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thesis abstract

Changes in small-mammal diversity and ecology in relation to landscape and climate change over the Neogene

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Abstract. The middle Miocene from 17 to 14 Ma was a time of elevated mammalian diversity in western North America that coincided with the regional development of topographic complexity and the last global warming interval of the Neogene. Understanding the evolutionary and ecological processes that govern past diversity trends and contribute to modern diversity gradients in relation to landscape and climate requires the integration of faunal and paleoenvironmental datasets across spatio-temporal scales. Using a variety of approaches, I analyzed small-mammal and environmental data to investigate diversity and dietary-ecology responses to changes in climate across space today and through time during the middle Miocene. I additionally utilized fossil-record simulations to assess the influence of variable preservation history on estimates of diversification rates in relation to landscape change. This thesis sheds light on how interactions between tectonic activity and climate warming influenced species richness and ecology from local to regional scales.

Keywords. Basin and Range Province, climate change, diversification dynamics, Neogene, paleoecology, rodents, topography

Introduction

A striking diversity gradient in relation to areas of high elevation and topographic complexity has been demonstrated for birds, mammals, and vascular plants, with mountains emerging as global biodiversity hotspots today (Myers et al. 2000, Ruggiero and Hawkins 2008, Badgley 2010). In North America, mammal species richness per unit area rises steeply from the low-relief Great Plains to the topographically complex intermontane west, and species' range edges align strongly with geographic barriers (Fig. 1; Badgley and Fox 2000). This topographic diversity gradient (TDG) is the outcome of ecological, evolutionary, and biogeographic processes operating over a dynamic landscape and climate history. Although clear patterns have emerged, various hypotheses to explain the underlying mechanisms for the origin and maintenance of increased diversity in montane regions remain unresolved.

The evolution of western North American mammalian faunas has a complex history intimately linked with tectonic activity, climate change, and the development of topographically

complex and environmentally heterogeneous habitats over the last 30 million years (Badgley et al. 2014, Riddle et al. 2014). Gradients in mammal diversity in relation to mountains occur from local to continental scales. Along elevational gradients, strong ecotones influence the distribution of organisms according to their physiological tolerances and habitat preferences (Brown 2001, McCain 2005). At broader spatial scales, complex topographic fabric influences climate patterns and vegetation composition, and facilitates high regional turnover in species composition (Kerr and Packer 1997, Badgley and Fox 2000, Coblenz and Riitter 2004). Finally, over geologic time, the history of landscape change, barrier formation, and species dispersal influences the production, accommodation, and extinction of species within the region, leading to significant net changes in diversity (Badgley 2010, Hoorn et al. 2010).

The Cenozoic fossil record of mammals in North America reveals a dynamic and intermittent TDG, suggesting that the pattern of elevated diversity in topographically complex regions is not a persistent feature over geologic time (Finarelli and

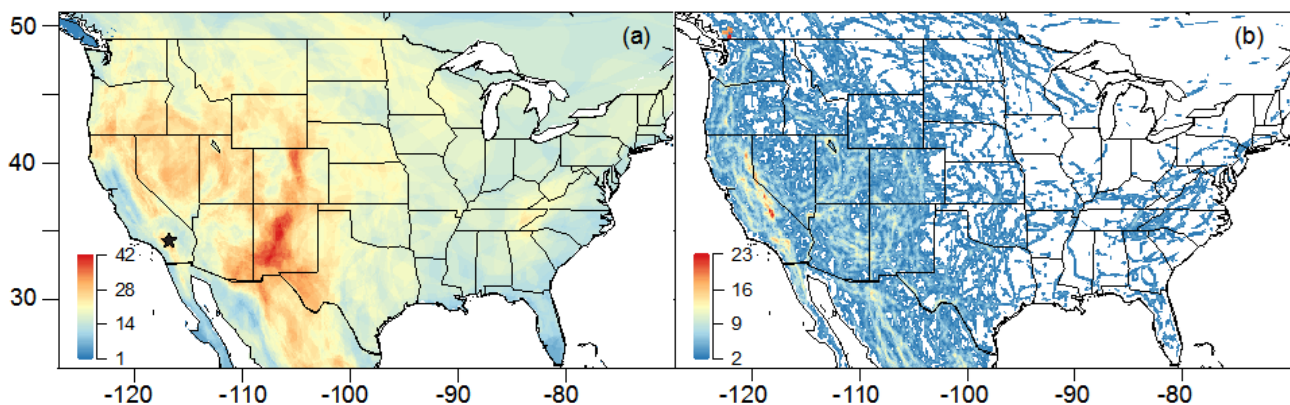


Figure 1. (a) Species richness of extant rodents and (b) distribution of overlapping range boundaries for two or more species, based on species' ranges compiled at 0.1-degree resolution. Geographic-range data are from NatureServe (Patterson et al. 2007). Today, both species density and spatial turnover are greater in the region of recent tectonic activity and high topographic complexity. The star in (a) denotes the location of the primary fossil and paleoenvironmental records investigated in this research. (Figure modified from Badgley et al. in press)

Badgley 2010). Peak mammal diversity in western North America and a strong TDG occurred in the middle Miocene from 18 to 14 Ma (Fig. 2; Badgley et al. 2014), during an interval of intense tectonic activity that generated the topographic complexity – alternating mountain ranges and basins – that characterizes the Basin and Range Province today (McQuarrie and Wernicke 2005). While barrier formation during this time likely promoted allopatric speciation, concurrent global warming during the Miocene Climatic Optimum, or MCO, (Zachos et al. 2008) also likely promoted geographic-range shifts into and across the intermontane western region, increasing regional diversity and influencing faunal composition across spatial scales. Contemporaneous changes in regional vegetation, such as the expansion of grasslands, and the development of modern biomes, including desert ecosystems, in western North America added complexity to the regional landscape during the Neogene (Fox and Koch 2003, Strömberg 2011). This influenced mammalian habitats and dietary resources (Janis et al. 2004, Jardine et al. 2012). The dynamic nature of regional species diversity in relation to landscape and climate change also had implications for the processes governing community assembly (Mittelbach and Schemske 2015). Thus, the TDG today and in the past reflects the combined outcome of multiple processes operating over local to regional scales.

The central goal of my research is to link regional-scale biogeographic processes with local-scale ecological dynamics in small-mammal faunas over the Neogene, and specifically during the middle Miocene diversity peak in western North America (Smiley 2016). My primary research questions are as follows: (1) Does species ecology vary predictably in relation to climate and vegetation across space and through time? (2) How did local ecosystems change through the MCO warming? (3) Did species richness, composition, and ecology respond to changes in local environments during this time? (4) Is high species richness facilitated by increases in local species richness or high species turnover across space? (5) How do changes in fossil preservation impact our ability to reliably infer diversification dynamics from the fossil record? I focused on extant and fossil rodents because they are taxonomically and ecologically diverse in North America, demonstrating a strong TDG gradient today and during the middle Miocene (Finarelli and Badgley 2010). Furthermore, rodent lifestyles are tightly linked with the characteristics of their local habitats, and they play critical roles (e.g., seed dispersion, prey base) in the maintenance of ecosystems in western North America and worldwide (Badgley and Fox 2000, Terry and Rowe 2015). By assessing evolutionary and ecological processes operating across spatial scales in the past, this research contributes to our under-

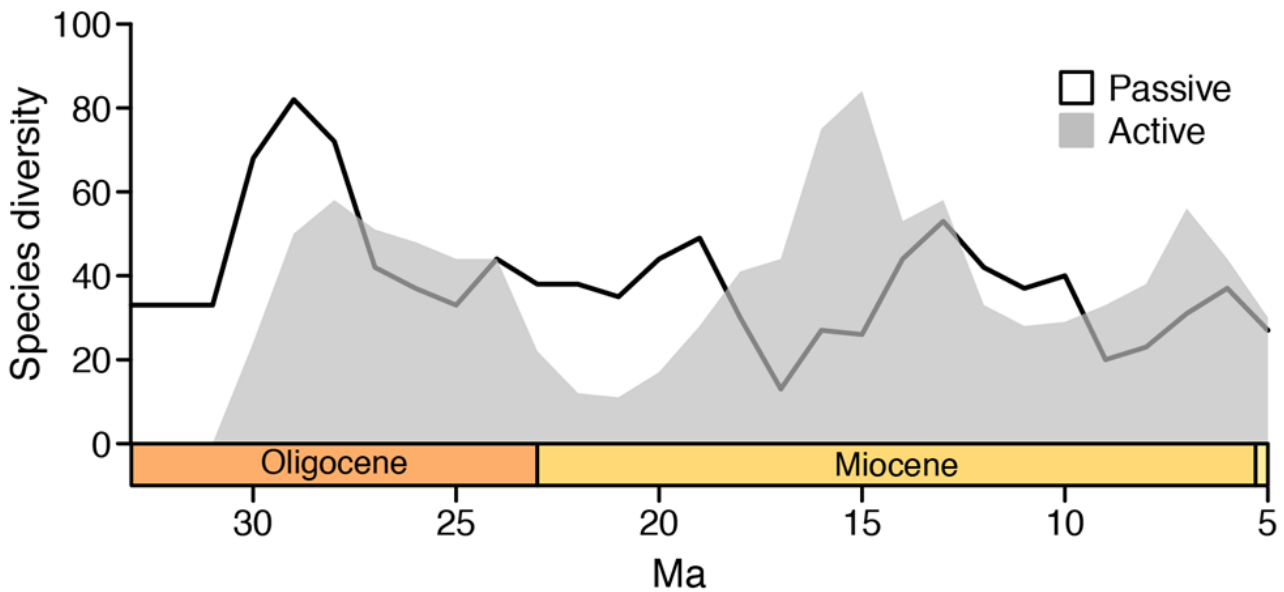


Figure 2. Rodent species richness through time for 1-Myr time bins for the topographically complex, tectonically active region (west of the Rocky Mountain Front Range) in transparent gray and for the low-relief, tectonically passive region (Great Plains and east) outlined in black. Peak mammal diversity for the active region coincided with intense tectonic extension and global warming during the middle Miocene. The passive region did not show a corresponding peak during that interval. Both records were dynamic through time, and the topographic diversity gradient was only intermittently present. Species diversity was calculated assuming that species ranged through first and last occurrences within a region and using the methods of Finarelli and Badgley (2010). Fossil-occurrence data were obtained from the MIOMAP database for North American fossil mammals (Carrasco et al. 2007). (Figure modified from Smiley, in review)

standing of how diversity patterns are shaped over deep time.

Materials and methods

The most complete continental fossil record spanning the MCO within western North America occurs in the Mojave Desert of southern California. Work over several decades has generated a rich fossil record from this region, including abundant small-mammal remains from three primarily middle Miocene formations. The Barstow, Crowder, and Cajon Valley formations are temporally well constrained (Reynolds 1991) and archive the influences of tectonic activity and climate change on mammal diversification and paleoecology at the basin scale. In addition, paleoenvironmental data from paleosol (fossil soil) units in the Crowder and Cajon Valley formations serve to illuminate local environmental changes and habitat heterogeneity during the MCO.

Approaches for assessing the ecological attributes of species in the past have expanded rapidly over the past few decades and include sta-

ble isotope analysis and quantitative dental and morphological metrics in relation to dietary ecology (Passey and Cerling 2006, Eronen et al. 2010). In particular, small-mammal datasets are increasingly accessible through novel analytical techniques, such as *in situ* laser ablation mass spectrometry and μ CT scanning of minute fossil teeth (Evans et al. 2007, Hynek et al. 2012). Relatively large sample sizes found in small-mammal assemblages from formations such as the Crowder and Cajon Valley are especially valuable for inferring species-level ecology and ecological interactions in the fossil record. However, these approaches often must be validated in modern ecosystems before application to the fossil record. To address how dietary ecology varies across species' ranges within topographically complex and environmentally heterogeneous regions today, I first sampled the carbon, nitrogen, oxygen, and hydrogen isotopic composition of hair from two extant rodent species that occur across western North America (Smiley et al. 2015). I applied classification and regression tree analysis to generate rodent-diet

isoscapes models – or ‘mice-oscapes’ – in relation to climatic gradients and C₃ (cool, mesic-adapted) and C₄ (warm, arid-adapted) grass distributions.

Armed with a framework for applying stable isotope approaches to small-mammal assemblages from the fossil record, I then assessed how species diversity and ecology responded to basin-scale climate and vegetation changes during the MCO, focusing on the geological and paleontological records from the Crowder and Cajon Valley formations. First, I combined field sampling and laboratory analyses to develop a multi-proxy record of paleoenvironmental conditions through time from each formation (Smiley et al. in revision). I analyzed paleosol elemental geochemistry to estimate paleoprecipitation, phytoliths (silica bodies produced by plants) to infer the relative abundances of forest, C₃-grass, and C₄-grass vegetation, and the carbon isotopic composition of preserved soil organic matter to assess local changes in aridity. Then, I compiled records of large- and small-mammal diversity and species composition across basins and through time to compare with the reconstructed paleoenvironments of the Crowder and Cajon Valley formations.

Utilizing *in situ* laser ablation mass spectrometry, I then evaluated the carbon and oxygen isotopic composition of tooth enamel from fossil rodents preserved in the small-mammal assemblages (Smiley et al. in preparation). These isotopes can be used to assess the consumption of C₃ and C₄ vegetation among species as well as infer water-resource use or habitat moisture conditions over space and time (Cerling et al. 2004, Koch 2007). I additionally assessed the ecology of small-mammal fossils based on two dental measurements, the hypsodonty index (relative crown height) and occlusal surface area, as dietary and body-size indicators (Damuth and MacFadden 1990, Williams and Kay 2001). I then compared interspecific variation in dental isotopic composition and morphology within fossil assemblages to modern co-occurring rodent species to posit how community assembly based on species dietary niche may have differed under past environmental conditions.

Finally, because fossil productivity has been shown to covary with diversity in the Basin and Range Province (Badgley et al. 2014, 2015), I utilized modeling approaches to examine how changes in preservation probability impact our ability to reliably infer rodent diversification dynamics over the Neogene (Foote 2000, Liow et al. 2010). Based on data from the North American fossil and continental rock records, I simulated fossil records under several diversification and preservation scenarios (Smiley, in review). I converted phylogenies generated from birth–death models to simulated fossil records by removing phylogenetic information and recording species durations over 1-myrr time intervals. Diversification scenarios included constant speciation and extinction rates, variable and tectonically-driven increases in speciation rates, and diversity-dependent speciation rates. I then degraded the simulated fossil records according to five preservation scenarios, based on common trends (e.g., increasing rock record towards the present) or derived from fossil occurrences and rock area (Foote and Raup 1996, Peters 2008). Using presence–absence-based diversification metrics (Foote 2000), I then examined how well the simulations captured origination, extinction, and diversification rates with an imperfectly sampled fossil record.

Results and Discussion

The work summarized herein coupled analyses of basin-level environmental change and small-mammal ecological response with regional patterns in small-mammal composition and diversification during the MCO. My work enhances our understanding of the processes underpinning the TDG in deep time, and in particular demonstrates how elevated diversity during this time is accommodated across spatial scales.

In order to apply stable isotopic analyses to the small-mammal fossil record, I first determined how isotopic composition depicts species diets and ecological interactions across heterogeneous habitats today. Spatial variation in carbon isotopic composition reflected diets that covaried most strongly with seasonal temperature and precipitation gradients, accurately predicted the distribu-

tion of C₃ and C₄ grasses, and recorded spatial and temporal heterogeneity in these grass resources (Smiley et al. 2015). The nitrogen isotopic composition of rodent hair suggested a moisture influence on their diets, while enrichment in oxygen and hydrogen isotopic composition relative to local meteoric water (i.e., water derived from precipitation) is consistent with the observation that non-obligate drinkers (e.g., kangaroo rat, *Dipodomys ordii*) rely on highly evaporated water sources, such as seed moisture. I additionally found significant differences in carbon isotopic niches between species along these environmental gradients, indicating that stable isotopes can distinguish small-mammal dietary ecology, even among closely related herbivorous species, and guide our understanding of resource-use differences that may facilitate species' coexistence.

By evaluating variation in environmental conditions and species ecology across space today, I was then able to better interpret changes in these relationships in the fossil record and through geologic time. Integrating the geological (phytoliths, paleosol elemental geochemistry, and isotopic composition of preserved soil organic matter) and paleontological records of the Crowder and Cajon Valley formations, I found the earliest evidence of C₄ vegetation in the Mojave region of southern California, evidence for a forested and mesic ecosystem (~800 mm.yr⁻¹ of precipitation), and high habitat heterogeneity within and across basins (Smiley et al. in revision). Crowder and Cajon Valley assemblages recorded locally diverse large and small-mammal faunas during the middle Miocene (e.g., up to seven co-occurring, ecologically similar rodent species at ~17 Ma), indicating that high alpha diversity contributed to the MCO diversity peak. Furthermore, exceptionally low faunal similarity across the Crowder, Cajon Valley, and nearby Barstow formations indicates that high turnover in species composition across space also contributed to elevated diversity during the middle Miocene. Faunal exchange across alternating basins and ranges, even within a single region, may have been reduced during the tumultuous history of tectonic activity and landscape change during this time, leading to high faunal provinciali-

ty in western North America (Badgley et al. 2015).

The stable isotopic composition of rodent fossils recorded finer-scale variation in vegetation than did environmental proxies and documented an increase in C₄-grass consumption despite little apparent change in the availability of this resource on the local landscape (Smiley et al. in preparation). The integration of isotopic and morphological data from fossil rodents also allowed me to gain insight into past ecological interactions and dietary niche partitioning. Contrary to the prediction that ecological niche differentiation should be necessary to support high species diversity within these assemblages, I found significant overlap in both stable isotopic composition and dental morphology among co-occurring species. Interspecific overlap in dietary ecology during the MCO contrasts with rodent species co-occurring in present-day western ecosystems, which exhibit substantial differences in both isotopic composition and dental properties. This work contributes to filling a gap in our knowledge of small-mammal paleoecology and community assembly during past climate and habitat change, specifically during a critical time in the formation of the faunal assemblages that characterize the Basin and Range Province today (Riddle et al. 2014).

While focus on the Mojave region helps to elucidate local-scale dynamics, a gap in the fossil record prior to the MCO over much of western North America, including southern California, limits our ability to evaluate regional changes in diversity and ecology over longer timescales (Badgley et al. 2015). For these reasons, I assessed whether or not we can correctly infer shifts in diversification rates under variable degrees of preservation (Smiley et al. in review). While variation in preservation rates distorted diversification patterns in certain scenarios, most degraded records were able to recover underlying diversification dynamics. Exceptions to this general finding include intervals when preservation rate changed substantially (e.g., a preservation pulse from 10% to 50% between consecutive 1-myr time bins), which may impart a temporary, false signal of elevated speciation or extinction rates. In these cases, estimated diversification rates are more relia-

ble indicators of underlying dynamics than independent estimates of speciation or extinction. These results indicate that elevated diversification rates in relation to tectonic activity during the middle Miocene are likely to be evident in the fossil record.

By studying species richness and composition from local to regional scales, this body of work provides insight into the processes shaping the peak in mammal species richness during the MCO and reveals the influence of climate and vegetation change on species' ecology. While sampling effects may also play a role in shaping the Miocene diversity pattern, fossil-record simulations suggest that the species-richness peak during the MCO is not due solely to the effects of preservation. From both paleontological and molecular perspectives, the middle Miocene was a critical interval in the assembly of western small-mammal faunas (Riddle et al. 2014). Understanding the influence of landscape and climate change on local-scale ecological interactions, community assembly, and regional species-pool dynamics remains a critical research goal for illuminating the history of Basin and Range faunas further (Blois et al. 2013, Mittelbach and Schemske 2015).

This research also contributes an important paleoecological perspective on the mechanistic underpinnings of the topographic diversity gradient during the middle Miocene interval of climate warming and landscape transformation, while also highlighting the reciprocal insights achieved from data integration of the fossil and modern records. The fossil record provides our most direct link to ecosystem dynamics during substantial climate and environmental change in the past (Fritz et al. 2013, Finnegan et al. 2015). And in today's world, information from the past is critically important to strengthening our predictions of how ecosystems are likely to change in the coming centuries.

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