

Cenozoic comparisons of diversity and disparity in the context of tectonic regime: A case study in North American rodents

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ABSTRACT

The tectonic evolution of landscape topography is an important driver of biotic evolution throughout Earth's history. Studies of extant diversity have shown a higher diversity of mammals in topographically complex regions, suggesting that landscape complexity plays a role in generating taxonomic diversity. However, this relationship is poorly understood, especially over geologic time scales. Previous work has posited that heterogeneous topography should lead to increased species diversity as a result of new niche spaces into which lineages may speciate. This is in comparison to homogeneous landscape topography, which offers fewer and less varied niche spaces and thus less ecological opportunities for diversification. It is also thought that barriers to species and individual movement created by mountainous landscapes may divide populations, leading to speciation by restricting gene flow. These two models can be distinguished by their effects on morphological disparity. If niche differentiation is important to the process, we would expect increased morphological disparity in association with heterogeneous landscape topography, whereas the allopatry model predicts no greater morphological disparity over the complex landscape, only taxonomic diversification. We explore these models in the tectonically active and passive regions of North America in rodents from 25 to 0 Ma. We investigate diversity and disparity trends and examine the effects of climate, landscape heterogeneity, and environmental shifts on these patterns. We find that morphological and taxonomic evolution are not impacted by topography in a predictable way, and find that homogeneous landscapes host taxonomic and morphological diversity surpassing that of heterogeneous landscapes for much of the last 19 million years in North America. Furthermore, diversity and disparity trends are both coupled and decoupled during this period, signifying that taxonomic and morphologic increase and decrease are discordant through time. Our results support the finding that the relationship between landscape heterogeneity and species diversity has not remained constant through geologic time.

1. Introduction

The drivers of taxonomic diversity, morphological disparity, and their relationship to one another are poorly understood, and have been investigated across many floras, faunas, and geologic periods. In particular, biotic responses to abiotic drivers have been a topic of interest for the past several decades ([Simpson, 1964](#); [Barnosky, 2001](#); [Hillebrand and Azovsky, 2001](#); [Alhajer et al., 2020](#)). The response of biodiversity to climatic fluctuations and variations in the physical landscape have also received particular attention ([Alroy et al., 2000](#); [Irl et al., 2015](#)). The drivers of these responses are not well understood, and current work seeks to address the modern phenomenon of increased faunal diversity in topographically complex highlands compared to

adjacent lowlands, with a focus on rodents ([Badgley and Fox, 2000](#); [Badgley, 2010](#); [Badgley et al., 2017](#); [Antonelli et al., 2018](#); [Smiley et al., 2020](#)).

[Finarelli and Badgley \(2010\)](#) demonstrated in a study of North American fossil species distribution data that mammalian species richness is strongly correlated with landscape complexity, which they inferred to be driven by the Cenozoic history of tectonic activity. Topographically complex landscapes are thought to promote the origination of new species both as a result of novel niche space availability, which encourages ecomorphological evolution and taxonomic diversification, and as a result of topographic barriers to migration that facilitate allopatric speciation (examples of topographic diversity gradient in birds: [Davies et al., 2007](#); fish: [Willis et al., 2005](#); invertebrates: [Garrick,](#)

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2011; and mammals: [Finarelli and Badgley, 2010](#); [Badgley et al., 2017](#)).

Given that the relationship between topographic complexity and diversity is quite clear in modern assemblages, one might expect that diversity would correlate with tectonic activity (the process generating landscape complexity) across geologic time scales; however, that relationship is not entirely clear ([Simpson, 1964](#); [Badgley, 2010](#); [Finarelli and Badgley, 2010](#)). In particular, species richness in the topographically homogeneous and tectonically inactive Great Plains region of North America (i.e., the passive region east from the Front Range of the Rocky Mountains to the Mississippi River; or PR following [Finarelli and Badgley, 2010](#)) is greater than that of the topographically complex and tectonically active western region (i.e., the active region west from the Front Range to the Pacific coast; AR) through much of the Cenozoic, with the AR exceeding the PR in diversity only during the middle Miocene period of significant tectonism and climate warming ([Finarelli and Badgley, 2010](#)). In fact, according to the IUCN (International Union for Conservation of Nature), rodent species in the AR today outnumber those in the PR by about 163 species to 87, respectively ([IUCN, 2020](#)).

The clear distinction in topographic complexity and precise geographic boundary between these two regions allows for the investigation of several possible scenarios for taxonomic diversification in these settings. In the PR, we would expect that in hypothesis (1) landscape homogeneity provides relatively little variety in niche openings into which taxa may speciate, resulting in relatively low diversity. In the AR, we may expect one of two scenarios: hypothesis (2) the geographic speciation model, assumes that taxa are passively speciating as a result of geographic barriers causing physical separation, known as vicariance. In this case, populations undergo speciation resulting from allopatry and genetic drift. As a result, we would expect taxonomic diversity to increase without accompanying increases to morphological disparity. Hypothesis (3), which we call the ecological speciation model, assumes that taxa are speciating as a result of adaptive pressures from a changing landscape. As novel niche space becomes available, taxa diversify both morphologically and ecologically to fill these new niche spaces and speciation occurs in this sense. Thus, in the AR, we would expect taxonomic diversity and morphological disparity to increase in tandem in this scenario as taxa radiate morphologically to adapt ecologically to these new environments. In addition, it is probable that body mass impacts the way in which rodents interact with the landscape. Larger-bodied rodents, such as some sciurids and castorids, may have an easier time navigating topographically heterogeneous landscapes, which may affect the body mass distributions that we find in either region. We also expect that climate change should influence morphological disparity given that past studies have found varying effects of climate change on biodiversity, and we would also expect these effects to be reflected in measures of morphological disparity ([Janis et al., 2000](#); [Janis et al., 2004](#)).

In this study, we explore the breadth of biodiversity present on the landscape through the study of morphological diversity, also known as morphological disparity, and attempt to parse its drivers ([Foote, 1997](#); [Erwin, 2007](#)). Morphological disparity describes the variety of morphological forms which are occupied and relies on the observed morphology of specimens rather than taxonomic methods, which can be prone to various biases such as taxonomic naming ([Isaac et al., 2004](#); [Gwinn et al., 2016](#)), geopolitical ([Harris and Froufe, 2004](#); [Murphy, 2021](#)), and unequal sampling efforts ([Jones et al., 2012](#)). Morphological disparity offers a taxon-free metric which captures some aspect of the breadth of morphospace occupied or the average dissimilarity among the taxa or individuals considered ([Briggs et al., 1992](#); [Foote, 1992, 1993](#); [Erwin, 2007](#)). We examine the disparity present in the morphological trait of body size. Body size is an important aspect of morphology, as size represents a critical component of morphology, which is typically defined as the study of structure and form. Body size governs the biological processes and interactions that an individual engages in, including energy consumption, diet, home range size, and others ([Makarieva et al., 2004](#); [Codron et al., 2007](#); [Tucker et al., 2014](#)).

As such, morphological disparity may offer a more ecologically meaningful perspective of the total diversity achieved on a landscape, especially in comparison to measures such as taxonomic diversity.

We also closely consider the relationship between taxonomic diversity and morphological disparity and what it can reveal about the drivers of these relationships. Foote investigated the nature and direction of the changes in diversity and disparity in the Blastoida and Trilobita and found that morphological disparity and taxonomic diversity increase in tandem as clades arise and diversify ([Foote, 1992, 1993](#)). During clade decline, however, Foote describes two major patterns of diversity and disparity: (1) taxonomic decrease concurrent with sustained or increasing levels of morphological diversity, and (2) simultaneous taxonomic and morphological decrease ([Foote, 1992, 1993](#)). The first case is thought to be a result of non-selective extinctions (i.e., extinctions that target forms and branches of the phylogenetic tree at random). Non-selective extinctions decrease taxonomic diversity and could have varying effects on morphological disparity ([Foote, 1992](#); [Grunert et al., 2019](#)). In some cases, morphological disparity experiences no change alongside decreasing diversity as a result of extinctions equally impacting all parts of the morphological spectrum ([Foote, 1993](#)). In other cases, disparity will increase alongside decreasing diversity. This is thought to be the result of continued diversification through morphospace as a clade ages ([Briggs et al., 1992](#); [Foote, 1993](#)). An example of scenario (1) can be observed in the Cambrian trilobite family Pteroccephaliidae, in which increasing disparity accompanied taxonomic decrease thought to be a result of either random extinction or extinction targeting mean forms ([Hopkins, 2013](#)). In the second scenario (2), simultaneous taxonomic and morphological diversity decrease is thought to be a result of elevated extinction and/or reduced origination in particular regions of morphospace ([Foote, 1993](#)). Examples of this scenario can be observed in the Paleozoic trilobite clades Proetida, Phacopida, and Scutelluina, in which morphological extremes are preferentially undergoing increased extinction and/or reduced origination, resulting in simultaneous taxonomic and morphologic decrease ([Foote, 1993](#)). These patterns are a few of many which describe taxonomic diversity change alongside morphological change, and while Foote describes these patterns in the Blastoida and Trilobita during clade diversification and decline, we use these patterns as a basis to parse the nature of diversity and disparity change in North American rodents. Foote examined these trends over large stratigraphic intervals and on a global scale, while we aim to consider these diversity and disparity patterns in the largest order of mammals on a continent-level scale.

The Miocene of North America marks a time of significant climatic change and encompassed periods of both warming (e.g., the Middle Miocene Climatic Optimum ca. 16–14.8 Ma, or millions of years ago) and cooling (e.g., the Middle Miocene Climatic Transition beginning ca. 14.8 Ma; [Flower and Kennett, 1994](#); [Zachos et al., 2001](#); [Zachos et al., 2008](#)). Climate and factors like topography are deeply interconnected and work together to create complex environmental conditions. Climate factors are frequently determined by latitude, prevailing winds, and temperature, which can be greatly altered by topographic conditions including elevation, slope, and aspect ([Kauffman, 2003](#)). Global climate change paired with topographically heterogeneous landscapes can lead to geographic range shifts in elevation and/or latitude, as well as changes in origination and extinction rates, and to evolutionary processes ([Badgley, 2010](#); [Chen et al., 2011](#)). Climate warming is thought to generate faster speciation and/or lower extinction rates, as well as increased metabolic rate, greater energy availability ([Erwin, 2009](#)). Together, these factors have important ramifications for biodiversity and the global environment.

The North American landscape was characterized by active tectonism from the Paleocene through the Miocene, with the most significant tectonic events occurring during the middle Miocene ([Trimble, 1980](#); [Dickinson, 2006](#); [Finarelli and Badgley, 2010](#)). This tectonic activity occurred primarily in the region west of the Front Range of the Rocky

Mountains and included events such as Great Basin extension (ca. 17.5 Ma; Dickinson, 2006), Snake River Plain volcanism (ca. 16–0.6 Ma; Dickinson, 1997, 2006), Colorado Plateau uplift (ca. 20 Ma; McQuarrie and Chase, 2000), and the eruption of the Columbia River flood basalts (ca. 17–14 Ma; Zoback et al., 1994; Dickinson, 2006). Tectonic activity reached a peak during the middle Miocene and tectonic events declined significantly thereafter. In comparison, the region east of the Front Range to the Mississippi River (i.e., the Great Plains region) experienced relative tectonic stability throughout this time, punctuated by periodic ash falls from volcanic eruptions to the west (ca. 65–17 Ma, to a lesser degree from 17 to 0 Ma; Trimble, 1980; Diffendal, 1991). Consequently, these differing tectonic regimes are reflected in the landscape topography of each of these regions, which remains apparent to this day with remarkably increased landscape complexity in the West compared to the adjoining Great Plains. The interaction of the effects of climate change and tectonic activity have been previously proposed as a driver to diversification in mammals (Finarelli and Badgley, 2010).

It is against this backdrop that we investigate diversity and disparity in North American rodents, which have been a focus for studies of the effect of landscape complexity on mammalian diversity (Badgley, 2010; Finarelli and Badgley, 2010; Badgley et al., 2017; Smiley et al., 2020). Rodents are small-bodied mammals and highly susceptible to barriers to migration, have a short generation time, and are abundant on the North American landscape and in the fossil record. Rodents constitute 40% of extant mammalian diversity and 20% of published fossil mammal diversity over the last 25 million years (Kay and Hoekstra, 2008; Alroy et al., 2019). Past work has also shown that rodents exhibit a topographic richness gradient in the present day, with ambiguous findings in the Miocene record (Badgley, 2010; Finarelli and Badgley, 2010; Badgley et al., 2017). In this study, we investigate past biodiversity through the lens of morphological disparity. We build on past studies of taxonomic richness in these settings by closely examining corresponding trends in morphological diversity. We explore three hypotheses for taxonomic diversity and morphological disparity change in the AR and PR and examine the ways in which diversity and disparity interact with climatic change tectonic regime.

2. Materials and methods

We obtained species-level fossil rodent occurrence data from the MIOMAP ($n = 1194$, 308 unique species from 14 families) and FAUNMAP I and II databases ($n = 6761$, 56 unique species from 9 families), which we merged with species average first molar area measurements obtained from the Paleobiology Database (FAUNMAP Working Group, 1994; Carrasco et al., 2005; Graham and Lundelius Jr., 2010; Alroy et al., 2019). We sorted these data into one million-year time bins (spanning from 25 Ma to 1 Ma) using the range-through assumption based on the first appearance datum and the last appearance datum for a taxon, and excluding singletons. We grouped taxa into two geographic regions: the tectonically active region or the tectonically passive region following the regional boundaries outlined by Finarelli and Badgley (2010; Figure 1). Taxa were placed into one or both regions based on the localities in which they occur. We omitted indeterminate specific identifications. We estimated body mass from first molar area following the body mass-molar area regression equation for rodents in Legendre (Legendre, 1986; Janis, 1990; Hopkins, 2008; Freudenthal and Martín-Suárez, 2013). Tooththrow dimensions are accurate predictors of interspecific trends in rodent body mass, thus for a study of this scale, first molar area is an appropriate predictor of body mass (Hopkins, 2008). We consider body mass as it captures size, which represents a basic component of morphology. Body size, in turn, correlates with many ecological and life history variables (e.g., home range size, population size and density, diet, trophic level, locomotor mode; reproductive rate; adult size; Robinson and Redford, 1986; Millar and Hickling, 1991; Pusey et al., 2005; Price and Hopkins, 2015; Ofstad et al., 2016; Pineda-Munoz et al., 2016). This makes body mass an ideal indicator of

morphological size diversity and also reflective in some ways of ecological diversity. Modern rodent occurrences were obtained from the IUCN database using geographic range maps. Rodent species with geographic ranges extending into the AR were placed into this region, and those with ranges extending into the PR were placed into the PR region. Species with ranges overlapping both the AR and PR were placed into both regions. Modern rodent body masses were obtained from the PanTHERIA database and placed in the 0 Ma time bin ($n = 199$; IUCN, 2020; Jones et al., 2009). Because these data are direct measurements of specimens rather than estimates based on dental regressions, caution should be used when making direct comparisons between modern and fossil data. Mean and median body mass estimates across all taxa were then calculated for each region and time bin.

From these data, species richness was calculated along with three measures of morphological disparity including the sum of ranges (SOR), sum of variances (SOV), and mean distance from centroid (mean DFC; Ciampaglio et al., 2001; Wills et al., 1994; Halliday and Goswami, 2016; Grunert et al., 2019). We capture taxonomic diversity through species richness, which is based on sums of species occurrence data in each region. We calculated disparity metrics in each region using the mean estimated (or measured for modern data) body mass of species. SOR was calculated for each region and captures the total range of morphospace occupied by individuals or taxa within a time bin and thus describes the breadth of morphospace occupation (Ciampaglio et al., 2001; Wills et al., 1994; Halliday and Goswami, 2016). SOV was also calculated for each region and describes the sum total of squared deviation from the mean character value, giving a sense of the spread of values through that range (Ciampaglio et al., 2001; Wills et al., 1994; Halliday and Goswami, 2016). SOR and SOV calculations exclude modern data. Mean DFC was calculated for each time bin in each region and captures the mean character distance of each specimen from the centroid of all specimens within a time bin, which quantifies how far a species or individual lies on average from the central tendency of the larger assemblage (Ciampaglio et al., 2001; Wills et al., 1994). Disparity in body mass captured in this way should reflect the magnitude and extent of morphological variation in rodents during this time period and give greater depth to descriptions of biodiversity.

Correlation tests were then performed on first differences of diversity (taxonomic richness) and disparity (mean DFC metric) to gauge the degree of correlation between change in diversity and disparity in each region. First differences for diversity in the AR and PR were calculated and plotted, along with first differences for disparity in the AR and PR, and diversity and disparity in both the AR and PR. We performed a Shapiro-Wilk test for normality and a Kendall rank correlation test, which tests for statistical dependence between two variables. We examined and compared the changes in each measure for each region, and determined their degree of correlation, if any. We did this by examining the first difference changes in each time bin and determining the type of relationship shared by the diversity and disparity metrics: coupled or decoupled. Coupled relationships indicate that diversity and disparity are positively or negatively correlated, and increase or decrease in tandem. Decoupled relationships indicate that diversity and disparity don't vary in a consistent direction for any length of time, and respond independently of one another. Lastly, we tested for correlation between diversity and disparity in the AR and PR with global temperature using averaged stable isotope records ($\delta^{18}\text{O}$) as indicators for global temperature (Westerhold et al., 2020).

3. Results

3.1. Body mass change through time

Mean and median body mass has varied significantly in both the AR and the PR over the past 25 million years. We find that mean body mass tends to increase through time from the Miocene into the Pliocene-Pleistocene in both regions, apart from intermittent periods of

decrease (Fig. 2A). Mean body mass remains relatively low for much of the Miocene, and in fact, the smallest mean body masses attained during our study period appear during the 18 Ma time bin in both the AR and PR. This pattern is driven by the loss of larger-bodied taxa belonging to the families Castoridae (such as *Fossorcastor fossor*) and Geomyidae (such as *Gregorymys curtus*, *G. formosus*, and *Pleurolicus sulcifrons*). At the same time, we observe the appearance of small-bodied taxa belonging to the families Heteromyidae (such as *Cupidinimus halli* and *Perognathus minutus*), Dipodidae (such as *Megastomus gladiolifex*), Eomyidae (such as *Pseudotheriomys cuyamensis*), and Sciuridae (such as *Nototamias hulberti*). Beginning at around 12 Ma, both regions begin to increase in mean body mass before falling during the latest Miocene-early Pliocene, driven first by the appearance of large castorids (such as *Dipoides*) and the loss of small dipodids (such as *Macrogathomys nanus*), and then again by the loss of large castorids (such as *Dipoides*) and sciurids (such as *Spermophilus wilsoni*). Both regions then begin increasing into the late Pliocene-early Pleistocene, growing by an order of magnitude, and eventually attaining the highest mean body masses observed in this study, largely due to the appearance of several large-bodied taxa, including large-bodied castorids (like *Dipoides* and *Procastoroides*), cricetids (like *Ondatra*), and erethizontids (like *Erethizon*). Median body mass (which is less influenced by the appearance and disappearance of a few exceptionally large-bodied taxa) in the PR is highest during the Middle to Late Miocene and peaks at 8 Ma, while median body mass in the AR is highest during the Early Miocene and peaks at 21 Ma. Beyond these periods, median body mass remains relatively stable for the duration of our study period (Fig. 2B). The range of body mass appears to generally increase through time and is comparable between the AR and PR (Fig. 2C).

3.2. Patterns in diversity and disparity

We found that diversity and disparity vary through time, and are not consistently correlated over time and space. The most obvious feature of both taxonomic richness and disparity over the study interval is a substantial increase in the late Pliocene and Pleistocene. Patterns of taxonomic richness are variable in the AR and PR and tend to fluctuate prior to the Pliocene, rising through the early Miocene to a high in the middle Miocene, then generally dropping until the dramatic rise beginning in the early Pliocene (Fig. 3A). Morphological disparity is at a moderate value in the early Miocene, before dropping quite low in the middle Miocene, when taxonomic diversity is high, and then rising in the late Miocene with a decrease in richness before increasing dramatically into the early Pliocene and then dropping in the Pleistocene in both regions (Fig. 3B).

In general, the patterns we recovered indicate that morphological disparity was higher in the PR compared to the AR for much of the past 19 million years. Both SOR and SOV values indicate that the PR occupies both a broader range of morphospace as well as exhibits more variance (Table 1). Most strikingly, calculations of mean DFC show that disparity during the Pliocene far exceeded that of the Miocene by two orders of magnitude in both regions (Fig. 3B). But despite this, morphological disparity in the modern day is comparable to levels achieved during the Miocene, suggesting that the Pliocene rodent assemblages differed dramatically from those before and after this time.

Table 1
The sum of ranges and sum of variances are shown for the AR and PR. The sum of ranges represents the sum total range of body masses occupied in all time bins in each region and the sum of variances represents the sum total variance in all time bins in each region. Calculations of SOR and SOV do not include modern data (0 Ma time bin).

Morphological disparity values for AR and PR, not including 0 Ma bin		
	AR	PR
SOR	2.47E5	4.28E5
SOV	3.76E8	1.22E9

In the AR, there are three time periods in which disparity appears to be relatively high compared to the baseline levels. These occur at 21 Ma, 8 Ma, and from 4 to 3 Ma (Fig. 3 BCE). In the PR, there are fewer obvious periods of high morphological disparity; rather, there seems to be a trend of uniformly low disparity from 25 Ma to about 9 Ma, at which point there is a trend of increase until 2 Ma. Despite this overall low level of disparity, this period is interspersed by patterns of both increase (from 17 Ma to 15 Ma) and decrease in disparity (from 12 Ma to 9 Ma).

Taxonomic richness is higher in the AR for much of the Miocene, with PR richness exceeding the AR for only the earliest Miocene and from the end-Pliocene to the beginning of the Pleistocene (Fig. 3A). Since 5 Ma, richness has predominantly increased in both the AR and PR into the present day (Fig. 3A). In the present day, richness is higher in the AR than the PR, but this relationship has reversed periodically over the past 25 million years.

The Shapiro-Wilk test indicates our data come from a population that is not normally distributed. The Kendall rank correlation tests of first differences indicate little correlation between diversity and disparity within regions, as well as across regions (Fig. 4). A notable exception is the comparison of diversity first differences only between the AR and PR, in which the Kendall rank correlation test yielded a *p*-value of 0.02, indicating a statistically significant relationship in diversity between the AR and PR (Fig. 4 A). This implies that diversity in the AR and PR are correlated, and there is dependence between these two variables. The remaining comparisons do not indicate statistically significant relationships: disparity in the AR and PR do not share a statistically correlated relationship (Fig. 4B), and same with diversity and disparity in the AR (Fig. 4C), and diversity and disparity in the PR (Fig. 4D).

The relationship between diversity and disparity varies in both the AR and PR during this time period. We observe periods during which diversity and disparity are coupled and others in which they are decoupled (Fig. 5). Coupled trends, denoted in Fig. 5 by the letter “C”, describe periods during which diversity and disparity change in the same direction in a region, either by increasing or decreasing together. This pattern occurs in the AR from 3 to 7 Ma and from 8 to 17 Ma, and in the PR from 2 to 12 Ma and 16–17 Ma. Decoupled trends describe periods during which diversity and disparity change in the opposite direction (one increasing while the other decreases or vice versa), and are denoted in Fig. 5 by the letter “D” and gray shading. This pattern occurs in the AR from 0 to 3 Ma, 7–8 Ma, and 17–25 Ma in the AR, and in the PR from 0 to 2 Ma, 12–16 Ma, and 17–25 Ma. Alongside these patterns, major climatic events are shown with isotopic data from Westerhold et al. (2020; Figure 5C). And the correlation test of $\delta^{18}O$ isotope records and diversity and disparity in the two regions do not indicate significant correlation between this temperature proxy and either diversity or disparity (Fig. 6).

SOR and SOV values are higher in the PR than the AR (Table 1). This indicates that in a broad sense, the PR surpasses the AR in the range of morphospace occupied and in the variance of the samples. This is largely in line with our findings in mean DFC, which show that PR disparity surpasses that of the AR for much of the past 25 million years (Fig. 3B). In comparison, diversity is higher in the AR for much of the past 25 million years (Fig. 3A; Finarelli and Badgley, 2010).

4. Discussion

4.1. Body mass patterns

Body mass change in North American rodents through the last 25 Ma is most remarkable across the Miocene-Pliocene boundary, which could represent the appearance of morphologies novel to North America (Vermeij, 1991). The maximum mean rodent body mass of the past 25 million years (5.6 kg) is reached in the PR at 2 Ma (Fig. 2A). However, median body mass does not record a similar spike at that time. This indicates that the mean body mass is influenced strongly by a few exceptionally large taxa in the Plio-Pleistocene, but the distribution of

body masses is relatively unaffected. The Pliocene is unique in the diversification of existing rodent ecologies, such as that of semi-aquaticism, hopping, and burrowing, as well as the appearance of exceedingly large body masses and our results may be recording this signal (Samuels and Hopkins, 2017). Previous work has found elevated beta-diversity in the Great Plains (as compared to the Great Basin) as late as during the Barstovian North American Land Mammal Age (ca. 15.97–13.6 Ma), which is also supported by previous findings that modern biological concepts, such as the latitudinal diversity gradient in mammals, have arisen over the past 4 million years (Davis, 2005; Marcot et al., 2016). In this study, we also find notable changes during the time period from the late Miocene to Plio-Pleistocene, including increases of several orders of magnitude to diversity and disparity in both regions (Fig. 3). This lends evidence to a Late Cenozoic shift in the processes that govern biodiversity trends in mammals.

4.2. Relationships of diversity and disparity with climate and environmental changes

Global climate undergoes several shifts over the course of the last 25 million years (Fig. 5C). Warming during the Middle Miocene Climatic Optimum (ca. 16–14.8 Ma) is followed by cooling during the Middle Miocene Climatic Transition (beginning ca. 14.8 Ma). Temperatures again rise during the Late Miocene during the Tortonian Thermal Maximum (ca. 11 Ma), which is followed by the Mid-Pliocene Warm Period (ca. 3.3–3.03 Ma) and then general cooling through the Pleistocene and Holocene (from 2.6 to 0 Ma; Haywood et al., 2016; Westerhold et al., 2020). The trends we recover in disparity, and to a lesser degree, diversity, appear to broadly mirror trends in climate warming, as diversity and disparity both appear to increase alongside increasing global temperatures. For example, we find that disparity in both the AR and PR begins a regime of general increase at around 17 Ma before plateauing and increasing again at around 11 Ma coincident with the Tortonian Thermal Maximum. This increase at the Tortonian Thermal Maximum is more apparent in the AR, and less so in the PR. Similarly, the Mid-Pliocene Warm Period also coincides with an increase in disparity in both the AR and PR (Fig. 3). However, during time periods characterized by cooling trends, there is less of a relationship between disparity and global temperature change. Neither disparity in the AR nor the PR show signs of sustained decrease during the cooling of the Middle Miocene Climatic Transition, however, Plio-Pleistocene cooling does coincide with considerable decreases in disparity in both regions.

Diversity, on the other hand, appears to correspond with climate trends to a lesser degree. Diversity in the AR, for example, begins trending upward at around 21 Ma and reaches a maximum at the height of the Middle Miocene Climatic Optimum (Fig. 3A). Diversity in the AR then decreases throughout the Middle Miocene Climatic Transition and then increases during the Tortonian Thermal Maximum and the Mid-Pliocene Warm Period. However, diversity then remains high despite patterns of climate cooling into the Pleistocene. Diversity in the PR exhibits similar patterns to the AR since the Plio-Pleistocene but does not align with the AR for much of the Miocene. This suggests that disparity appears to have a more predictable relationship with global temperature, while diversity, especially in the PR, has a more complicated and unpredictable relationship with global temperature. Despite these patterns, neither diversity nor disparity in either region appear to share a strong statistical correlation with oxygen ($\delta^{18}\text{O}$) isotope records (Fig. 6; Westerhold et al., 2020).

The PR during this period also experienced a significant shift in habitat. By the late Arikarean (ca. 21.9 Ma), the PR underwent a transition from closed forests to C3 grass-dominated habitats (Strömberg, 2006). And between about 8 Ma to 2 Ma, the PR was characterized by the expansion of C4 grasslands (Strömberg and McInerney, 2011). Together these environmental shifts represent the appearance of novel ecological niche space. New niche spaces can facilitate the innovation of novel morphologies through diversification

of species into previously unavailable niches. For example, past studies have shown that the shift to C4 grasslands preceded or coincided with morphological change in a variety of North American taxa (Strömberg, 2006; Samuels and Hopkins, 2017). The most well-studied event is perhaps the evolution of high-crowned teeth in ungulates in association with increased airborne grit or a shift from a browsing-dominated diet to grazing (Strömberg, 2006). This transition has also been recovered in small mammals, which exhibit parallel increases to crown height as well as locomotor shifts to burrowing, jumping, and cursoriality, all of which are locomotor modes associated with open grasslands (Samuels and Hopkins, 2017; Jardine et al., 2012). In turn, it has also been asserted that certain ecological roles are oftentimes associated with certain ranges of body mass. The consumption of grass is generally associated with larger body size, while the consumption of seeds or insects is associated with smaller body sizes (Case, 1979). Similar generalizations can be made for locomotor mode: quadrupedalism is associated with larger body sizes and open habitats and bipedalism with smaller body sizes and closed habitats (Vasquez, 1996). Considering this, we would expect average body mass to increase at the same time as grassland expansion, which is supported by our data with the appearance of numerous large-bodied castorids (such as *Dipoides* and *Eucastor*), cricetids (such as *Ondatra*), and sciurids (such as *Paenemarmota*, *Spermophilus*) in the PR between 8 and 4 Ma. These taxa can also be classified as herbivores and consume various types of plant material. These morphological shifts align with changing environmental conditions, which lead to novel niche space becoming available and may result in morphological innovation to fill these niche spaces. This morphological expansion is reflected in the morphological disparity observed in the PR and in general, we find that these environmental shifts to more open habitats align with increasing disparity in the PR and is also reflected in the ecological roles present on the landscape. The AR, on the other hand, which did not experience a similar ecological shift during this time, does not seem to exhibit the same morphological expansion. Instead, disparity largely decreases from 8 Ma to 5 Ma.

4.3. Tectonism

The AR was characterized by active tectonism for much of the Miocene with a pronounced increase in activity from 17 to 14 Ma (for a summary of significant North American tectonic events over the past 30 million years, see Fig. 1 in Badgley et al., 2017; McQuarrie and Wernecke, 2005; Dickinson, 2006). This period of active tectonism coincides with the period of highest Miocene diversity in the AR, as noted by Finarelli and Badgley (2010), but not disparity. The PR does not follow this pattern of elevated diversity through the Middle Miocene (Fig. 3A). Disparity in both regions begin a regime of general increase beginning at 18 Ma, which plateaus in the AR but continues to increase in the PR until 12 Ma (Fig. 3C). If tectonism in the AR contributes to increased niche space and subsequent diversification, we would expect concurrent morphological and taxonomic expansion, resulting in diversity and disparity increasing together. We observe this at times in the AR during the middle Miocene and into the Pliocene, such as from 11 Ma to 7 Ma. This scenario most closely matches the ecological speciation model, where landscape changes appear to advance taxonomic and morphologic diversification in tandem (i.e., “C”, coupled in Fig. 5A). At the same time, the PR does not experience the same landscape shifts and niche expansion, meaning that taxonomic and morphologic diversification may not be driven in the same way as in the AR. In the PR, diversity and disparity change independently of one another during the Middle Miocene (“D”, decoupled in Fig. 5B). This scenario most closely corresponds with the outcome of the geographic speciation model, where we observe taxonomic diversity increasing without accompanying increases to morphological disparity. However, the drivers of this pattern in the PR are uncertain, being that there are no obvious geographic or environmental drivers.

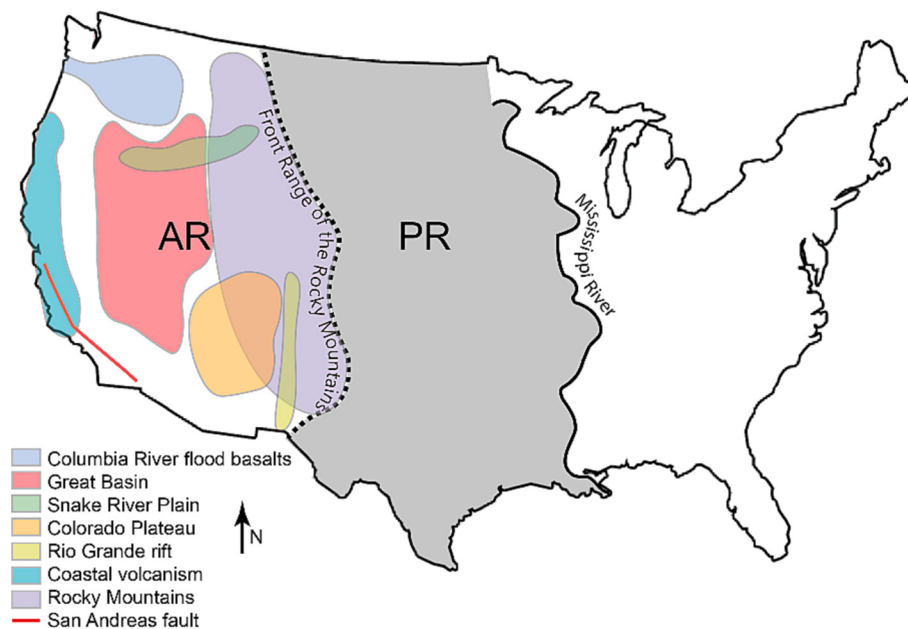


Fig. 1. Study regions and tectonic areas of interest are shown on a map of the United States. The tectonically active region (AR; [Finarelli and Badgley, 2010](#)) includes the area west of the Front Range of the Rocky Mountains, labeled “AR”. The tectonically passive region (PR; [Finarelli and Badgley, 2010](#)) is shown in the region bounded by the Front Range and the Mississippi River, denoted by gray shading and the label “PR”. Regions of tectonic activity are shown in color.

4.4. Decoupling of diversity and disparity

We find that at varying times over the past 25 million years, diversity and disparity have been both coupled and decoupled and the relationship between diversity and disparity has varied both through time and across tectonic regimes. The Kendall rank correlation tests indicate that comparisons of diversity and disparity first differences within the AR are not significantly correlated, suggesting that diversity and disparity are decoupled in this region ([Fig. 4C](#)). Similarly, diversity and disparity first differences within the PR are not significantly correlated, also indicating decoupling ([Fig. 4D](#)). Disparity first differences in the AR and PR are also not significantly correlated but yielded a Kendall's tau of 0.15, indicating a slightly stronger, yet statistically insignificant correlation. This indicates that disparity in these two regions is changing asynchronously. Diversity first differences in the AR and PR, however, were found to be significantly correlated ([Fig. 4A](#)). This linkage indicates a relationship between diversity in the AR and diversity in the PR, which could suggest analogous drivers of diversity in both regions, or, given their geographical connectedness, it is possible there is interchange between them that is contributing to diversity in both regions. This is supported by the presence of some species in both regions. The lack of correlation between disparity in the AR and PR indicates that disparity does not share a similarly connected relationship across these regions, which is unsurprising given that we do not find correlation between diversity and disparity in either the AR or the PR. This also lends support to our finding that diversity and disparity are decoupled for periods during the past 25 million years in both the AR and PR, indicating that taxonomic diversity and morphological disparity have the potential to develop independently of one another, which most closely matches the geographic speciation model.

In addition to coupling and decoupling patterns, the nature and direction of the relative changes in diversity and disparity are also informative. Some time periods exhibit coupled trends in diversity and disparity, in which diversity and disparity change in tandem. Periods of concordant increase may be time periods characterized by taxonomic increase driven by ecomorphological diversification, resulting in increases to diversity and disparity in tandem. We observe this pattern in the AR during 11–8 Ma and from 5 to 3 Ma, and in the PR from 9 to 6 Ma

and again from 5 to 2 Ma ([Fig. 5](#)). These periods coincide with times of climatic warming, increasing primary productivity, and environmental change ([Janis et al., 2000](#); [Strömberg and McInerney, 2011](#); [Westerhold et al., 2020](#)). Another contributing factor may be immigration from other continents, which would result in increased taxonomic diversity as well as an influx of novel morphologies ([Vermeij, 1991](#)).

Coupled decrease in diversity and disparity indicates that extinctions are occurring along with morphospace contraction. A possible driver of this contraction could be a response to low levels of landscape disturbance or decreased primary productivity ([Janis et al., 2000](#); [Kondoh, 2001](#)). In relation to taxonomic diversity, studies have found that species richness in mammals can track the levels of primary productivity on the landscape, and that decreases in species richness may occur alongside declines in primary productivity due to losses in nutritional availability ([Brown, 1973](#); [Abramsky and Rosenzweig, 1984](#); [Janis et al., 2000](#); [Bailey et al., 2004](#)). Similar studies on the relationship between morphological disparity and ecological factors such as primary productivity have not been performed. However, as a result of decreased primary productivity we might expect that the organisms, especially ecological specialists which depend on certain types of flora, would not be able to survive as readily in an environment with decreased primary productivity and food availability which would lead to decreases in both richness and morphological disparity. This pattern aligns with Foote's second pattern of diversity and disparity, in which we observe simultaneous taxonomic and morphological decrease in which specific morphologies or clades go extinct non-randomly ([Fowler and MacMahon, 1982](#); [Foote, 1992, 1993](#)). In our sample of rodents, we see examples of this pattern in the AR between 24 and 22 Ma and 7–5 Ma and in the PR between 19 and 18 Ma and 12–9 Ma ([Fig. 5](#)). These periods appear to correspond with relatively high extinction rates in their respective regions, and in the PR, this pattern corresponds with the expansion of C3, and later C4 grasslands ([Finarelli and Badgley, 2010](#); [Strömberg, 2006](#); [Strömberg and McInerney, 2011](#)). Future work could examine these patterns in other mammalian lineages.

We also observe instances of Foote's first major pattern of diversity and disparity, in which diversity and disparity are decoupled and taxonomic decrease occurs concurrently with sustained or increasing levels of morphological diversity. We find evidence of increasing

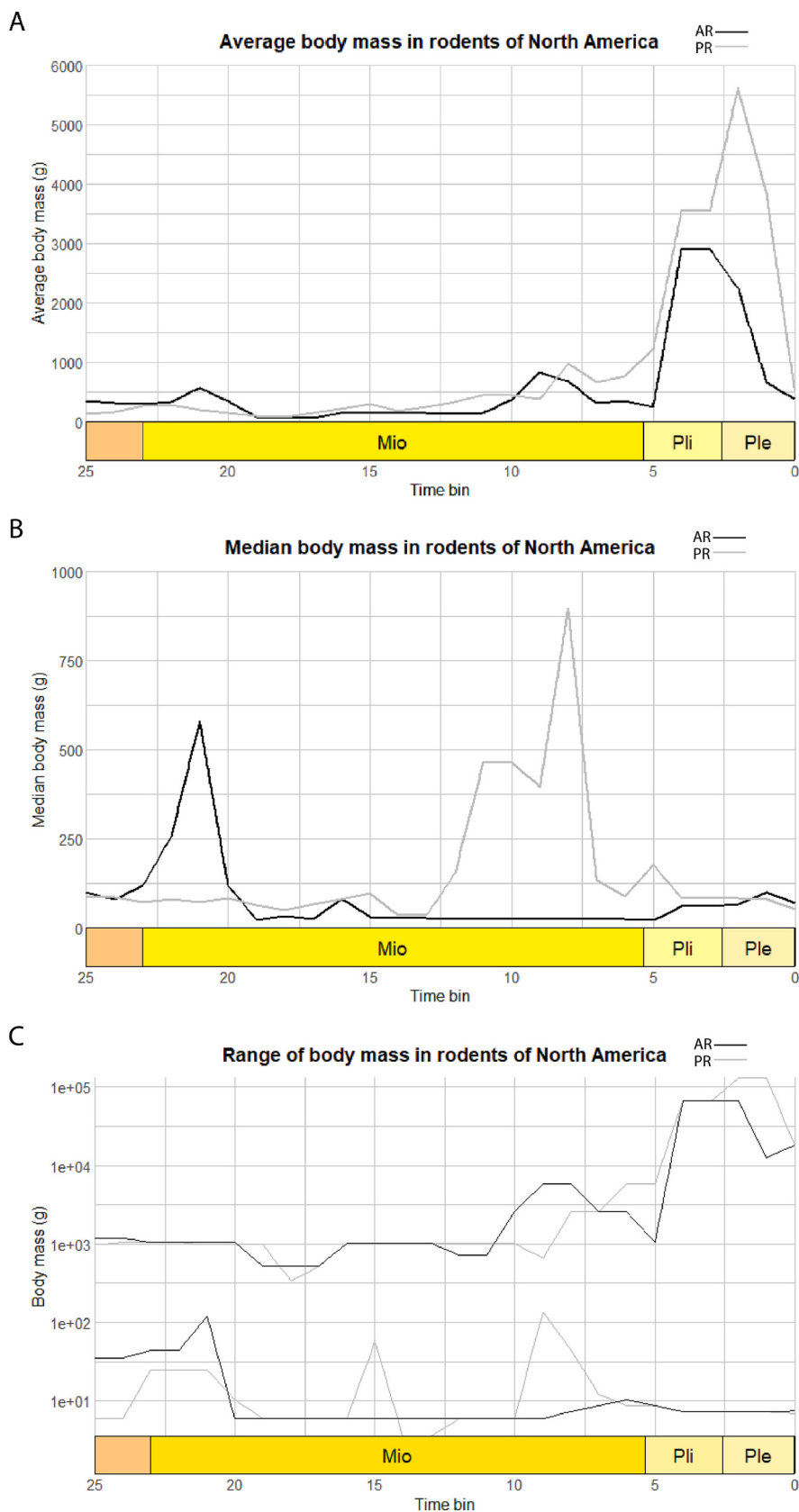


Fig. 2. (A) Mean, (B) median, and (C) ranges of estimated body mass in grams for North American rodents. Body masses were estimated from a regression of first molar area and an average was taken for each million-year time bin from 25 Ma to the present day. The black line shows data for the active region and the gray line for the passive region.

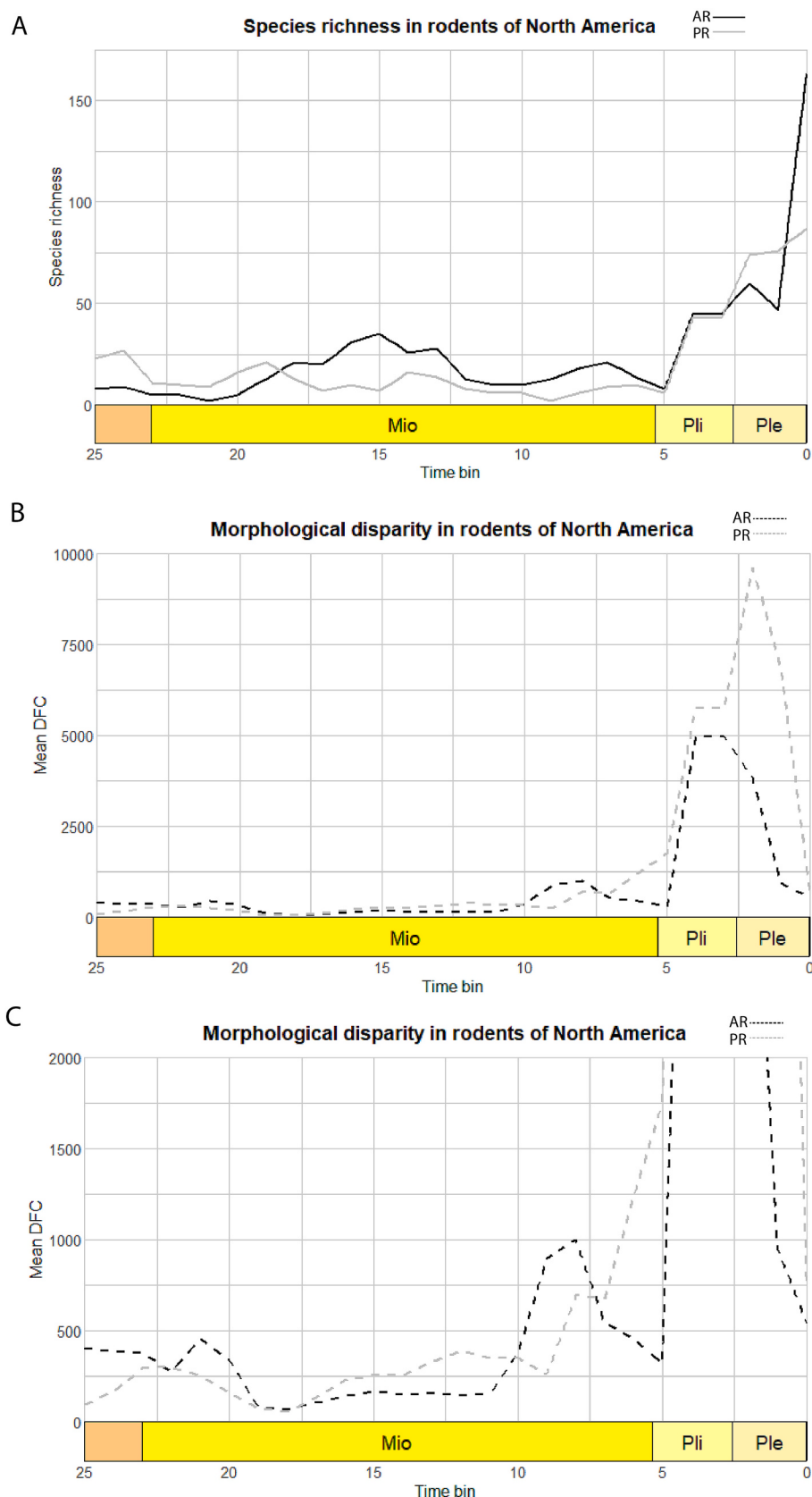


Fig. 3. (A) Taxonomic diversity and (B, C) morphological disparity in body mass for North American rodents in time bins from 25 Ma to the present day. Taxonomic diversity is measured in counts of species richness. Morphological disparity is captured through the mean distance from centroid, a measure of the mean distance from the mean body mass in each time bin and region. (C) shows plot (B) with the y-axis scaled to the data in the bins from 25 Ma to 5 Ma. Data from the AR are shown with black lines, and the PR with gray. The active region is shown with black and the passive region with gray, solid lines show diversity (species richness) and dotted lines show disparity (mean DFC).

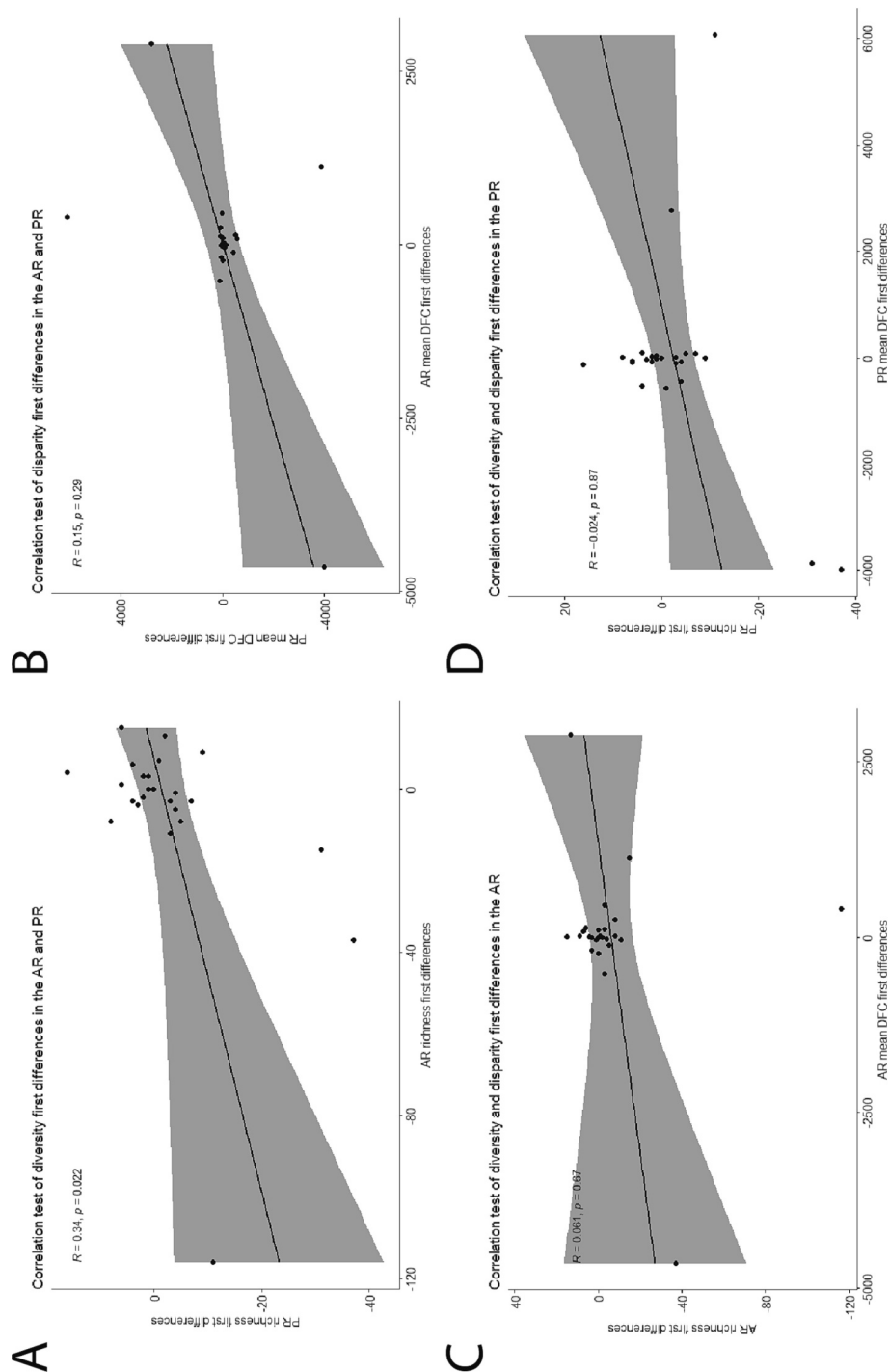


Fig. 4. Scatter plots of first differences for diversity and disparity in the AR and PR along with regression lines and 95% confidence intervals. Kendall's tau statistic (R) and p-values for Kendall's rank correlation test are shown. (A) Diversity first differences in the AR vs. PR. (B) Disparity first differences in the AR vs. PR. (C) AR diversity vs. disparity first differences. (D) PR diversity vs. disparity first differences.

disparity alongside decreasing diversity several times in both the AR and PR (such as from 22 to 21, 12–10 Ma in the AR, and 24–22 and 14–12 Ma in the PR; Fig. 5). This pattern indicates that fewer taxa are present, relative to the time bins preceding and following this period, but they are expanding in their occupation of morphospace, suggesting greater ecological breadth. This pattern is thought to be the result of continued diversification through morphospace as a clade ages and may represent periods where the assemblages are being targeted by random extinctions. In fact, per-lineage net diversification rates indicate that these periods coincide with relatively high rates of extinction in both the AR

and PR (Finarelli and Badgley, 2010).

Grunert et al. (2019) examined patterns of diversity and disparity change in therocephalians across the Permian-Triassic extinction and discovered that diversity and disparity are decoupled across this boundary. The authors found that the number of species decreases and remains low following the mass extinction, whereas disparity initially drops at the boundary before making a recovery in the Triassic. In other words, taxonomic decrease is occurring immediately prior to morphological expansion possibly as a result of novel niche space becoming available following the loss of many species on the landscape (Grunert

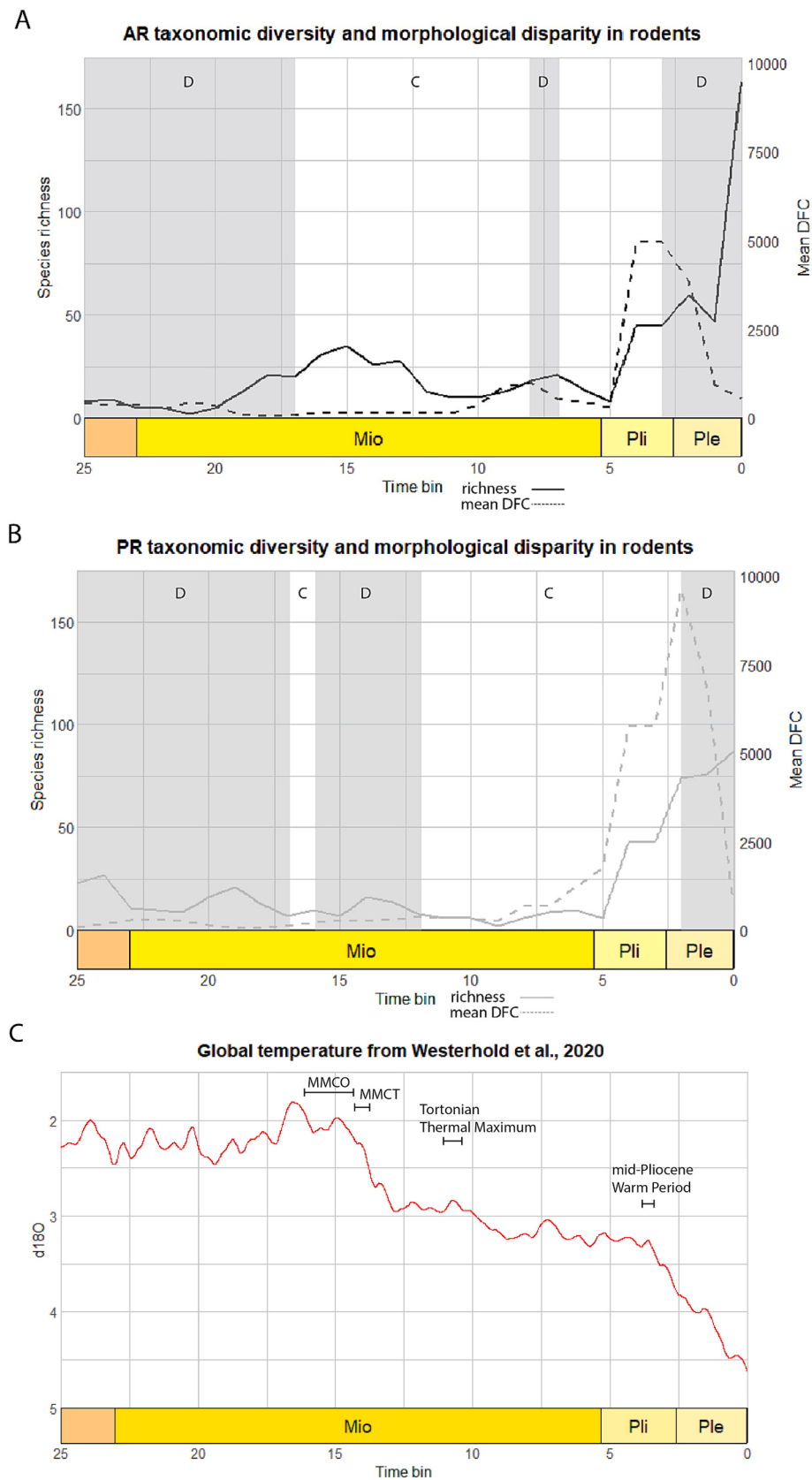


Fig. 5. The relationships between diversity and disparity in the AR (A; black lines) and PR (B; gray lines). Periods during which diversity and disparity are coupled are denoted by the letter “C” and periods during which diversity and disparity are decoupled are denoted by the letter “D” and gray shading. Solid lines show species richness (diversity), and dotted lines show mean DFC (disparity). Isotopic data from [Westerhold et al. \(2020\)](#) are shown along with major climatic events (C).

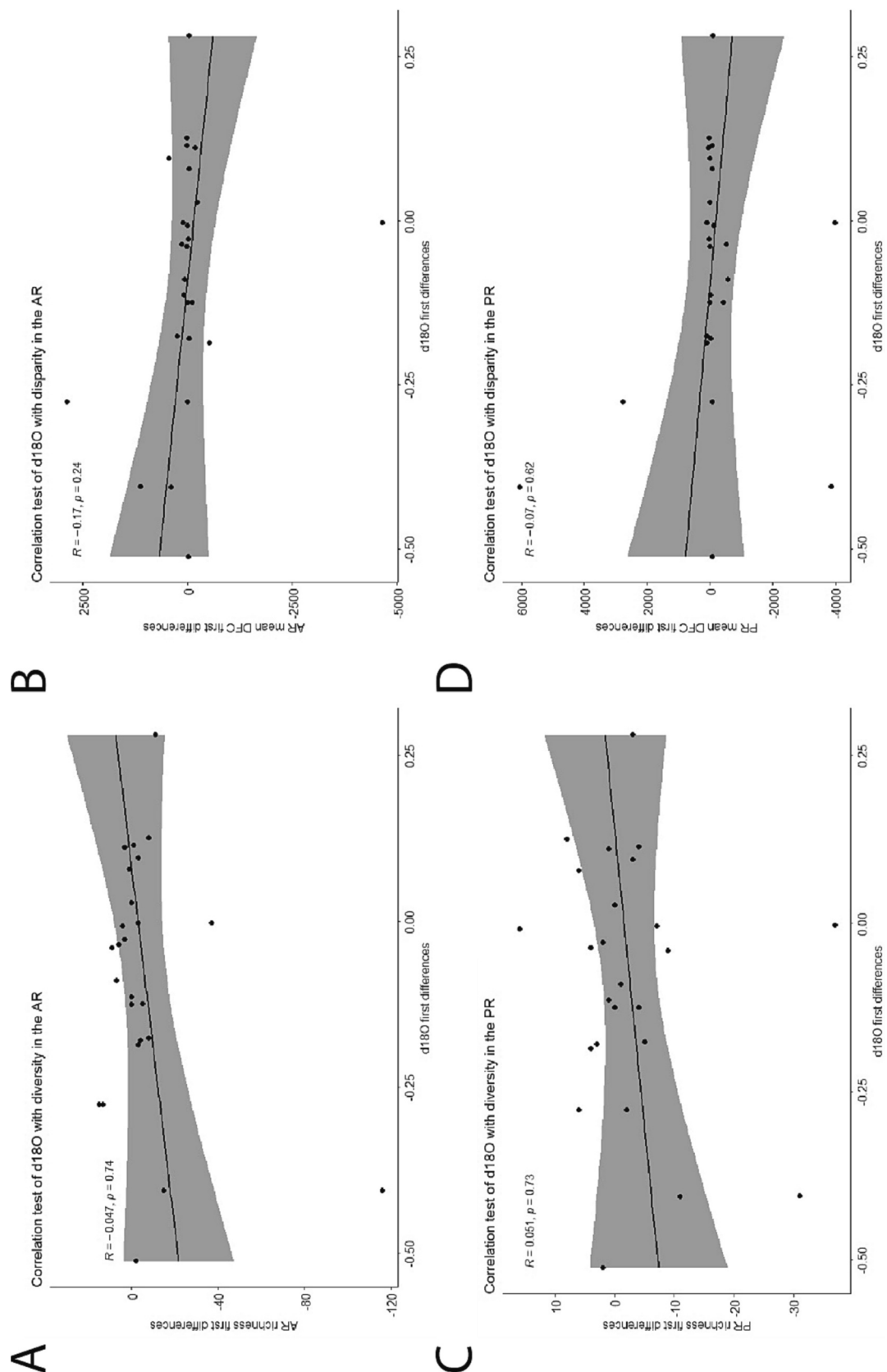


Fig. 6. Scatter plots of first differences for diversity, disparity, and $\delta^{18}\text{O}$ isotope records in the AR and PR along with regression lines and 95% confidence intervals. Isotope records are from [Westerhold et al. \(2020\)](#). Kendall's tau statistic (R) and p-values for Kendall's rank correlation test are shown. (A) $\delta^{18}\text{O}$ and diversity first differences in the AR. (B) $\delta^{18}\text{O}$ and disparity first differences in the AR. (C) $\delta^{18}\text{O}$ and diversity first differences in the PR. (D) $\delta^{18}\text{O}$ and disparity first differences in the PR.

et al., 2019). We might expect a similar scenario in the AR following tectonic activity, which may be acting locally as an ecological disturbance, with novel niches arising in the aftermath and morphologies diversifying to fill these niches. And in fact, we observe generally decreasing richness beginning at 15 Ma concurrent with nearly unchanged disparity until about 11 Ma in the AR, at which point both diversity and disparity begin to trend upwards (Fig. 5 A). This could be evidence for geographic speciation, whereby geographic barriers cause physical separation, and we observe diversity increases without corresponding increases to disparity in the AR.

SOR and SOV represent broad-scale regional measures of the total range and total variance occupied by the taxa present in the AR and PR and we find that both these values are higher in the PR than in the AR during the past 25 million years. This finding, and our findings in mean DFC which indicate disparity in the PR exceeds disparity in the AR for much of the past 25 million years, do not align with our proposed models for speciation in the AR and PR, in which we predicted PR diversity and disparity would be low as a result of comparatively homogeneous landscape structure. We propose that a combination of factors may be contributing to this finding. It may be that the lack of tectonic activity in the PR over the last 25 Ma has contributed to prolonged periods of relative environmental stability, which may allow for not only species proliferation and longevity, but also morphological expansion. It may also be that, despite low topographic relief, the PR exhibits more habitat diversity than expected, which is supported over multiple measures of morphological disparity.

It is clear that throughout the period from 25 Ma to the present day in North America, rodents achieve several patterns of diversity and disparity change through time. We recovered scenarios similar to those described by Foote, as well as novel patterns of diversity and disparity change, possibly driven by ecological factors characteristic of assemblages outside the periods of extreme faunal turnover investigated by Foote (1992, 1993). Interestingly, we find that diversity and disparity are largely uncorrelated and appear to respond independently of one another at times. Diversity and disparity also interact with ecological factors and appear to be driven in some part by habitat diversification. Despite these findings, there are several limitations to the data in this study and the conclusions that can be drawn from it. Uncertainty should be noted in the ages of both tectonic and climatic events as well as rodent occurrences, which can be biased by incomplete preservation. For this reason, the species richness is underrepresented in the fossil record. And as such, more recent periods are assumed to be better sampled than those in the deep past. The patterns presented in this study should be examined with these caveats in mind. Future study should focus on small-scale studies with well-sampled fossil records and regional-scale climatic data. Despite this, diversity and disparity change through time in this continental setting reveal much about both morphological and ecological innovations and how these relate to taxonomic growth in times of changing environmental and landscape conditions, allowing for a more nuanced analysis of how these factors affect niche occupation and its drivers.

5. Conclusions

Taxonomic diversity and morphological disparity in North American rodents exhibit complex relationships with climatic and tectonic factors. Despite tectonic drivers and topographically complex landscapes, morphological disparity is lower in the AR compared to the PR across several metrics. We observe both of our hypothesized scenarios in the AR: geographic and ecological speciation, both of which appear in the AR following the middle Miocene period of heightened tectonic activity and climate warming. In addition to this, a prominent pattern in the PR shows exceedingly high morphological disparity from the late Miocene into the Pleistocene, which suggests that environmental change, such as the spread of grasslands, may contribute to species proliferation, as well as morphological expansion. Notably, we recover a compelling signal of

exceedingly elevated diversity and disparity during the Pliocene-Pleistocene in both regions. Despite differing patterns in the AR and PR, there appears to be some linkage between the two regions resulting in correlated taxonomic diversity.

We used a relatively broad indicator of morphology in body mass, and future study should focus on quantitative analyses of skeletal shape as well as size. Despite this, our findings suggest that morphological disparity evolved independently from taxonomic diversity in rodents, and their relationship with one another is highly variable and may be dependent upon numerous factors. These relationships do not appear consistent across our period of study and require further investigation to fully parse diversity and disparity with associated abiotic factors.

CRediT authorship contribution statement

Amanda W. Peng: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Samantha S.B. Hopkins:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Westerhold et al 2020 d18O isotopic data (Reference data) (PANGAEA)

PanTHERIA (Reference data) (Figshare)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2024.112033>.

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