variables in the Basin and Range region since 36 Ma ago. Number of mammalian species, sediment-accumulation rates (SARs) from all sedimentary Macrostrat packages, deformation rates, and area-change rates per 0.5 Ma for the entire Basin and Range. Eo, Eocene; Plio, Pliocene; Q, Quaternary.
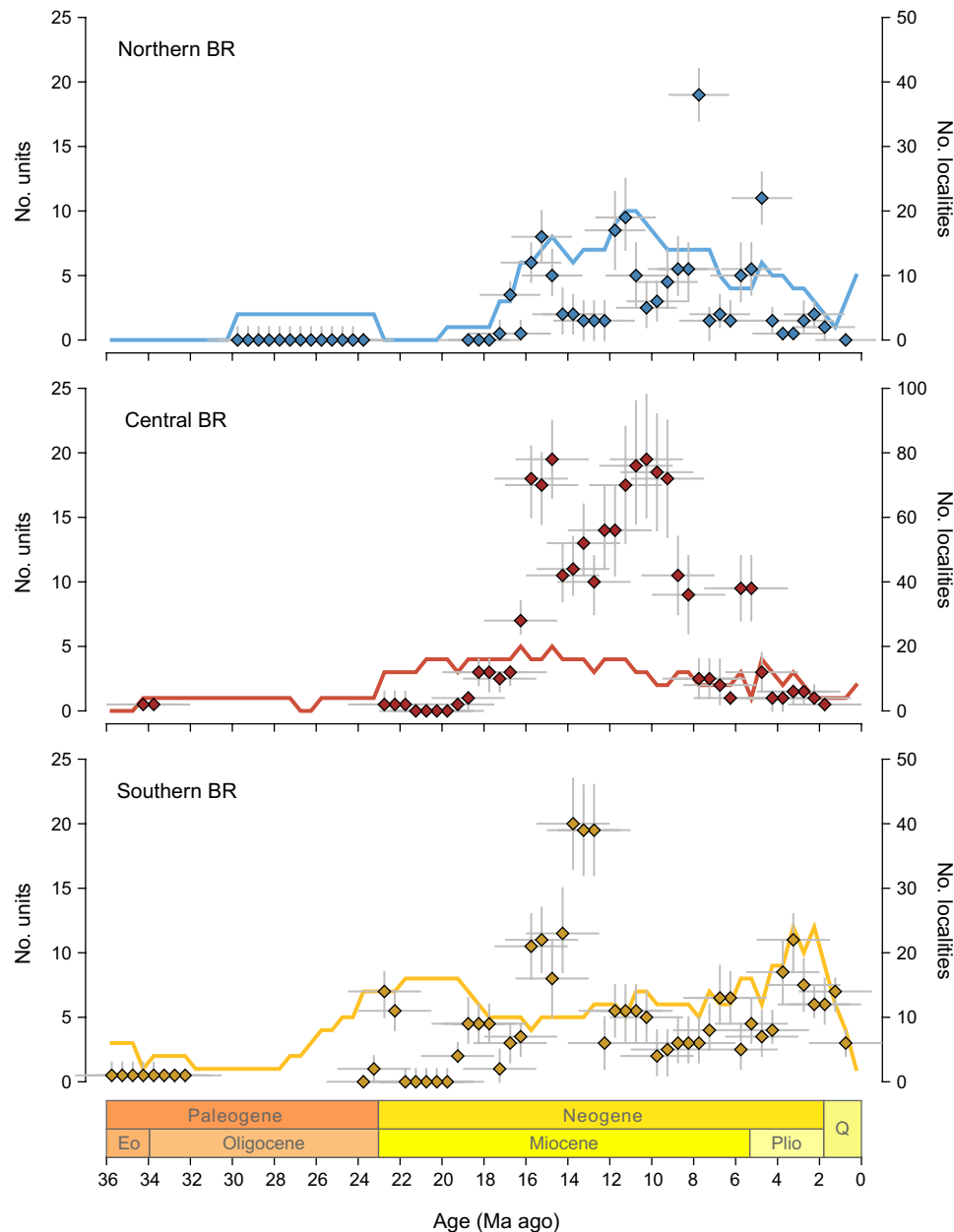
Fig. 3. Number of fossiliferous units and fossil localities for subregions of the Basin and Range. Number of fossil localities (diamonds) per 0.5-Ma time bin compared to number of fossiliferous units through time. Vertical error bars represent lower 2.5% and upper 97.5% estimates of bootstrapped localities, and horizontal error bars represent average uncertainty of locality ages; age uncertainties are the average of age ranges of all pre-Holocene localities for Northern (1.4 Ma), Central (1.7 Ma), and Southern (1.7 Ma) Basin and Range (BR). Number of localities from the most recent time bin are omitted. Eo, Eocene; Plio, Pliocene; Q, Quaternary.

at 18.5 Ma ago, and in mean SAR of fossiliferous units at 17.0 Ma ago (Fig. 2 and Table 1). For the interval from 36 to 0 Ma, significant changes in both the mean SAR of all Macrostrat packages and of nonfossiliferous Macrostrat packages occurred at 4.0 Ma ago. Because many Quaternary packages by definition have short durations, the SAR for the most recent 0.5-Ma time bin was an order of magnitude higher than the highest pre-Quaternary SAR value. Excluding the most recent time bin shifted significant changes in mean SAR for all Macrostrat packages and nonfossiliferous packages to 18.0 and 7.5 Ma ago, respectively (Table 1). Although modern mammal

species richness in the BR (193 species) is substantially higher than pre-Quaternary richness (mean number of species from 36.0 to 0.5 Ma ago = 20), excluding the most recent time bin did not change the timing of significant changes in mean number of species (Table 1).

Timing and magnitude of species richness and landscape processes vary among BR subregions

In the Northern BR, mammalian species richness and SAR were low through the Late Eocene and Oligocene until they abruptly

Table 1. Results of change-point analysis for the Basin and Range. Change points are given as ages of significant change in means for deformation rates (km/Ma), area-change rates (km²/Ma), SAR (m/Ma) of nonfossiliferous and fossiliferous sedimentary packages from Macrostrat and fossiliferous units from literature sources, and mammalian-species richness for (A) the entire Basin and Range, and the (B) Northern, (C) Central, and (D) Southern subregions. For each variable, *t* statistic, lower and upper 95% confidence intervals (CIs), and *P* value of Welch's *t* test comparing means of intervals before and after each change point are given.

	Age (Ma ago)	*t* statistic	95% Lower CI	95% Upper CI	*P*
(A) Basin and Range					
Deformation rates	23.0	9.495	54.415	83.419	<0.001
Area-change rates	18.5	16.489	1011.884	1292.853	<0.001
SAR, all Macrostrat packages to 0.5 Ma ago	18.0	10.776	2543.394	3711.485	<0.001
SAR, nonfossiliferous Macrostrat packages to 0.5 Ma ago	7.5	4.025	1122.623	3696.900	0.001
SAR, fossiliferous Macrostrat packages to 0.0 Ma ago	17.0	11.760	1410.243	1991.621	<0.001
SAR, fossiliferous units to 0.0 Ma ago	17.0	14.378	1957.445	2594.465	<0.001
Number of mammal species to 0.0 Ma ago	17.5	7.444	29.429	52.106	<0.001
(B) Northern Basin and Range					
Deformation rates	16.5	9.168	10.090	15.726	<0.001
Area-change rates	17.5	10.227	322.457	478.883	<0.001
SAR, all Macrostrat packages to 0.5 Ma ago	18.0	13.962	1252.698	1673.311	<0.001
SAR, nonfossiliferous Macrostrat packages to 0.5 Ma ago	18.0	6.064	330.188	655.097	<0.001
SAR, fossiliferous Macrostrat packages to 0.0 Ma ago	17.0	14.584	862.262	1141.832	<0.001
SAR, fossiliferous units to 0.0 Ma ago	16.5	17.148	1500.462	1904.827	<0.001
Number of mammal species to 0.0 Ma ago	17.5	3.722	6.239	21.246	<0.001
(C) Central Basin and Range					
Deformation rates	22.0	9.509	55.483	64.442	<0.001
Area-change rates	21.0	19.906	540.050	660.344	<0.001
SAR, all Macrostrat packages to 0.5 Ma ago	9.5	4.022	850.042	2708.345	<0.001
SAR, nonfossiliferous Macrostrat packages to 0.5 Ma ago	7.5	3.707	862.446	3265.373	0.0026
SAR, fossiliferous Macrostrat packages to 0.0 Ma ago	24.5	9.357	370.622	572.463	<0.001
SAR, fossiliferous units to 0.0 Ma ago	23.5	10.227	360.525	536.604	<0.001
Number of mammal species to 0.0 Ma ago	17.0	5.855	11.324	23.364	<0.001
(D) Southern Basin and Range					
Deformation rates	27.0	9.662	11.366	17.278	<0.001
Area-change rate	21.0	8.324	446.179	727.911	<0.001

	Age (Ma ago)	t statistic	95% Lower CI	95% Upper CI	P
SAR, all Macrostrat packages to 0.5 Ma ago	17.5	4.789	224.584	549.952	<0.001
SAR, nonfossiliferous Macrostrat packages to 0.5 Ma ago	26.5	−2.799	−650.887	−94.769	0.011
SAR, fossiliferous Macrostrat packages to 0.0 Ma ago	18.5	8.767	322.522	513.437	<0.001
SAR, fossiliferous units to 0.0 Ma ago	24.5	5.372	228.630	504.957	<0.001
Number of mammal species to 0.0 Ma ago	16.5	4.722	11.669	29.324	<0.001

increased at ~17 Ma ago. Deformation rates and area-change rates first increased at ~36 Ma ago and varied little until the Late Oligocene (Fig. 4). Although sedimentary packages formed in this subregion through this interval, few sedimentary units with mammalian fossil records formed at this time, resulting in low species richness before the Early Miocene (Fig. 5, A and B). Trends in mammalian species richness were correlated with deformation rates and area-change rates; first differences were not correlated, and a 1.5-Ma lag in area-change rate ($r = 0.31$) was detected (table S2). Species-richness trends were strongly correlated with SAR of all sedimentary packages (Spearman's $\rho = 0.82$) and SAR of fossiliferous units ($\rho = 0.87$), and first differences were significantly correlated (table S1). Change-point analysis detected significant changes in the mean number of mammal species at 17.5 Ma ago and in the mean SAR of fossiliferous units at 16.5 Ma ago. Significant changes in mean deformation rates occurred at 16.5 Ma ago and in rate of area change at 17.5 Ma ago. For the interval from 36 to 0.5 Ma ago, the mean SAR of all Macrostrat packages and mean SAR of nonfossiliferous Macrostrat packages increased at 18.0 Ma ago (Table 1).

In the Central BR, mammalian species richness was low until the Middle Miocene. Deformation rates in the Central BR first rose at ~24 Ma ago, following steadily increasing rates of area change through the Oligocene. Thickness and SAR of both nonfossiliferous and fossiliferous Macrostrat packages closely followed the initiation of deformation in this subregion in the Early Miocene (Figs. 4 and 5D). In the Central BR, species richness was strongly correlated with deformation rates ($\rho = 0.82$) and area-change rates ($\rho = 0.79$) and moderately correlated with SAR of fossiliferous units and SAR of all sedimentary packages (table S1). First differences of these variables were not significantly correlated, with the exception of SAR of all sedimentary packages. Deformation rates slightly lagged species richness by 0.5 Ma ($r = 0.74$), and species richness lagged area-change rates by 1.0 Ma ($r = 0.65$). Species richness lagged SAR of fossiliferous units by 4.5 Ma ($r = 0.58$; table S2). Change-point analysis showed significant changes in the mean number of species at 17.0 Ma ago and in SAR of fossiliferous units at 23.5 Ma ago. Significant changes in deformation rates occurred at 22.0 Ma ago and in rate of area change at 21.0 Ma ago. Mean SAR of all Macrostrat packages increased at 9.5 Ma ago, and mean SAR of nonfossiliferous packages increased at 7.5 Ma ago, when the most recent time bin was excluded (Table 1).

In the Southern BR, mammalian species richness was low until the Early Miocene. Rates of deformation and area change first began

to increase in the Early Oligocene (Fig. 4), and sedimentary packages accumulating through the Oligocene were predominantly non-fossiliferous (Fig. 5F). Thickness and SAR of fossiliferous units increased in the Southern BR by the beginning of the Miocene. Overall, changes over time in landscape variables in the Southern BR were moderately correlated with species richness. SAR of all sedimentary packages was correlated with species richness ($\rho = 0.60$; table S1), and no lag was detected in these trends. Species richness lagged deformation rates ($r = 0.29$) by 7.0 to 7.5 Ma, area-change rates ($r = 0.27$) by 3.5 to 4.0 Ma, and SAR of fossiliferous units ($r = 0.44$) by 5.5 Ma (table S2). Change-point analysis detected significant changes in mean species richness at 16.5 Ma ago. Mean SAR of fossiliferous units increased significantly at 24.5 Ma ago. Significant changes in mean deformation rates occurred at 27.0 Ma ago and in rate of area change at 21.0 Ma ago. Mean SAR of all Macrostrat packages and nonfossiliferous packages increased at 17.5 and 26.5 Ma ago, respectively, when the most recent time bin was excluded (Table 1).

DISCUSSION

Landscape features, as shaped by tectonics and climate, have an important influence on species distributions. Landscape evolution processes, in particular those that generate complex topography, are also linked to the generation of the sedimentary record through erosion and weathering of uplifted terranes and deposition in subsiding basins. Fossil preservation is incumbent on burial, so increased rates of sediment accumulation should lead to an increase in species richness of the fossil record through increased fossil productivity (11). Comparing patterns of species richness and indicators of landscape evolution processes shows that landscape change was an important influence on the sedimentary and fossil records of the BR.

Across the BR, high mammalian species richness in the Middle Miocene coincided with substantial changes in landscape evolution processes. Between 18 and 15 Ma ago, species richness, SAR, deformation rates, and area-change rates doubled or tripled (Fig. 2). For the entire BR, the Neogene peak in species richness occurred between 16 and 14 Ma ago, exceeded only by the richness of the last 0.5 Ma. Badgley et al. (8) also found that mammal diversity in the Great Basin (a subset of the BR) peaked between 16 and 14 Ma ago and differed significantly from earlier and later time intervals. Similarly, SAR of all sedimentary packages had a mid-Miocene peak
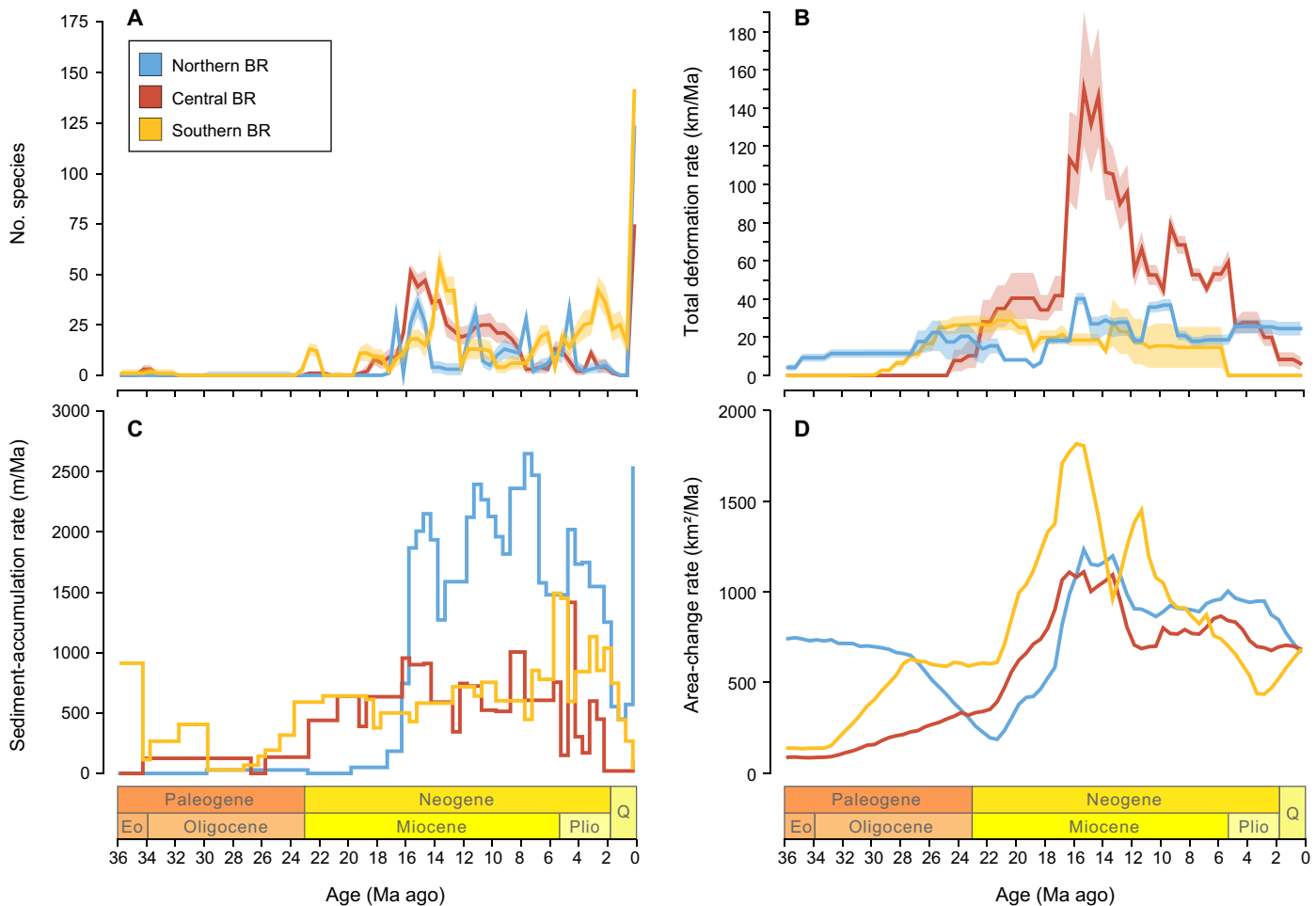
Fig. 4. Changes in mammalian species richness and landscape evolution variables per 0.5 Ma for subregions of the Basin and Range. (**A**) Median number of mammalian species—shading represents lower 2.5% and upper 97.5% estimates of number of species based on bootstrapped age uncertainty of localities; (**B**) deformation rates—shading represents lower and upper rate estimates from (5, 58–61, 63–68); (**C**) total SAR of fossiliferous units; and (**D**) area-change rates for the Northern, Central, and Southern Basin and Range (BR). Eo, Eocene; Plio, Pliocene; Q, Quaternary.

that slightly preceded the onset of increasing species richness. Rates of deformation and area change also peaked in the Middle Miocene through the interval of elevated species richness (Figs. 2 and 4).

Across the entire region, the staggered timing of significant change in means detected through change-point analysis (Table 1) suggests that variables may be linked through a progression of landscape changes and responses. Mean species richness increased at 17.5 Ma ago and overlapped with an increase in mean sediment thickness and accumulation rates at 18.0 Ma ago. These changes were preceded by increased mean deformation rates at 23.0 Ma ago and mean area-change rates at 18.5 Ma ago (Fig. 2 and Table 1). The timing of these changes suggests that species richness may have increased in response to changing landscape evolution processes, potentially because speciation rates and geographic-range shifts were higher during intervals of heightened tectonic activity (1, 9), or because preservation rates increased in conjunction with higher SAR (11). High deformation rates in the Early Miocene would have led to increasing area over the extending BR region. Expanding area would have been an important influence on species richness (10), as species richness was correlated with area-change rates while

controlling for deformation rates [$\rho_{partial}$ = 0.67; the converse case showed no correlation ($\rho_{partial}$ = −0.02)]. Partial correlation of SAR of all Macrostrat packages and area-change rates were also significant with deformation rates controlled ($\rho_{partial}$ = 0.69; $\rho_{partial}$ of the converse case = −0.27), indicating that increased sediment accumulation may have been more closely related to areal increase due to extension than to fault activity. The accumulation of fossiliferous units, however, was only moderately correlated with deformation ($\rho_{partial}$ = 0.42 with area controlled) and area-change rates ($\rho_{partial}$ = 0.39 with deformation controlled), indicating similar responses to changes in deformation and area. Sediment accumulation would have increased as highlands eroded and basins filled. More fossils may have been buried in the emerging basins by elevated SAR (9), contributing to the Middle Miocene peak in species richness. If such a progression of events and responses in landscape processes led to high richness and enhanced fossil preservation over the BR, then a similar relationship of species richness to SAR and other landscape evolution processes should be evident in each subregion. Instead, the increase in species richness differs in time relative to tectonic processes in each subregion (Fig. 4).
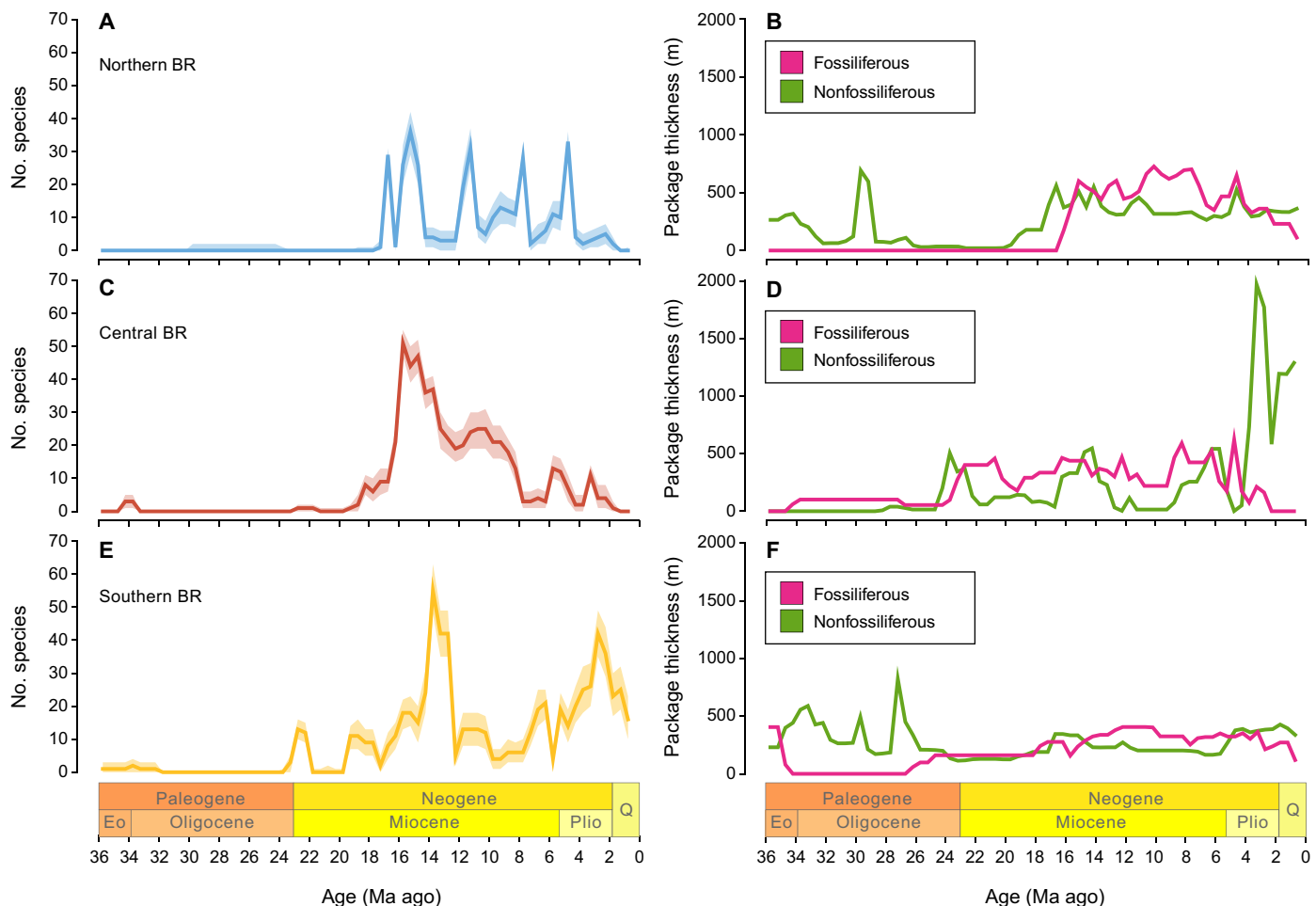
Fig. 5. Mammalian species richness and sediment thickness for each subregion of the Basin and Range to 0.5 Ma ago. Number of mammalian species and thickness of nonfossiliferous and fossiliferous Macrostrat packages per 0.5 Ma for the (**A** and **B**) Northern, (**C** and **D**) Central, and (**E** and **F**) Southern Basin and Range. Shading in (A, C, and E) represents lower 2.5% and upper 97.5% estimates of bootstrapped species richness per 0.5 Ma. Eo, Eocene; Plio, Pliocene; Q, Quaternary.

The mid-Miocene spike in richness occurred in each subregion within a narrow interval but did not coincide with significant shifts in SAR, deformation rates, or area-change rates. Significant changes in species richness for the Northern, Central, and Southern BR occurred between 17.5 and 16.5 Ma ago (Fig. 4A and Table 1). In the Northern BR, increased species richness was synchronous with major changes in rates of sediment accumulation, deformation, and area change. In the Central and Southern BR, however, major change-point shifts in SAR, deformation rates, and area-change rates preceded the increase in species richness by up to 10.5 Ma (Table 1). There was, however, a marked increase in observed deformation rates in the Central BR at ~17 Ma ago, but this increase was not mirrored in the other subregions (Fig. 4B). This variation in timing differs from the aggregated pattern for the BR that suggests a closer relationship between species richness and changes in landscape and sediment accumulation (Fig. 2). Such a prolonged difference in timing between significant shifts in states of landscape change indicates that the increase in species richness in the Central and Southern BR was not a direct response to sedimentation history and landscape evolution processes. Increased mean sediment thickness and accumulation rates of fossiliferous units also preceded

richness by 6 to 8 Ma and were closer in timing to major shifts in mean deformation and area-change rates than to changes in mean species richness (Fig. 4 and Table 1). Increased SAR and thickness of fossiliferous units between ~24 and 22 Ma ago did coincide with increasing deformation rates and modest increases in mammalian species richness in the Southern BR (Fig. 4), indicating that fossil productivity increased with the onset of deformation relating to the collapse of the Mogollon highlands in central Arizona (Fig. 1) (6, 14). Relatively few fossil localities occurred within this interval, however, and this uptick was unlike the abrupt spike in richness and localities that occurred in the Middle Miocene in the Northern, Central, and Southern BR (Figs. 3 and 4). While increased sediment thickness and accumulation rates undoubtedly had an influence on fossil burial and preservation, they were not the main factors contributing to the Middle Miocene peak in mammalian species richness.

Mammalian species richness in the BR peaked during two warm intervals in the Miocene and Pliocene and declined during cooling intervals. The mid-Miocene spike in mammalian species richness coincided with the onset of the Middle Miocene Climatic Optimum (MMCO). This warm interval occurred from ~17 to 14 Ma ago

(8, 15), when global mean annual temperatures are reconstructed as ~3° to 7°C higher than modern temperatures (16, 17). In the BR region, mean species richness per time bin during the MMCO was higher than the average richness since the Late Eocene and was also elevated in each subregion (Table 2). In the Pliocene, high species richness overlapped with the early Pliocene Warm Period (PWP) from ~5 to 3 Ma ago, when global mean temperatures were ~ 3°C warmer than the present day (1, 15, 18). Both of these warm intervals were followed by climatic cooling, polar ice sheet expansion (15, 18), and the transition to drier conditions in North America (19). The post-MMCO climatic transition may have had a greater impact on species turnover than Plio-Pleistocene cooling, as species richness in the BR decreased through the end of the Miocene yet remained above the Neogene average after the PWP (Table 2). Badgley et al. (8) found that the highest diversification and origination rates of large and small mammals in the Great Basin occurred at 16 Ma ago during the MMCO, followed by the highest turnover and extinction rates at 13 Ma ago. Similar trends in rodent species diversification through the MMCO were found in other parts of western North America (11).

Although patterns of mammalian species richness through time strongly correspond to intervals of changing climate (8, 11), they are not completely divorced from landscape evolution and the preservation of the sedimentary record. Each subregion shows intervals of high richness alternating with intervals of low richness that vary slightly among subregions and roughly correspond to the number of localities (Figs. 3 to 5). Intervals of high and low richness are accentuated because our analyses include singletons, and we do not assume range-through in recording species richness. This approach emphasizes intervals of increased preservation, which are related to the number and timing of deposition of fossiliferous sedimentary units, which generally controls the number of fossil localities in each time bin (Fig. 3) (8). The pronounced variability between episodes of high and low richness through time generally indicates times of increased preservation of both the sedimentary and fossil records. These episodes of enhanced preservation should be closely tied to landscape and climate evolution, particularly when rates of change display substantial temporal and spatial variation.

Each subregion has different tectonic and sedimentation histories that vary in timing and magnitude. Changes in SAR and sediment thickness appear to be related to changes in deformation and area-change rates in each subregion (Fig. 4 and Table 1). Much of the extensional history of the BR was governed by rollback of the subducting Farallon slab beneath the North American plate, the evolution of the plate boundary, and the associated northward and

southward migration of the Mendocino and Rivera triple junctions, respectively (4, 5, 14). Consequently, major tectonic episodes in the BR were diachronous, progressing from northeast to southwest in the Northern BR during the Early Eocene to Early Miocene, and from east to west in the Southern BR during the Late Eocene to Middle Miocene (14). These events were important drivers in the timing of erosion and deposition of sediment (20). Individual basin histories are obscured at the coarse spatial resolution of our analyses, but we may be able to infer how the regional history of landscape change affected the preservation of the fossil record. A prominent feature of the fossil record of the BR is the dearth of information before the Early Miocene. This may be a feature of poor sampling (8), but it also reflects differences in sediment accumulation and preservation in relation to tectonic evolution of the region.

Tectonic history may affect sedimentation in various ways, and its effects may differ at basinal and regional scales. The regional and subregional patterns of richness and sedimentation reflect broad changes in tectonic history but may not capture basin-scale processes that contribute to fossil preservation. At the basin scale, sedimentary facies change laterally in relation to active fault zones and temporally as tectonic activity waxes or wanes (21). Changes in sedimentary facies in relation to basin evolution affect the preservation of fossils in sedimentary successions (22). Very high SAR in some environments may not concentrate fossils, and rich fossil localities may instead form during intervals of lower SAR (22). Regional and subregional records integrate numerous basins at various stages of development, revealing broad patterns of landscape change. At regional scales, tectonic regime can determine the fate of sediment dispersal and accumulation (20), thereby affecting patterns of fossil preservation and biotic evolution (23).

One pattern common to each subregion is that most sediment packages accumulating during and following the early phases of topographic collapse do not preserve mammal fossils (Fig. 5). This pattern may be due to the characteristics of sediments in active tectonic areas, which tend to be coarse grained and not conducive to fossil preservation. Fossil preservation generally depends on rapid burial in fine-grained sediments. Coarse-grained sediments (gravel- to cobble-sized clasts) typically have poor preservation potential for vertebrate fossils. Sedimentary sequences in extensional basins typically reflect a transition from high-energy colluvial and alluvial deposits to lower-energy alluvial deposits through time (21). Over the BR region, sedimentary packages deposited between ~34 and 23 Ma ago consisted predominantly of conglomerate and breccia (Fig. 6). These packages were largely nonfossiliferous, and few fossil localities occurred during this interval (Figs. 3 and 5). Through the remainder of the Neogene, the proportion of breccia declined and finer-grained lithologies increased (Fig. 6). These coarser-grained sediments may represent colluvium and alluvium accumulating in basins during the initiation of highland collapse and extension. As deformation rates decreased over time and drainages evolved, landscape stability and sediment maturity increased, and conditions that favor fossil preservation became more widespread.

In addition, the changing style of extension and basin development in the BR may explain differences in sedimentation histories among subregions. In the Northern and Southern BR, deformation occurred in two phases: an early high-extension phase marked by low-angle detachment faulting, and a later low-magnitude phase characterized by high-angle block faulting (the Central BR did not undergo the same transition because of its position relative to the

Table 2. Mean mammalian species richness of the Basin and Range. Mean and SD of mammalian species richness for the entire study interval, 36 to 0 Ma ago; the Middle Miocene Climatic Optimum, 17 to 14 Ma ago; and the Pliocene Warm Period, 5 to 3 Ma ago.

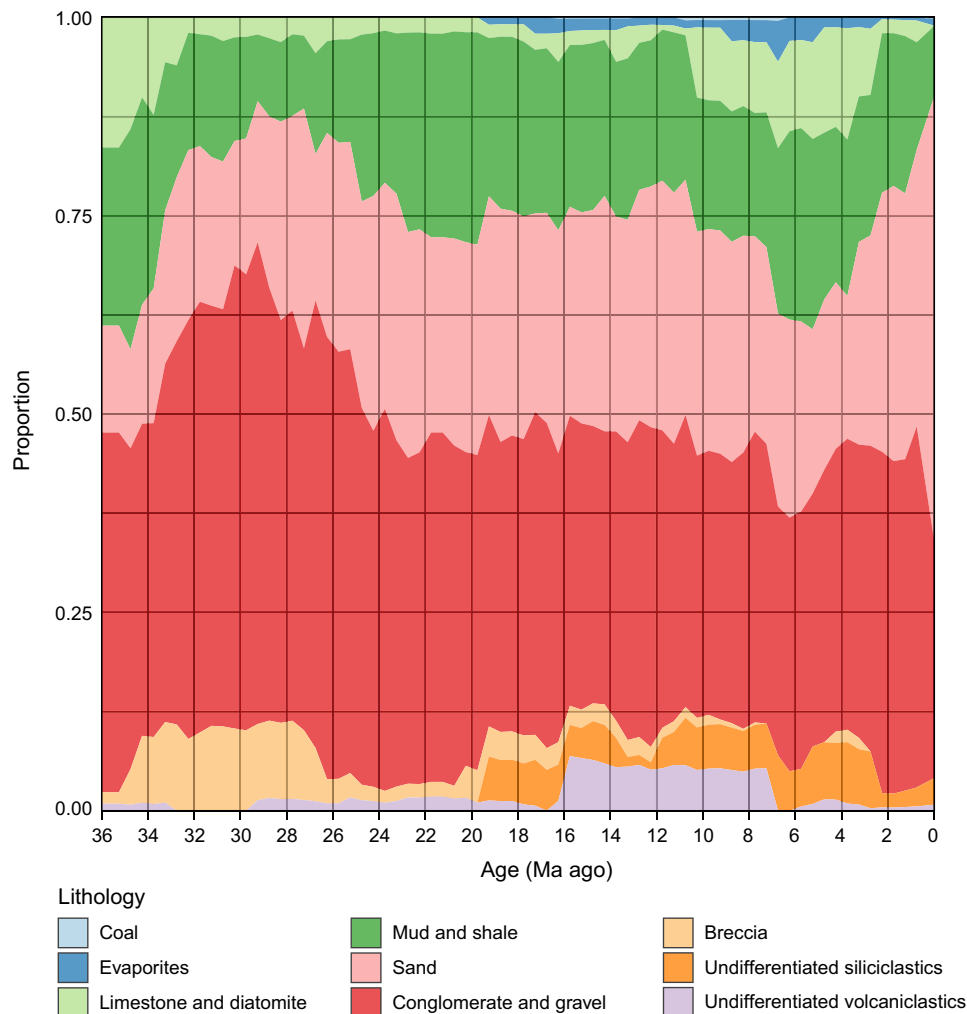| Time interval	Basin and Range	Northern BR	Central BR	Southern BR
36–0 Ma ago	22.4 ± 30.5	6.7 ± 16.6	9.1 ± 14.7	11.6 ± 19.7
17–14 Ma ago	53.9 ± 28.3	17.6 ± 14.9	31.0 ± 17.9	13.7 ± 7.3
5–3 Ma ago	33.0 ± 7.7	10.4 ± 13.0	6.8 ± 4.8	20.8 ± 4.9

Fig. 6. Lithology of all Macrostrat packages from the Basin and Range since 36 Ma ago. Proportion of thickness of all sedimentary Macrostrat packages per 0.5 Ma by lithology.

evolving plate margin) (*4*, *5*, *7*). Basins created during the early detachment phase were likely buried over time as highlands continued to collapse, and metamorphic core complexes were exhumed. The rapid exhumation and denudation of metamorphic core complexes from ~40 to 5 Ma ago (*4*, *14*) coincided with the accumulation of much of the nonfossiliferous sedimentary record in the BR (Fig. 5). Later high-angle block faulting of the extended terranes developed successor basins, which hold most of the Miocene to recent sedimentary and fossil records. Subsequent migration of fault zones and fault-block uplift may also have exhumed earlier basin fill, as has been interpreted for the Miocene Horse Camp Basin in Nevada (*24*). The timing of the transition in extensional regime, as well as phases of topographic collapse, differed among subregions and may explain why significant changes in mammal richness and landscape processes are synchronous in the Northern BR but asynchronous in the Central and Southern BR (Fig. 4).

Patterns of sediment accumulation in each subregion varied with the evolution of the landscape. Little continental sediment is preserved in the BR before the Late Eocene when the Nevadaplano and Mogollon highlands occupied the region (Fig. 1). In the Northern

BR, topographic collapse of the Nevadaplano and detachment faulting occurred between ~35 and 15 Ma ago (*5*, *6*) and coincided with moderate area-change rates and the sporadic accumulation of nonfossiliferous sedimentary packages (Figs. 4 and 5B). Much of the Late Eocene–Early Miocene sediment record of the Northern BR may have been eroded or buried during the early phases of extension. The initial collapse of the Nevadaplano was centered in the highest-elevation portions in Nevada and Utah (*14*); sediment shed from high elevations was diverted out of the region to the west and east (*20*, *25*) or was buried during the early detachment phase. Consequently, little sediment accumulated in the Northern BR until the transition to high-angle faulting at ~17.5 Ma ago (*4*), which was accompanied by major changes in SAR, deformation rate, and area-change rate (Fig. 4). In particular, the overall accumulation of sedimentary packages was more continuous after the transition, and fossiliferous units began to accumulate (Figs. 3 and 5).

The sedimentary history of the Southern BR is related to the collapse of the Mogollon highlands and the southward migration of the Rivera triple junction (*4*, *14*). Collapse of the Mogollon highlands and the onset of detachment faulting began ~30 Ma ago and

proceeded until ~14 Ma ago (4–6). During this interval, deformation rates and area-change rates were high, and thick packages of nonfossiliferous sediment accumulated during the early phase of collapse and faulting (~28 to 25 Ma ago; Fig. 5F). The highest rates of sediment accumulation occurred at this time (fig. S1), and few fossil localities formed during this phase (Fig. 3). Models show that well-developed southern drainages coming off the Mogollon highlands transported sediment westward to the California coast (20, 25). Fossil-bearing sediments in the Southern BR began to accumulate at ~23 Ma ago and continued through the Neogene (Fig. 3). The transition to block faulting in the Southern BR occurred ~12.5 Ma ago (4); our data show upticks in deformation and area-change rates around this time and may represent the transition to block faulting in this subregion (Fig. 4, B and D). SAR of fossiliferous units also slightly increased between 13 and 11.5 Ma ago, potentially in response to the transition in tectonic style, including the deposition of several mammal-bearing units and localities in the Rio Grande rift (Figs. 1 and 3).

The history of the Central BR reflects its location between the southern Nevadaplano, the northern Mogollon highlands, the southern Sierra Nevada mountains, and the evolving plate margin (Fig. 1) (4). Tectonic deformation in the subregion began at ~25 Ma ago (Fig. 4B) as the Mogollon highlands collapsed, and the East Pacific Rise was subducted along the southwestern coast (14). The accumulation of both nonfossiliferous and fossiliferous sedimentary packages in the Early Miocene closely followed the initiation of deformation in this subregion (Fig. 5D). The paucity of a sediment record before 25 Ma ago may be due to the higher elevation of the subregion before extension (6); the long-term preservation of sediments occurred only after the Central BR was extended, and its area steadily increased (Fig. 4D). The pulse of sediment accumulation at ~15 Ma ago is likely related to the strikingly high deformation rates in the Middle Miocene that accompanied core complex exhumation in western Arizona and Nevada (4, 14). The increase in sediment thickness and SAR after ~6 Ma ago (Fig. 5D and fig. S1) may be associated with the establishment of the modern Colorado River corridor and the deposition of associated sediments (20).

Elevation changes over the BR also likely affected the ultimate fate of sediment. Today, the Southern BR is roughly 1 km lower in elevation than the Northern BR (7). Reconstructed topographic models show that similar elevational differences existed throughout the Neogene and that the Central and Southern BR achieved lower elevations following highland collapse (6). Large drainage networks would have delivered greater amounts of sediment to the Central and Southern BR as extension progressed (20), and lower overall elevations could have increased the preservation potential of sediment in these subregions through the transition in extensional style.

We framed this study to focus on the history of mammalian species richness and sedimentation of the BR and its subregions (Fig. 1). The availability of data resources and existing studies limit our analyses to the BR of the United States, which excludes almost half the geographic extent of the region (4, 7). Even with this restricted focus, the amount of available lithological and structural data varies among subregions. These differences include a bias in the focus of previous work on the Northern BR, where fault kinematics and basin evolution are better studied than in other portions of the BR. The sedimentary and fossil records of the Southern BR may also be understudied, particularly the pre-Pliocene records outside the Rio Grande rift (26). Future, more comprehensive analyses

may incorporate the rock and fossil records of the entire region and investigate whether the patterns identified in the United States existed in the BR of Mexico.

Landscapes integrate a variety of tectonic- and climate-driven processes. Species respond to changing landscapes by altering their areal and elevational distributions, which can spur speciation and extinction mechanisms (1, 2). Drivers of speciation in the past are often difficult to disentangle from fossil preservation, especially when the processes that mold landscapes include drivers (topographic uplift, subsidence, and precipitation) and responses (erosion, sedimentation, and productivity) that affect the number of fossil occurrences and diversity of fossil faunas and floras. High mammalian species richness in western North America during the Middle Miocene occurred against the backdrop of significant tectonic and climatic activity. The collapse of the high-elevation Nevadaplano and Mogollon highlands was achieved through widespread extension and subsidence that created basins that accumulated sediment throughout the BR. The sweep of deformation across the region resulted in diachronous intervals of sediment accumulation in the Northern, Central, and Southern portions of the BR. Mammalian species richness through time tracked sediment accumulation but peaked during intervals of warm climate in the Miocene and Pliocene, indicating that species responses to climate ultimately were more pronounced than the effects of enhanced preservation in evolving landscapes. Preservation and landscape processes were important influences on the fossil record, but climate-driven effects on mammal richness are captured at regional and subregional scales. Analysis of local impacts of climate and landscape on basin sedimentary records will help test whether these patterns persist at finer scales.

MATERIALS AND METHODS
Study design
To compare the trends in mammalian species richness, sediment accumulation, and tectonic history for the BR, we used online databases and literature sources to compile mammalian species occurrences, lithological data, and tectonic data for the region between 36 and 0 Ma ago. We divided each record into 72 time bins with a duration of 0.5 Ma to compare changes in these variables through time for the entire BR and for the Northern, Central, and Southern subregions in the United States. Subregions (Fig. 1) were delineated along modern physiographic boundaries following (4, 5, 7) and based on topography, structural history, and bedrock lithology. Our analyses are predominantly restricted to the BR in the conterminous United States, where paleontological, geological, and tectonic data are readily available.

We obtained records of mammal occurrences from 1312 localities in the BR region (fig. S2) from 36 to 0 Ma ago from MioMap (12) and the Paleobiology Database (paleobiodb.org). We verified accepted species and genus taxonomy and corrected synonymies using the Paleobiology Database (data S1). Large-bodied mammal species include those belonging to Artiodactyla (excluding Cetacea), Carnivora (excluding Desmatophocidae, Otariidae, and Phocidae), Didelphimorphia, Edentata, Creodonta, Perissodactyla, Proboscidea, and "Ungulata"; small-bodied mammal species include those belonging to Chiroptera, Insectivora, Marsupialia, Lagomorpha, and Rodentia. We excluded species in the most recent time bin introduced through the Columbian exchange. We included occurrences of genera without identified species (e.g., *Herpetotherium* sp.) if these genera did not otherwise have identified species occurrences. As we

were interested in the effects of preservation on species occurrences, we did not assume range-through presence, and we included species with one occurrence (singletons). For each locality, we used the given age range listed in MioMap, and we excluded localities without absolute age estimates. We added locality ages from literature sources only when age estimates were unavailable in the MioMap dataset, and we constrained species occurrences from the Paleobiology Database to the estimated ages of the formations in which they occur, obtained from the literature. Age estimates of many localities span more than one 0.5-Ma time bin; for all pre-Holocene localities in our dataset, the average uncertainty in age is 1.7 Ma. To account for this uncertainty, we bootstrapped the age of each locality within its estimated age range and then tallied the species occurrences for that time bin using R (*27*) (see the Supplemental Materials). This procedure was repeated 10,000 times to generate the median, lower 2.5%, and upper 97.5% richness estimates per time bin. Similarly, we used the same bootstrap procedure to estimate the median, lower 2.5%, and upper 97.5% number of localities per time bin. We used the average pre-Holocene locality age range as uncertainty estimates on locality ages, determined separately for the Northern, Central, and Southern BR (Fig. 3).

We obtained lithological data from the Macrostrat online database (*13*) and literature sources. The Macrostrat database contains comprehensive records of gap-bound rock packages in North America, organized into columns that represent the bedrock and surficial geology over a specific area (fig. S2). Information for each package in the database includes lower and upper ages, lithology, minimum and maximum thickness, and column location. We downloaded packages formed between 40 and 0 Ma ago from the Macrostrat API (https://macrostrat.org/api/units?age_top=0&age_bottom=40&response=long&format=csv), removed superfluous columns, and extracted sedimentary packages from the BR province in Arizona, California, Idaho, Nevada, New Mexico, Oregon, Utah, and Texas (fig. S2). For our analyses, we calculated the maximum thickness of 246 sedimentary packages and the sedimentary portion of sedimentary and volcanic packages deposited between 36 and 0 Ma ago; for packages that began deposition before 36 Ma ago, we included only the calculated thickness deposited after 36 Ma ago (data S2). To the Macrostrat data, we added 58 sedimentary packages from the literature (*26*, *28–44*) to increase the representation of important fossil-bearing units that are absent from Macrostrat or to refine the geographic coverage of these packages. In addition to the Macrostrat dataset, we compiled records of 84 sedimentary units with mammal-fossil records from literature sources (*3*, *26*, *28*, *30*, *32–34*, *36–57*). The lithologic information in the MioMap dataset does not completely overlap spatially or temporally with the Macrostrat dataset. Because most of the mammalian species occurrences in MioMap are derived from these 84 fossiliferous units, analyzing them separately allows us to examine sedimentological trends in greater detail (data S3). These units included formally named geological formations and members, as well as informally named fossil-bearing beds. For each sedimentary package or unit, we calculated thickness (m) and SAR (m/Ma) per 0.5-Ma time bin from 36 to 0 Ma ago for the entire BR and for each subregion.

For tectonic deformation rates, we used estimates of the magnitude and timing of the horizontal component of fault-slip strain compiled in (*5*, *58–68*) for 72 fault systems in the Northern, Central, and Southern BR. We calculated total deformation rates (km/Ma) as the total displacement (km) divided by the duration of displacement

(Ma) for 0.5-Ma time bins from 36 to 0 Ma ago. We calculated the upper and lower errors on deformation rates by adding or subtracting the given uncertainties on displacement distances in kilometers. Area-change rates per 0.5-Ma time bin for each subregion from 36 to 0 Ma ago were calculated from (*6*, *14*) (data S4).

Quantitative analyses

Calculations of original data and first differences of species richness, SAR, deformation rate, and area-change rate were compared using Spearman's rank-order correlation and presented in table S1. We calculated lag correlations between variables to examine the synchroneity between time series. Lag correlations were calculated using Pearson's product-moment correlation with the cross-correlation function in the stats package in R 4.0.2 (*27*) and are given in table S2. Selected partial correlations were performed with the ppcor package (*69*) in R 4.0.2.

For each time series, we used change-point analysis to detect significant changes in means from one time bin to the next. We used the changepoint package (*70*) in R 4.0.2, with the cumulative sum test statistic for nonparametric data. We specified that the analysis detect only one significant change per time series to pinpoint the earliest significant change in means rather than the greatest overall change in the entire time series. We tested a variety of penalty methods, all of which returned similar change points; we ultimately chose not to implement a penalty as this setting gave the most consistent results. We used Welch's two-sided *t* tests to compare means for the intervals before and after each change point (Table 1). All R code and output of analyses are available at https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/R7HWGE.

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