

Change in North American mammal community structure
under late Cenozoic (~36 Ma – present) climate change

by

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Abstract

Patterns of biodiversity emerge as a product of numerous drivers including species sorting along modern and ancient environmental gradients, long-term climate changes, speciation and extinction events, the formation and weathering of mountain ranges, and plate tectonics. The fossil record is a natural experiment that records faunal change under myriad evolutionary, climatic, and tectonic processes. My dissertation focuses on changes in North American mammal community structure under conditions of long-term climate change during the Cenozoic. I ask three primary questions: Are patterns of biodiversity sensitive to the processes of fossilization? When did the modern latitudinal diversity gradient emerge and were changes driven by climate? How has community composition changed as rates of extinction fluctuated under climate change? How can we best search for the proximate climatic drivers (i.e. changes in spatial climate patterns) of diversity changes? I show, through the development of a novel simulated fossilization method, that measuring latitudinal richness gradients in the fossil record is problematic when rates of species loss are high. However, estimating the magnitude of the latitudinal diversity gradient is improved with the use of β diversity as a metric (so called latitudinal turnover gradients). I also show that the late Cenozoic (36 Ma – present) North American mammal diversity gradient varied but neared modern magnitudes only during the late Miocene and late Pleistocene. From ~15 Ma – 0.01 Ma, hoofed mammals show a decline in relatedness of species in North American communities, reflecting the phylogenetically dispersed extinction of dicot specialists as the global climate cooled. I make direct comparisons of a-historical and historical approaches to studying biodiversity change and suggest that understanding the contribution of macroevolution is requisite to

testing hypotheses on the formation of modern communities. I also address the need for a high resolution terrestrial paleoclimate record and show that stable oxygen isotopes from pronghorn (*Antilocapra americana*) enamel are excellent sources of data on seasonal changes in environmental waters. My dissertation is a critical step in answering “What factors have led to the emergence of communities as we know them today?” and understanding the role of climate change in shaping modern and ancient communities.

Statement of Contributions

Chapter 2 is currently neither published nor submitted. Christopher Hassall contributed early iterations of the simulated fossilization R code (Appendix C). Root Gorelick and Natalia Rybczynski provided comments on an earlier version of the manuscript.

I published Chapter 3 in *PLoS One* in 2014 with my co-authors Christopher Hassall, Root Gorelick and Natalia Rybczynski. I conceived and designed the study with advising from Natalia Rybczynski and Root Gorelick. Christopher Hassall contributed R code for the climate space models and simulated fossilization (which was later heavily altered by myself for Chapter 2). I performed all of the simulations and modelling. Natalia Rybczynski, Root Gorelick, and Christopher Hassall provided comments on the various iterations of the manuscript.

I published Chapter 4 in the *Biological Journal of the Linnean Society* in 2015 with my co-authors Root Gorelick and Natalia Rybczynski. I conceived and designed the study as well as performed all analysis. Root Gorelick and Natalia Rybczynski played an advisory role and provided comments on earlier iterations of the manuscript.

I submitted Chapter 5 to *Oecologia* in 2015 with my co-authors Sora Kim, Jeffrey Welker, and Mark Clementz. I conceived and designed the study, prepared and submitted all samples for isotopic analysis, and performed all statistical analyses. Sora Kim provided me with considerable training on preparation of enamel and bone for stable oxygen isotopic analysis. Jeffrey Welker measured over 1000 weekly Wyoming precipitation samples from the period of 1989-2012 for 9 stations across Wyoming. Both

Mark Clementz and Sora Kim played an advisory role as well as provided comments on earlier iterations of the manuscript.

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1 Chapter: Introduction

Spatiotemporal changes in organismal diversity have captivated both neontologists and palaeontologists alike (Blois and Hadly 2009). Contemporary ecological studies are illuminating the ways in which organismal diversity varies across the modern globe (Currie 1991; Currie and Fritz 1993; Currie et al. 1999; Hawkins et al. 2003; Currie et al. 2004; Qian et al. 2009; Qian and Xiao 2012). Particularly well-studied macroecological phenomena include latitudinal and altitudinal gradients in richness, community composition, body size, and geographic range size (Stevens 1989; Blackburn et al. 1999; Hawkins et al. 2003; Qian and Xiao 2012). These numerous studies broadly support a link between climate (e.g. rainfall, temperature, and by extension productivity) and terrestrial biodiversity (Hawkins et al. 2003). However, modern biodiversity patterns are a product of numerous contemporary and historical drivers including species sorting along modern and ancient environmental gradients, competitive interactions, dispersal, long-term climate changes, speciation and extinction events, the formation and weathering of mountain ranges, and plate tectonics (Blois and Hadly 2009).

Neontological approaches, by their exclusion of extinct species, cannot tell us how important historical events have been and how they have contributed to the formation of communities as we know them today. The fossil record, which is the result of a natural biodiversity experiment, might be an integral puzzle piece in understanding the myriad drivers of spatiotemporal patterns of biodiversity.

Temporal changes in biodiversity are becoming particularly relevant in the context of ongoing global climate change. Distributional studies over ecological timescales (<100 yrs) have recorded dramatic range shifts and expansions for a wide

range of terrestrial taxa (Parmesan and Yohe 2003; Chen et al. 2011). However, the full faunal response to climate change occurs on evolutionary timescales of thousands to millions of years over which the processes of speciation, extinction, and adaptation dramatically alter terrestrial faunas (Blois and Hadly 2009). The fossil record is the best source of data on long-term responses to climate change. Fortunately, improvements in databasing (e.g. the Paleobiology Database, the Miocene Mapping Project or MIOMAP, and the New and Old World (NOW) fossil mammal database), computational methods, and characterization of global climate (Zachos et al. 2001; Zachos et al. 2008) have increased the spatiotemporal scale of climate change studies that utilize the fossil record.

The study of paleobiodiversity has grown from describing changes in the numbers and types of organisms through time (e.g. Sepkoski's three marine evolutionary faunas; Sepkoski, 1981; 1984) to include characterizing the evolution of macroecological phenomena (Jablonski 1993; Davis 2005; Jablonski et al. 2006; Rose et al. 2011; Jablonski et al. 2013; Fraser et al. 2014b), trends in body size evolution (Smith et al. 2010; Secord et al. 2012), and patterns of macroevolution (Alroy 1996; Raia et al. 2011a; Raia et al. 2012; Fraser et al. 2015). The explosion of phylogenetic methods and thus phylogenetic hypotheses has also improved the study of paleobiodiversity by placing richness, morphological, and macroevolutionary changes into a phylogenetic context (Felsenstein 1985; Raia 2010; Raia et al. 2011a; Raia et al. 2012; Slater and Harmon 2013). The fossil record is therefore becoming a powerful tool for developing a baseline

of biological response to climate change and possibly predictions for modern animal responses (Blois and Hadly 2009; Barnosky et al. 2011).

In this dissertation, I explore changes in the structure of mid to late Cenozoic (~36 Ma – present) North American mammal communities with the purpose of characterizing the role of climate in shaping them. I hypothesize that climatic influences on modern spatial diversity patterns apply equally to spatial diversity patterns through time, i.e. that the underlying ecological processes are “ergodic.” I do not empirically test whether rates of community change in space are equal to rates of change in time but rather whether climate remains one of the primary explanatory variables. I have focused on metrics for community compositional change because they are more robust to time averaging in the fossil record (Kidwell 2013) and change more rapidly under climate change than other diversity metrics such as richness (Kent et al. 2011; Dornelas et al. 2014). Herein, I define a community as a temporally co-occurring unit of species (defined using a morphological species concept) normally delineated by their co-occurrence at a single fossil locality. An ecological community is not strictly equivalent to a community as I define it here given temporal (e.g. some localities might be time averaged over 1,000 years) and spatial averaging (Tomašových and Kidwell 2009; Kidwell 2013). I define a fossil locality as a named collection of fossils (i.e. a named location from which mammal fossils have been collected). Not all fossil localities are created equal; the extent of time and spatial averaging varies among them. Typically, patterns of community structure are retained despite temporal and spatial averaging (Tomašových and Kidwell 2009).

Throughout, I use the word diversity very broadly, using phrases such as “diversity patterns” to refer to patterns of richness or species composition. I also speak a

lot about the latitudinal diversity gradient, which I define broadly as the change in diversity, be it richness or community composition, from lower to higher latitudes. Latitude, being correlated with some measures of climate (Currie 1991), is therefore only an imperfect proxy for climate. The value of measuring a latitudinal diversity gradient rather than a climate diversity gradient has therefore been questioned throughout the duration of my doctoral program (i.e. the drunkards search a.k.a. the streetlight effect or searching for an answer in the easiest place to do so). Imperfect preservation and a paucity of time machines means that paleontologists are often required to use proxy data, particularly for climate. Although proxy data are by their nature indirect measures of phenomena, their accuracy is supported by a broad array of empirical research (e.g. (Royer et al. 2001; Kurschner 2008; Bradshaw et al. 2012)). Throughout this dissertation, particularly in Chapter 3, I use a global climate proxy from marine foraminifera (Zachos et al. 2008) as both a measure of the steepness of latitudinal climate gradient and of average terrestrial climate conditions in North America. For example, I assume that cooler climates are associated with steeper latitudinal climate gradients but, where possible, I support my assumptions using published proxy data (e.g. (Ballantyne et al. 2006; Ballantyne et al. 2010)) and climate models (e.g. (Micheels et al. 2011; Pound et al. 2012)). I therefore do not believe that this dissertation suffers from the streetlight effect, but do concede that I use imperfect proxy data, an apparent limitation that Chapter 5 takes the first steps in addressing.

1.1 Cenozoic climate in brief

At least eight major climate change events have impacted the evolution of North American terrestrial ecosystems: the Paleocene-Eocene Thermal Maximum (~56 Ma),

early Eocene climatic optimum (~54 Ma), Eocene-Oligocene transition (~33.5 Ma), late Oligocene climatic optimum (~25 Ma), mid Miocene climatic optimum (~15 Ma), late Miocene global cooling (~7 Ma), mid Pliocene climatic optimum (~3.5 Ma), and late Pleistocene global cooling (~0.01 Ma) (Fig. 1.1; (Zachos et al. 2001; Zachos et al. 2008)).

I start my discussion at the Eocene-Oligocene transition because my dissertation focuses primarily on late Eocene through late Pleistocene of North America. Below I focus primarily on Cenozoic climate and associated changes in North American mammal faunas. During the same interval, there is a general association between global climate and marine biodiversity (Marx and Uhen 2010; Mayhew et al. 2012). Non-mammalian vertebrate lineages that undergo diversification during the mid to late Cenozoic include the snakes, which appear to diversify in conjunction with small mammals, and some groups of birds including the passerines (Behrensmeyer et al. 1992).

The end of the Eocene epoch (~34 Ma) marks the end of the greenhouse world and the beginning of the global ice house. The Eocene-Oligocene transition is characterized by a dramatic global cooling and aridification (Zachos et al. 2001; Zachos et al. 2008), the formation of substantial ice sheets in Antarctica (Liu et al. 2009), a significant decrease in high latitude sea surface temperatures (Liu et al. 2009), decline in atmospheric CO₂ (DeConto and Pollard 2003; Pearson et al. 2009; Zhang et al. 2013), and increasing terrestrial seasonality as well potentially steeper latitudinal climate gradients (Novacek 1999). The wet, tropical ecosystems of the early to mid Eocene were supplanted by savannah woodland ecosystems in North America (Jacobs et al. 1999; Novacek 1999; Blois and Hadly 2009; Stromberg 2011).

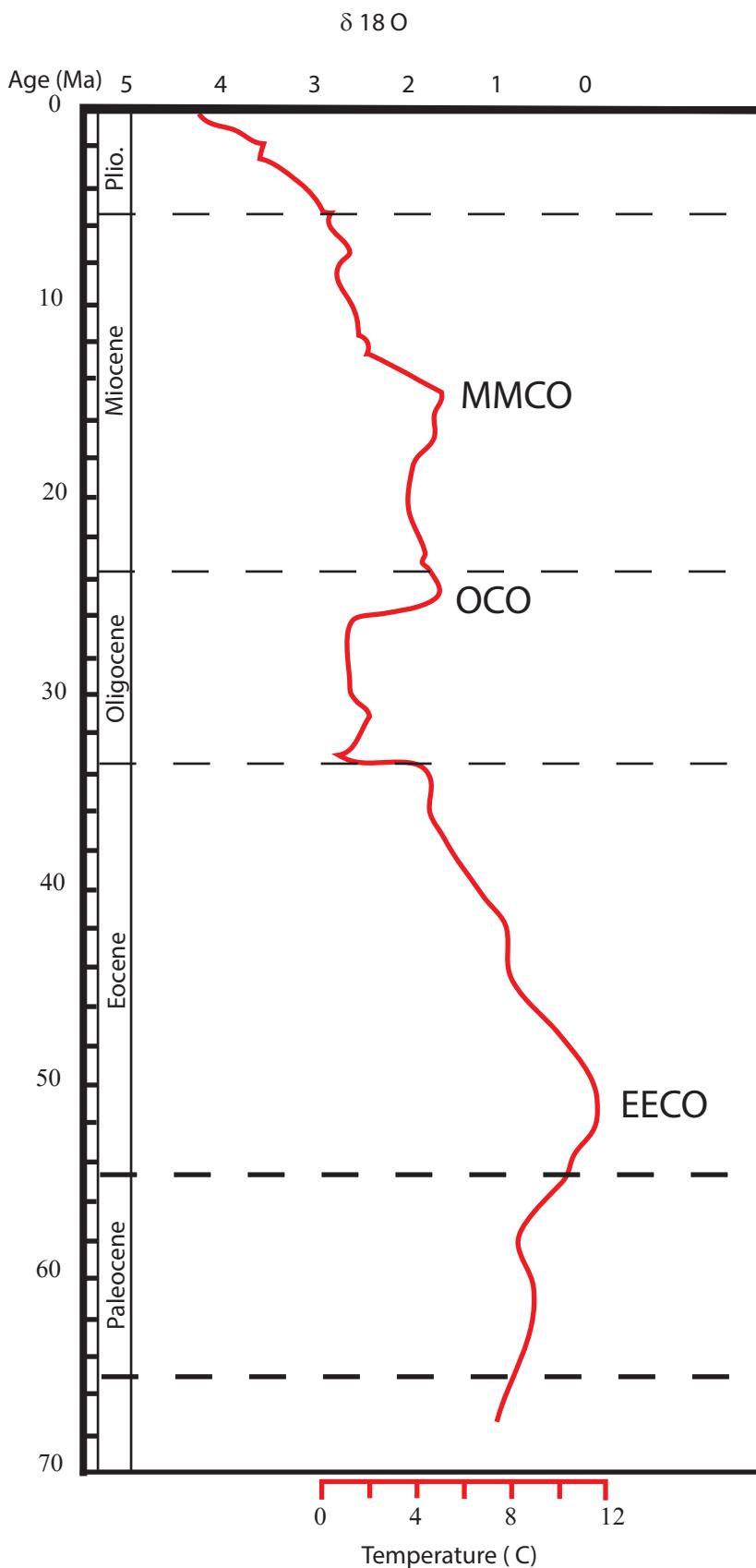


Figure 1.1 Cenozoic global mean temperatures estimated using $\delta 18\text{O}$ (\textperthousand) values from benthic foraminifera showing the early Eocene climatic optimum (EECO), Oligocene climatic optimum (OCO), and the mid Miocene climatic optimum (MMCO). Modified from Zachos et al. (2001).

Open habitat grasses may have undergone diversification during the Eocene-Oligocene transition and earliest Oligocene (Retallack 1997; Retallack 2007; Stromberg 2011) thus marking the beginnings of modern terrestrial ecosystems in North America. Mammalian lineages evolved characteristics typical of savannah vertebrates (i.e. lophodont or crested molars), while the remainder of the savannah fauna was populated by savannah-adapted taxa from Asia such as the selenodont artiodactyls and myomorph rodents (Webb 1977; Prothero 1994; Woodburne et al. 2009). Through the Oligocene the number of species with adaptations for specialized herbivorous diets (i.e. high crowned teeth) increased (Webb 1977).

The Miocene epoch is generally associated with the spread of grassland ecosystems and evolution of grassland taxa in North America such as grazing horses both of which are associated with mid to late Miocene global cooling and aridification (note: South American mammals show hypsodonty or high crowned teeth ~20 Ma before their North American counterparts that is not necessarily associated with the earlier evolution of grasslands) (Cerling et al. 1993; Stromberg 2002; Strömberg et al. 2013). Fossil animal, paleosol (ancient soils), and isotopic studies show that mid (15 Ma) Miocene North American ecosystems were relatively warm and wet (Jacobs et al. 1999; Janis et al. 2000; Retallack 2001; Zachos et al. 2001; Fox and Koch 2004; Janis et al. 2004; Zachos et al. 2008). Ecosystems in the central United States are reconstructed as woodland savannah (Jacobs et al. 1999) and an unprecedented abundance of browsing (tree or bush eating; brachydont) hoofed mammals suggests high plant primary productivity (Janis et al. 2000; Janis et al. 2004). Janis et al. (2000) implicate globally inflated atmospheric carbon dioxide for the high ungulate diversity, a hypothesis that is further supported by

mammalian enamel carbon isotopes, fossil leaf stomata densities, and alkenones (Van Der Burgh et al. 1993; Cerling et al. 1998; Passey and Cerling 2002; Zhang et al. 2013).

The late Miocene (7 Ma) of North America saw substantial decreases in continental mean annual precipitation, temperature, and atmospheric CO₂ (Van Der Burgh et al. 1993; Pagani et al. 1999; Kurschner 2008; Zhang et al. 2013). The Great Plains became more open and grassy and the replacement of C₃ plants with C₄ grasses drove substantial mammalian turnover at middle latitudes (Cerling et al. 1997; Cerling et al. 1998; Janis et al. 2000; Passey et al. 2002; Janis et al. 2004) (but see Fraser and Theodor 2013). Hoofed mammal diversity was markedly reduced, and new late Miocene ungulate communities were dominated by grazers (grass eaters; high crowned teeth) (Janis et al., 2000, 2004).

The Pliocene (~5 – 2.5 Ma) saw continued global cooling (Zachos et al. 2001; Zachos et al. 2008), declining atmospheric CO₂ (Zhang et al. 2013; Martínez-Botí et al. 2015), and the evolution of North American grassland steppe (Webb 1977). The further loss of browsing species from North American ecosystems was also associated with a decline in large grazing ungulate diversity (Webb 1977; Janis et al. 2000; Janis et al. 2004). The mid Pliocene (~3.5 Ma) is particularly interesting because it represents a brief warming period that had important impacts at high latitudes. Numerous paleoclimate proxies indicate that high Arctic temperatures were ~19°C warmer than the modern Arctic, suggesting surprisingly weak latitudinal temperature gradients in North America (Ballantyne et al. 2006; Ballantyne et al. 2010; Csank et al. 2011; Martínez-Botí et al. 2015). High Arctic plant and animal communities were therefore much more similar to their mid-latitude counterparts (Ballantyne et al. 2010; Csank et al. 2011; Rybczynski et

al. 2013). Climate cooling following the mid Pliocene climatic optimum and uplift of the Columbia and Costa Rica region had a strong impact on North American mammal communities through allowing a land connection at the Isthmus of Panama and thus the initiation of the Great American Biotic interchange. The majority of northward dispersals were xenarthrans, while there was a considerably more diverse southward dispersal of mammals (Woodburne 2010).

Climate cooling as well as the onset of marked glacial-interglacial cycles characterized the Pleistocene epoch (~2.5 – 0.01 Ma) (Zachos et al. 2001; Zachos et al. 2008). During glacial maxima large portions of North America were covered in ice (as far south as between 50°N and 40°N) (Carlson and Winsor 2012). Deglaciation was driven by changes in the Earth's orbital obliquity and resultant changes in northern insolation (Carlson and Winsor 2012; Tabor et al. 2015). The termination of the last glacial cycle is associated with melting of ice sheets and associated sea level increase, increases in atmospheric CO₂ to nearly pre-industrial levels, and freshwater forcing of the Atlantic meridional overturning circulation (Clark et al. 2012). In general, North American vegetation transitioned from cold adapted forest to grassland steppe in many regions (although there are numerous regional differences) (Clark et al. 2012). The Pleistocene is perhaps best known for numerous extinctions among the large mammals of North America, but less well known for declining evenness and richness of small

mammal communities that coincides with the onset of the last interglacial and the earliest human occupation of North America (Lyons 2003; Blois et al. 2010).

1.2 Structure of the thesis

In this dissertation, I make significant steps toward understanding the influence of long-term climate changes on macroecological phenomena. I make significant strides in understanding the interpretive limits of the fossil record with regards to macroecological patterns, what factors have led to the emergence of modern biodiversity patterns such as the ubiquitous latitudinal diversity gradients, and developing a framework for creating a comprehensive database of terrestrial paleoclimate proxies.

In the second chapter of my dissertation, I ask whether patterns of biodiversity are sensitive to the processes of fossilization. Understanding how biological signals are affected by the processes of fossilization, which introduce considerable spatiotemporal and taxonomic bias, is requisite to studying the deep time origins of macroecological phenomena. In my second chapter, I use an entirely novel method of simulated fossilization. Using range information for modern North American mammals, I create simulated fossil localities using a point sampling approach. The probability of a species entering the simulated fossil record is weighted based on their mean body size and geographic range size, i.e. small species with small geographic ranges are down-weighted. To determine the effects body and range size bias on measuring macroecological phenomena in the fossil record, I iteratively created simulated North American mammal fossil records and quantified the slope of the latitudinal richness gradient as well as the magnitude of community turnover (i.e. change in identity of species in the community) along the same axis. The method I present in Chapter 2 is a

significant step toward robust comparison of fossil and modern patterns of biodiversity. It enables users to generate single or multiple sets of simulated fossil localities with the same spatial distribution as real fossil localities and thus to directly compare biodiversity patterns. My second chapter is also a significant step toward developing a robust framework for studying the evolution of macroecological phenomena.

My reasons for analyzing both the richness and community composition are twofold. The latitudinal richness gradient is well studied among extant animals and has thus been the focus of a number of paleomacroecological studies (e.g. (Rose et al. 2011). The foremost purpose of the second chapter is therefore to understand whether the traditional measure of the latitudinal diversity gradient (i.e. richness change) is robust to fossil record bias. I also analyzed community compositional change across latitudes because, as mentioned above, measures of community compositional change may be more robust to fossil record bias (Tomašových and Kidwell 2009; Kidwell 2013) and respond more quickly to changes in climate (Dornelas et al. 2014). In Chapter 2 (as well as Chapter 3, which is outlined below), I will refer to the change in community composition along the latitudinal axis as the “latitudinal turnover gradient.” Typically, a gradient is a rate of change in measurable value (e.g. richness, temperature) over a given distance. A latitudinal turnover gradient, as defined here and elsewhere (Bowman, 1996; Koleff et al. 2003) refers to the rate of change in community composition or similarity/dissimilarity among sites along a latitudinal axis. I discuss the methodology I use for measuring the latitudinal turnover gradient in Chapter 2.

In Chapter 3 of this dissertation, I applied the methods I explored in Chapter 2 to the late Cenozoic (36 Ma – present) mammal fossil record of North America. I tested

whether long-term climate changes have influenced the evolution of the latitudinal turnover gradient in North American mammals. Although some recent works have attempted to characterize the mammalian latitudinal diversity gradient in deep time (e.g. (Rose et al. 2011), no previous study has used community structure as a diversity metric nor characterized gradient change on as long a time-scale. I suggest that we can develop new models that are historically, evolutionarily, and phylogenetically cognizant through the combined study of both modern and ancient patterns of biodiversity. My approach is therefore also unique because I make direct comparisons between the fossil record, modern record, and projections for modern mammals under various scenarios for anthropogenic climate change.

The study of phylogenetic community structure is one means of exploring community response to climate change that is cognizant of evolutionary history. In my fourth chapter, I ask how phylogenetic community composition has changed as rates of extinction fluctuated under historical climate change. I used phylogenetic relatedness among species as a community composition metric and asked whether long-term climate changes may have structured North American Cenozoic hoofed mammal communities. I am the first to quantify the phylogenetic community structure of North American fossil mammals, to characterize changes over such a long time scale, and to look for both climatic and macroevolutionary drivers of change. Chapter 4 is a significant contribution to understanding the formation of modern communities and climate change response because it explicitly addresses the role of extinction.

Climate may play a central role in shaping spatial and temporal patterns of diversity. In modern ecosystems, climate gradients, potentially through the mechanism of

abiotic species sorting, are particularly important in structuring spatial diversity patterns (Rohde 1991; Fraser 1998; Mitchell 2000; Hawkins et al. 2003; Peres-Neto et al. 2012; Qian and Ricklefs 2012). For example, steep diversity gradients are typically associated with steep climate gradients. In Chapter 5, I ask how we can best search for the proximate climatic drivers (i.e. changes in spatial climate patterns) of diversity changes. To fully test whether the coupling of climate and diversity is time invariant, paleobiologists require a terrestrial climate record with high spatial and temporal resolution. In Chapter 5, I explore the utility of stable oxygen isotopic values ($\delta^{18}\text{O}$) values from pronghorn enamel for reconstructing seasonal changes in $\delta^{18}\text{O}$ values from rainfall. Although numerous terrestrial paleoclimate records exist (*inter alia* stable oxygen and carbon isotopes from fossil hard tissues and paleosols, plant macrofossils, pollen) and have been sampled in North America, no single record is spatiotemporally complete enough to reconstruct climate gradients. One significant limitation of using the mammal hard tissue $\delta^{18}\text{O}$ record is that not all species record the same water sources with the same spatial and temporal resolution. Chapter 5 takes the first steps toward developing a physiologically cognizant model for using the mammal stable isotopic record to reconstruct climate gradients.

2 Chapter: Can latitudinal richness gradients be measured in the terrestrial fossil record?

2.1 Abstract

Studying the deep time origins of macroecological phenomena can help us to understand their long-term climatic and macroevolutionary drivers. Given the considerable taxonomic and spatiotemporal bias of the fossil record, it behooves us to understand how much biological information is present in fossil data. I devise a novel simulated fossilization approach, weighting the probability of each species appearing in the fossil record based on their mean body size and estimated geographic range size. I then estimate the magnitude of the latitudinal diversity gradient recorded in the simulated fossil record both before and after reducing the percentage of species that are successfully fossilized. Estimating the slope of the latitudinal richness gradient is particularly sensitive to the loss of species with small mean body size and small geographic ranges. By contrast, estimating the magnitude of the latitudinal faunal turnover gradient is much less sensitive to species loss but more sensitive to the identity of species lost from the simulated fossil record. The simulated fossilization approach presented herein allows for direct comparison of past and present latitudinal diversity gradients.

2.2 Introduction

Latitudinal richness gradients (LRGs; i.e. loss of richness from low latitudes to high) are nearly ubiquitous among modern terrestrial organisms, having been observed in many groups including angiosperms, birds, mammals, insects and other invertebrates (Currie and Fritz 1993; Currie et al. 1999; Engle and Summers 1999; Condit et al. 2002;

Hawkins et al. 2003; Qian et al. 2009; Baselga et al. 2012; Condamine et al. 2012). Until relatively recently, terrestrial LRGs have been studied primarily among extant organisms (Fraser et al. 2014a; Mannion et al. 2014). The study of LRGs in deep time (millions of years) is motivated by interest in the origins and evolutionary history of marine and terrestrial macroecological phenomena (Roy et al. 1998; Jablonski et al. 2006; Rose et al. 2011; Jablonski et al. 2013) as well as the influence of climate, tectonics, and macroevolution (Rose et al. 2011; Fraser et al. 2014a; Mannion et al. 2014). The fossil record is a natural experiment that potentially records the evolutionary history of LRGs. However, the link between biodiversity change and its driving mechanisms is filtered through the processes of fossilization, which introduce considerable bias (Kidwell and Flessa 1996; Kidwell and Holland 2002; Tomašových and Kidwell 2009; Tomasovych and Kidwell 2010; Benton et al. 2011; Miller et al. 2014). Our understanding of fossil LRGs therefore hinges on the assumption that we can apply methods of sampling correction to reduce the influence of bias, thus interpreting remaining patterns as biologically relevant.

Characteristic fossil record biases include, but are not limited to, body and range size bias, geographic bias in sampling effort, depositional environmental bias, and rock record volume bias (Benton et al. 2011; Mannion et al. 2011). At individual fossil localities, bias against species of small body and geographic ranges sizes are well documented (Kidwell and Flessa 1996; Kidwell and Holland 2002; Cooper et al. 2006). Between 5% and 50% of species in small size classes can go missing from the marine fossil record (Cooper et al. 2006). In terrestrial ecosystems, depending on their trophic group, 30 to 80% of small species are lost from death assemblages (Kidwell and Flessa

1996); less abundant species (e.g. species higher in the food chain) with small geographic ranges are similarly less likely to enter the fossil record (Benton et al. 2011).

In North America, the numbers and geographic coverage of terrestrial fossil localities increase toward the present (e.g. from the Miocene and to the Pleistocene, the number of high latitude fossil localities increases dramatically), which is problematic given the positive correlation between species diversity and area (the so called species-area effect) (Barnosky et al. 2005). Further, regional sampling changes through time (e.g. the early Cenozoic North American mammal record is mostly limited to the Great Plains and Central Lowlands of North America), which is problematic due to likely topographic differences and thus biodiversity differences among regions (Davis 2005; Badgley 2010). Our interpretation of biodiversity time-series is made further difficult by rock record bias; outcrop area is often correlated with terrestrial vertebrate taxic diversity (Benton et al. 2011; Mannion et al. 2011). It therefore behooves us to understand how the numerous biases typical of the fossil record affect our ability to detect changes in macroecological phenomena through time.

In recognition of fossil record bias, paleoecologists use a variety of compensatory approaches including rarefaction, sub-sampling, and model selection (Rose et al. 2011; Benson and Mannion 2012; Fraser et al. 2014b; Mannion et al. 2014; Fraser et al. 2015). Although these compensatory methods reduce sample size differences among localities and time periods (Valentine et al. 2013), the extent to which true biodiversity patterns are retained after fossilization and whether applying rarefaction allows apparent diversity patterns to be interpreted as biological signal remain unknown.

Herein, I divide “latitudinal diversity gradient” into two components, latitudinal richness gradients (i.e. change in the number of species) and latitudinal turnover gradients (i.e. change in the species composition of communities). The distinction is important because, species composition can turnover entirely with no change in richness and show more rapid change than richness under environmental perturbation (Dornelas et al. 2014). Estimates of community turnover are also more robust to the formation of death assemblages (Tomašových and Kidwell 2009). Although both richness and community composition vary along environmental gradients (Qian and Ricklefs 2007; Qian et al. 2009; Qian and Ricklefs 2012), they are not necessarily correlated. For the purposes of this paper, I use extant North American mammals as a test case because they show a negative LRG (Fig. 2.1A) that is well explained by latitudinal changes in climate (McCoy and Connor 1980; Currie 1991; Kaufman 1995; Badgley and Fox 2000). North American mammals also show considerable latitudinal change in community composition (Fig. 2.1C) that is often attributed to abiotic species sorting (Qian et al. 2009; Kent et al. 2011), a process whereby community composition is partly determined by the environmental tolerances of constituent species (Qian et al. 2009; Soininen 2010). Furthermore, the Cenozoic (65 Ma - present) terrestrial mammal fossil record is the focus of numerous paleoecological studies given its relevance to understanding the evolution of modern mammal communities (Alroy et al. 2000; Davies et al. 2011; Raia et al. 2011b; Figueirido et al. 2012; Price et al. 2012; Raia et al. 2012; Cullen et al. 2014; Fraser et al. 2014b). Although I focus on mammals, the method I develop here allows for the rigorous

comparison of modern and fossil communities for any terrestrial group with a fossil and modern record (e.g. birds, herps).

To address whether latitudinal diversity gradients measured using the fossil record might be reflective of the true gradients from which they are drawn, I developed a simulated fossilization approach. Using the modern mammal record (i.e. spatially referenced geographic range data), I created simulated fossil localities based on the geographic distribution of real North American fossil localities and introduce body and geographic range size bias as well as variations in sampling effort (0, 25, 50, 75% species loss). I generated fossil localities iteratively and re-calculated the slope of the LRG for each sampling effort as well as the magnitude of the latitudinal turnover gradient.

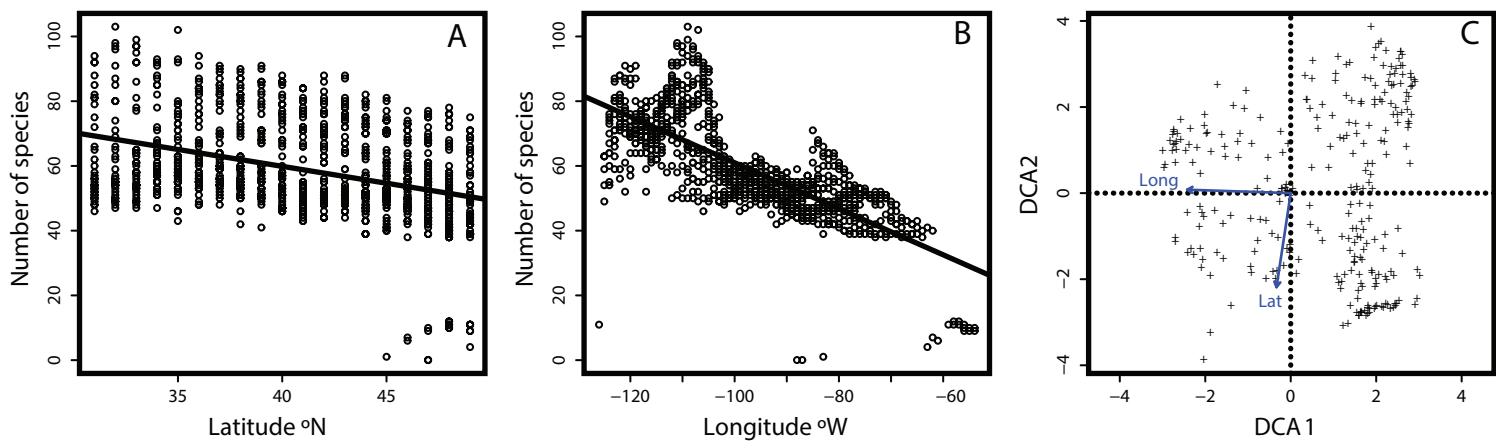


Figure 2.1 Modern North American mammal diversity gradients, (A) latitudinal richness gradient, (B) longitudinal richness gradient, and (C) latitudinal and longitudinal gradients in community turnover.

2.3 Materials and Methods

I downloaded spatially referenced geographic range data for modern North American mammals from NatureServe Canada (Patterson et al. 2007). The dataset included 1668 species after the exclusion of a small number of unreadable or corrupted files. Due to the focus on North America, I omitted any species with southern hemisphere ranges that did not cross the equator as well as species with fewer than 20 occurrences (705 species included; Appendix B). I sampled the ranges of extant North American mammals at a series of 5,066 points corresponding to a 1° grid. I calculated total richness in each grid cell and regressed richness against latitude to estimate the slope of the modern mammal latitudinal richness gradient in the continental United States and southern Canada (30° – 50° N). As a measure of faunal turnover with latitude (herein termed the latitudinal turnover gradient or LTG) of modern North American mammals, I used detrended correspondence analysis (DCA) (Kent et al. 2011; Oksanen et al. 2012), which was applied to a grid cell by species occurrence matrix.

DCA is a form of indirect gradient analysis, which is often used in ecological studies to quantify the degree of community change along environmental gradients (Ejrnæs 2000) but has been infrequently applied to the fossil record (Fraser et al. 2014b). DCA is an ordination method, thus each fossil site with its complement of species occupies a particular position along the first and second axes. Often, the position of each sampled site along the first DCA axis is correlated with the environmental variable of interest (in this case, latitude) (Bowman 1996). However, I have used the envfit function from the vegan R package (Oksanen et al. 2012), which fits environmental vectors to the ordination, effectively testing for a relationship with the position of each site in

ordination space. The result is a vector or series of vectors, which have both direction (the gradient) and length (importance of the gradient) as well as how much of the variation among sites is explained by the environmental variable (R^2 ; herein referred to as the magnitude or strength of the latitudinal turnover gradient). High values of R^2 and vector lengths indicate strong LTGs (Tuomisto and Ruokolainen 2006). In this context, R^2 values are precisely correlated with the vector lengths, which are scaled based according to the correlation between the environmental vectors and the ordination (Oksanen et al. 2012). Slopes are not associated with the fitted environmental vectors. I use the DCA approach as opposed to other methods of measuring community turnover (e.g. calculating faunal similarity or dissimilarity among grid cells or latitudinal bands, distance decay of similarity) (Soininen et al. 2007; Qian et al. 2009) because DCA can be applied to continuous distributions of extant species as well as arrays of unequally distributed fossil localities.

I then tested for the effects of typical fossil record biases by developing a simulated fossilization re-sampling approach in R (R Development Core Team, 2015).

2.3.1 Simulated fossilization of modern mammals

To create “fossil localities” from the modern mammal record, I used an iterative, point sampling approach with the maptools, sp, gpclib, ggplot2, rgeos, and MASS R packages (Venables and Ripley 2002; Pebesma and Bivand 2005; Peng 2007; Bivand et al. 2008; Lewin-Koh and Bivand 2008; Wickham 2009; Bivand and Rundel 2012). To ensure that I generated “fossil localities” with comparable spatial distributions to the North American fossil record for mammals, I used the late Miocene (~7 Ma; Hemphillian North American Land Mammal Age) as a model. My choice to use the late Miocene is

somewhat arbitrary but my simulated fossilization code allows for input of fossil locality data from any time period. My approach can also be easily modified for any continent and any group for which there is sufficient extant distribution data. I fit frequency distributions (normal, gamma, or β) to the latitudinal and longitudinal distributions of fossil localities from the late Miocene. I then created locality-by-species occurrence matrices using GIS to return the species present at each “fossil locality.” I repeated the procedure 10,000 times for each set of analyses, with and without bias (Appendix C). I performed all analyses both including and excluding bats.

2.3.1.1 Simulating fossil record bias

I weighted the probability of North American mammal species appearing in the simulated fossil record based on geographic range size, body size, and phylogenetic affinities. Range size probability weights were based on the fraction of North America occupied by each mammal species (i.e. species range size divided by total size of North America). Due to incompleteness of body mass data, I used a simple a cut off of 15 kg above which species were given a 95% chance of appearing in the “fossil record.” Species less than 15 kg were divided into herbivores (i.e. non-carnivoran clades), carnivores (i.e. members of Carnivora), and bats. Small herbivores were assigned a 60% chance of appearing in the fossil record while small carnivores and bats were assigned a 21% chance based on studies of modern death assemblages (Kidwell and Flessa 1996; Kidwell and Holland 2002). The probabilities I have used here are based on field studies of live-dead assemblages in African savannas but certainly do not represent the only possible weightings. Probabilities can therefore be easily altered by the user. I calculated joint probabilities for each species appearing in the simulated fossil record by multiplying

the geographic range size and body mass weightings for each species. I then sampled the extant mammal simulated fossil record assuming 100%, 75%, 50%, and 25% rates of sampling effort.

I calculated total richness at each simulated fossil locality both before and after application of rarefaction. Due to computational load, I only applied the Jackknife rarefaction method from the fossil R package (Vavrek 2012) and re-calculated the LRG slope. Additionally, I used a latitudinal band method, in which I divided North America into bands at 2° intervals, calculated richness within each band, both with and without Jackknife rarefaction, and calculated the slope of the LRG. I did not employ the additional method of grouping localities by geologic formation because modern mammal ranges are not restricted to geologic formations.

I also applied DCA as above to estimate the magnitude of the latitudinal turnover gradient (LTG) both with and without simulated fossil record bias. Rarefaction, as a method developed to improve the comparability of richness estimates among sites, cannot was not applied.

2.3.1.2 Model selection

I used an information theoretic approach (automated model selection using dredge from the MuMIn R package (Bartoń 2013)) to model change in LRG slope and the LTG among iterations and under simulated fossil record bias. I included the median latitude and longitude of all simulated localities, the area sampled (km^2), and species sampling rate as independent variables in all of the full models. I also extracted winter (December, January, February) temperature and mean annual precipitation data from Climate Wizard (www.climatewizard.org) for the period of 1951-2006 (Girvetz et al. 2009). I calculated

the slope of the temperature and precipitation richness gradients and variance in faunal turnover explained by precipitation and temperature as well as median, maximum, and minimum temperature and precipitation at each of the simulated fossil localities. Best-fit models were selected using AICc. I only investigated main effects and did not include interaction terms to reduce computation time.

2.4 Results

I estimated the slope of the modern North American mammal latitudinal richness gradient (LRG) to be -1.04 ± 0.08 (standard error) between 30°N and 50°N (Fig. 2.1A) and the longitudinal richness gradient to be -0.71 ± 0.02 (Fig. 2.1B). I estimated the magnitude of the latitudinal turnover gradient in the same region as 0.63 ($p = 0.001$) and the longitudinal turnover gradient as 0.76, indicating strong gradient in community change for modern mammals (Fig. 2.1C).

I found considerable variation in estimates of latitudinal richness gradient (LRG) slope and latitudinal turnover gradient. In general, most of the variation is explained by change in the correlation between diversity and temperature across the landscape (Table 2.1A; Fig. 2.2). In other words, where climate is strongly associated with richness, I found steep LDGs and *visa versa*. Only a small percentage of the variation in the LRG and LTG was explained by changes in the mean location of the simulated fossil localities (Table 2.1A). Additional unexplained variation reflects the fact that latitude is not a perfect surrogate for the climate gradient in North America. The results are similar when bats are excluded (Table 2.1B).

Reducing the species sampling rate of the simulated mammal fossil record from 100% to 25% increased the estimated slope of the LRG (Fig 2.2A-B). In fact, reducing

the species sampling rate increased the proportion of positive slope estimates (i.e. richness apparently increased with latitude; Fig. 2.3A-B). Application of rarefaction restores some of the signal, but not enough to recover the typically negative LRG of modern North American mammals (Fig. 2.3A-B). Species sampling rate is therefore one of the top explanatory variables in the fitted models (Table 2.1C-D). Using the method of dividing simulated fossil localities among latitudinal bands produced generally poor estimates of the LRG (Fig. 2.3C-D) and little variation was explained by those models (Table 2.1C-D).

LTG estimates do not appear weaker as species sampling rate is reduced both with and without the inclusion of bats (Fig. 2.4A-B). Accordingly, species sampling rate explained much less model variance for LTGs than for LRGs (Table 2.1C-D).

Table 2.1 Best fit generalized linear models relating estimates of latitudinal richness gradient magnitude measured as the slope of the latitudinal richness gradient (LRG) and magnitude of the latitudinal turnover gradient (LTG) to metrics for the geographic coverage of simulated fossil localities. (A) unbiased simulated fossil record with bats, (B) unbiased simulated fossil record with bats, (C) biased simulated fossil record with bats, and (D) biased simulated fossil record without bats.

Dependent Variable	Total variance explained (%)	Independent variables of best fit model	Variance explained (%)	t value	p value
(A)	LRG slope	TRG	50.69	-35.60	< 0.001
		Area	7.35	8.17	< 0.001
		Maximum temperature	2.39	-5.77	< 0.001
		Minimum temperature	1.27	7.34	< 0.001
		Median latitude	1.07	6.15	< 0.001
		PRG	0.63	4.39	< 0.001
	LRG slope (bands)	PRG	4.59	5.04	< 0.001
		Median latitude	3.29	5.46	< 0.001
		Maximum precipitation	2.05	1.88	0.06
	LTG magnitude	TTG	27.09	18.44	< 0.001
		PTG	20.36	-15.24	< 0.001
		Area	1.09	-2.78	0.01
		Median latitude	1.07	-4.86	< 0.001
		Maximum precipitation	1.02	-3.42	< 0.001
		Maximum temperature	0.55	-1.64	0.10
(B)	LRG slope	Median longitude	0.19	2.26	0.02
		TRG	47.48	-33.58	< 0.001
		Area	6.93	8.46	< 0.001
		PRG	1.89	9.12	< 0.001
		Maximum temperature	1.84	-5.14	< 0.001
		Median latitude	0.98	5.50	< 0.001
	LRG slope bands	Minimum temperature	0.97	6.21	< 0.001
		PRG	7.97	7.41	< 0.001
		Median latitude	3.59	5.67	< 0.001
	LTG strength	Maximum precipitation	2.85	2.02	0.04
		Area	1.20	-3.72	< 0.001
		Maximum precipitation	1.10	-3.79	< 0.001
		Median latitude	1.03	-4.72	< 0.001
		PTG	20.75	-16.00	< 0.001
(C)	LRG slope	TTG	26.87	18.63	< 0.001
		TRG	46.66	-566.19	< 0.001
		25% species loss	18.80	-0.49	0.62
		50% species loss		14.58	< 0.001
		75% species loss		25.20	< 0.001
		PRG	3.65	42.77	< 0.001
		Area	1.93	81.01	< 0.001
		Maximum temperature	1.36	7.56	< 0.001
		Minimum temperature	0.45	67.68	< 0.001
		Median longitude	0.40	-38.79	< 0.001
		Median latitude	0.37	79.76	< 0.001
		Minimum precipitation	0.21	9.95	< 0.001
	LRG slope bands	Maximum precipitation	0.16	-42.06	< 0.001
		25% species loss	7.71	-10.43	< 0.001
		50% species loss		-11.37	< 0.001
		75% species loss		-33.10	< 0.001
		Median latitude	1.53	65.76	< 0.001
		TRG	0.78	3.11	0.002
(D)	LTG magnitude	PRG	0.55	54.60	< 0.001
		Minimum temperature	0.53	-42.78	< 0.001
		Median longitude	0.06	-9.88	< 0.001
		Maximum precipitation	0.06	-7.77	< 0.001
		Area	0.06	-2.32	0.02
		Median latitude		1.53	65.76
		Maximum temperature		0.53	-42.78
		Median longitude		0.06	-9.88
		Maximum precipitation		0.06	-7.77

		Minimum precipitation	0.04	-6.41	< 0.001
		Maximum temperature	0.03	7.45	< 0.001
LTG strength	35.60	TTG	22.88	299.20	< 0.001
		25% species loss	5.56	-0.25	0.80
		50% species loss		-10.67	< 0.001
		75% species loss		-24.19	< 0.001
		PTG	3.62	-102.39	< 0.001
		Median latitude	1.55	-74.67	< 0.001
		Maximum precipitation	1.10	-59.96	< 0.001
		Maximum temperature	0.59	-15.21	< 0.001
		Area	0.14	22.60	< 0.001
		Minimum temperature	0.08	-12.06	< 0.001
		Minimum precipitation	0.06	2.93	0.003
		Median longitude	0.02	5.10	< 0.001
<hr/>					
(D)					
LRG slope	68.85	TRG	50.72	-604.24	< 0.001
		25% species loss	10.87	-7.96	< 0.001
		50% species loss		2.31	0.02
		75% species loss		2.04	0.04
		Area	3.33	90.88	< 0.001
		Maximum temperature	2.05	21.33	< 0.001
		PRG	0.49	57.00	< 0.001
		Minimum temperature	0.38	39.91	< 0.001
		Median latitude	0.38	76.72	< 0.001
		Median longitude	0.26	-36.67	< 0.001
		Minimum precipitation	0.20	12.99	< 0.001
		Maximum precipitation	0.17	-20.57	< 0.001
LRG slope bands	8.23	Median latitude	3.21	95.45	< 0.001
		PRG	2.14	83.47	< 0.001
		25% species loss	1.97	-6.74	< 0.001
		50% species loss		-18.99	< 0.001
		75% species loss		-17.94	< 0.001
		TRG	0.34	-11.18	< 0.001
		Minimum temperature	0.26	-28.60	< 0.001
		Median longitude	0.12	-11.47	< 0.001
		Area	0.07	4.59	< 0.001
		Minimum precipitation	0.07	12.92	< 0.001
		Maximum temperature	0.05	-6.89	< 0.001
LTG strength	36.87	TRG	25.08	294.45	< 0.001
		PRG	7.03	-122.96	< 0.001
		Maximum precipitation	1.88	-83.83	< 0.001
		Median latitude	1.78	-83.68	< 0.001
		25% species loss	0.36	-7.42	< 0.001
		50% species loss	0.36	-13.29	< 0.001
		75% species loss	0.36	-13.92	< 0.001
		Area	0.31	42.18	< 0.001
		Maximum temperature	0.27	-10.91	< 0.001
		Minimum precipitation	0.11	23.39	< 0.001
		Median longitude	0.03	2.10	0.04
		Minimum temperature	0.03	-2.58	0.01

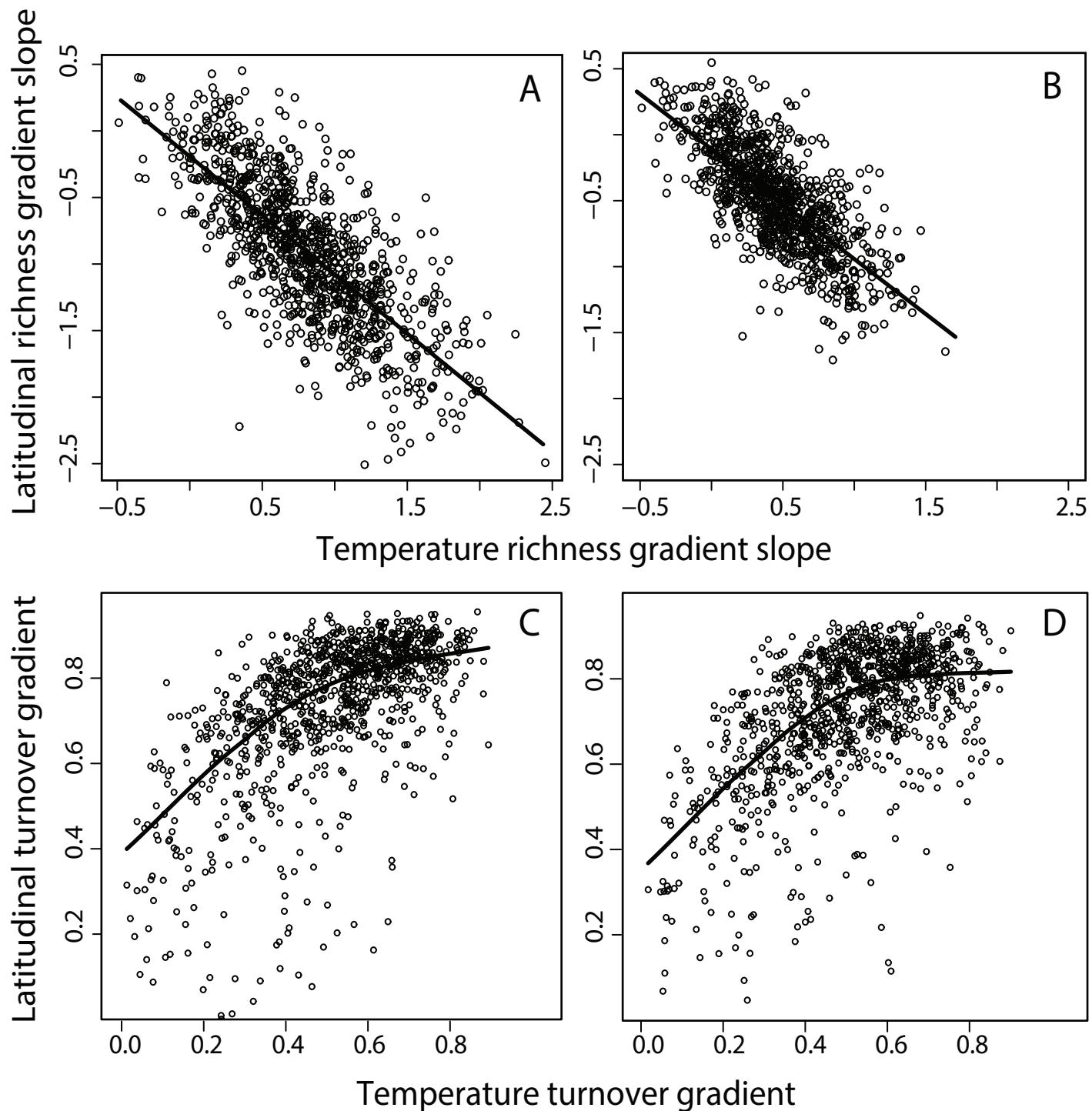


Figure 2.1 Correlation of (A) estimated latitudinal richness gradient slopes with slopes of the mammal temperature richness gradient, and (B) estimates of the latitudinal turnover gradient with estimates of the temperature turnover gradient for modern North American mammals. A temperature turnover gradient refers to faunal turnover along a spatial gradient in temperature. All estimates are derived from single iterations of simulated fossilization with complete species sampling.

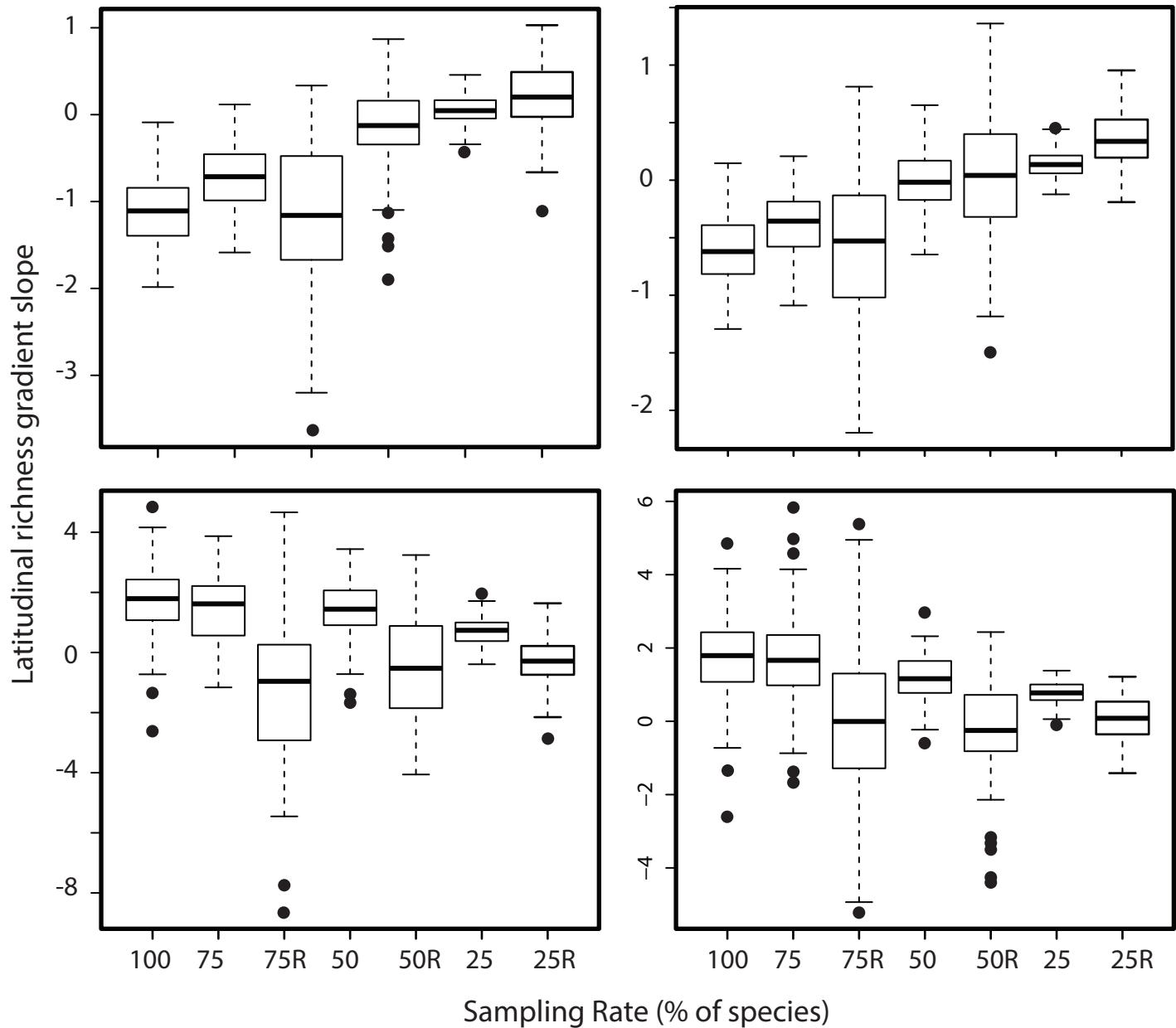


Fig. 2.3 Box plots of estimated North American mammal latitudinal richness gradient slope when species sampling is reduced from 100% to 25% with and without the application of rarefaction (R), (A) LRG slope estimates when richness is estimated on a per locality basis with bats and (B) without bats, (C) LRG slopes estimates when richness is estimated within latitudinal bands with bats and (D) without bats.

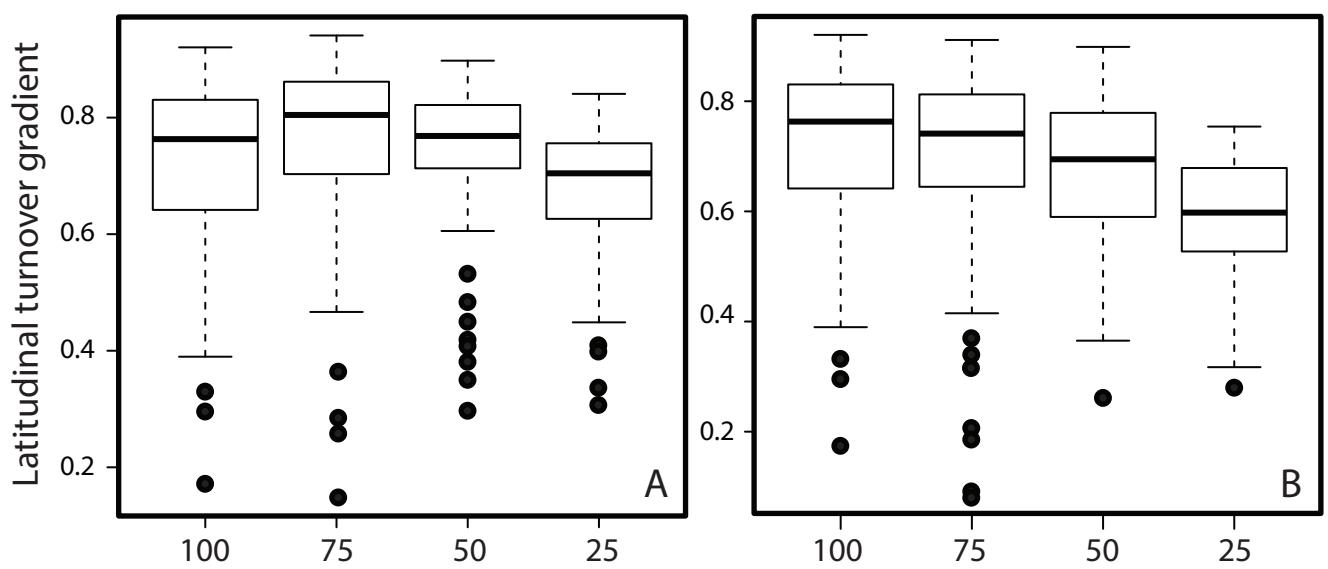


Fig. 2.4 Box plots of estimated North American mammal latitudinal turnover gradient magnitude when species sampling is reduced from 100% to 25% (A) with and (B) without bats.

2.5 Discussion

Interest in the origins of macroecological phenomena in deep time is burgeoning (Mannion et al. 2014). However, the fossil record is characterized by considerable taxonomic, temporal, and spatial bias (Benton 2010). Herein, I used a simulated fossilization approach to test whether estimates of the latitudinal richness gradient (LRG) and latitudinal turnover gradient (LTG) of modern North American mammals are robust to loss of small bodied, small ranged species. In general, I found that LRG estimates are highly impacted by loss of diversity during simulated fossilization. In many cases, simulated fossil record bias completely obliterated evidence of the negative LRG of modern North American mammals, a phenomenon that is not ameliorated by the application of rarefaction. In contrast, the LTG showed considerably less loss of signal when species sampling rate fell; estimates of the magnitude of latitudinal diversity gradient were less affected by the loss of species from the simulated fossil record.

Modern North American mammals show a significant decline in richness between 30°N and 50°N (-1.04 estimated slope of richness vs. latitude regression line; Fig. 2.1A) (Currie 1991) and from the west to east coasts (-0.71 estimated slope; Fig. 2.1B). Peaks in mammal diversity occur in the high altitude regions of Arizona and New Mexico (~35°N and 110°W), as well as at the most southern parts of the Appalachian region (~32°N and 85°W; Georgia and Alabama) (Fig. 2.1A-B). Modern mammal richness gradients are also associated with significant latitudinal ($R^2 = 0.63$) and longitudinal ($R^2 = 0.76$) faunal turnover gradients (Fig. 2.1C). That is, there is considerable change in richness and community composition on both the south-north and west-east axes. The best-supported models suggest that climate and productivity are the primary drivers of the latitudinal

diversity gradient (Currie and Fritz 1993; Currie et al. 1999; Engle and Summers 1999; Condit et al. 2002; Hawkins et al. 2003; Qian et al. 2009; Baselga et al. 2012; Condamine et al. 2012). The longitudinal gradient in North America reflects the east-west elevation gradient and tendency for topographically complex regions to show steeper richness and β diversity gradients (Badgley and Fox 2000; Badgley 2010).

On average, simulated fossilization without bias yielded a negative LRG (-1.11 mean estimated slope; Fig. 2.3A-B) and strong LTG ($R^2=0.74$; Fig. 2.4A-B) when diversity was compared across individual localities. Only small amounts of variation were explained by changes in the sampled area and median latitude and longitude of the simulated fossil localities (Table 2.1A-B). The majority of variation in the estimated LRG and LTG was explained by change in the correlation between diversity and temperature across the landscape (Table 2.1A-B). Where the relationship between diversity and temperature was tightest, I found steeper LRGs and LTGs. The “latitudinal band” method produced very poor approximations of the mammal LRG (1.73 estimated slope; Fig. 2.3C-D). When I excluded bats, I found broadly similar patterns before applying simulated fossil record bias.

When I introduced increasing bias against small-bodied, narrow-ranged species, I estimated a shallower LRG on average for North American mammals (Fig. 2.3A-B). Variation among iterations (i.e. each new set of simulated fossil localities) was generally greater than within iterations (i.e. variations in which particular species are lost; Fig. S2.1) suggesting that estimation of the LRG slope is not impacted by the loss of particular taxa but rather by the distribution of localities and the size of the species pool that is not fossilized. In fact, as I reduced the species sampling rate using simulated

fossilization, I retrieved a higher proportion of positive estimates for the LRG slope (Fig. 2.3A-B).

Positive LRG slopes are particularly interesting because early Cenozoic North American mammals may have shown flat or positive LRG (note that this is consistent with contemporary climate reconstructions) (Rose et al. 2011). Species sampling rate explained a large proportion of the model variance (Table 2.1C-D) suggesting, that fossil record bias could be the primary process leading to apparently positive latitudinal richness gradients.

Flattening of the LRG as species sampling rate decreased is likely explained by both Bergmann's rule, i.e. the increase in mean body size with latitude (McNab 1979; Blackburn et al. 1999; Freckleton et al. 2003), and Rapoport's rule, i.e. the increase in mean geographic range size with latitude (Fig. 2.5) (Stevens 1989; Kaufman 1995; Whittaker et al. 2001). Between 30°N and 50°N, there is an apparent increase in the mean and variation of mammal geographic range sizes (measured here as species occupancy or the number of grid cells occupied by a species; Fig. 2.5), which is most often attributed to loss of productivity toward the poles (Stevens 1989; Blackburn et al. 1999). Selective removal of small bodied, narrow-ranged species from the simulated fossil record means disproportionate loss of low latitude species and a flattening of the estimated LRG slope.

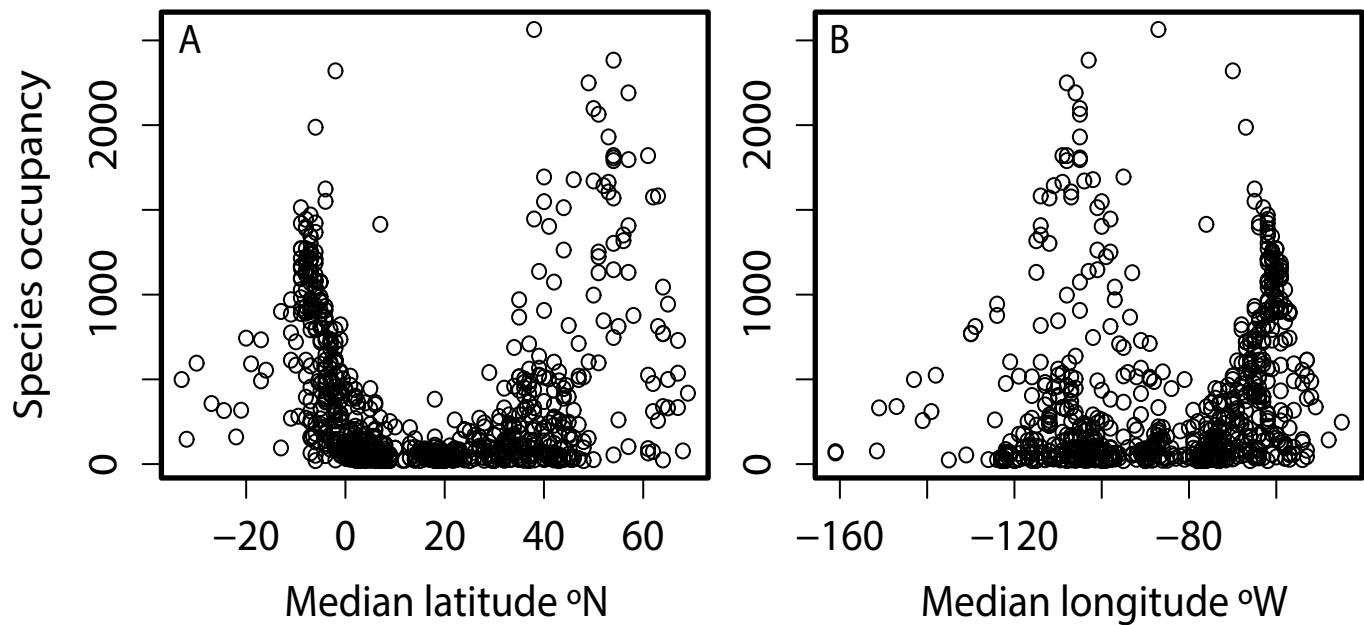


Fig. 2.5 Relationship of species geographic range size measured as species occupancy or the number of grid cells occupied with the median latitude of each species geographic range.

Mean LTG estimates remained high even after loss of 75% of species from the simulated fossil record (Fig. 2.4A-B) although they were slightly higher than estimated prior to the application of simulated fossilization (0.61; Fig. 2.1C). Slight overestimation of LTGs results from the discontinuity introduced by the creation of simulated fossil localities. Only a small amount of variation in LTG estimates was explained by area and the mean latitude and longitude of the simulated fossil localities (Table 2.1C). Unlike the latitude richness gradient, variation within iterations was greater than among them (Fig. S2.2), suggesting that shifts in the geographic placement of the fossil localities are less influential than the identity of the species that are never “fossilized.” That is, the removal of loss of particular species or groups of species might have a disproportionate impact on LTG estimates. When bats were excluded, mean estimated LTG declined as species sampling was reduced, but converged on the LTG estimate for the unbiased modern North American mammal record (Fig. 2.4B).

2.5.1 Conclusions

Studying the deep time origins of macroecological phenomena can help us understand their long-term climatic and macroevolutionary drivers. Given the considerable taxonomic and spatiotemporal bias of the fossil record, it behooves us to understand how the inference of macroecological patterns from the fossil record are impacted by typical biases. I used a simulated fossilization approach to show that estimated of the latitudinal richness gradient slope of modern North American mammals is particularly sensitive to the loss of small-bodied, narrow-ranged species from the fossil record. By contrast, estimates of latitudinal turnover gradients are much less sensitive to species loss than they are to the identity of species that are never fossilized.

Furthermore, the simulated fossilization approach presented herein allows for the direct comparison of modern diversity gradients with gradients measured in the past. My approach allows users to estimate the modern North American mammal diversity gradient using a similar (or exact same) distribution of localities to the fossil record, when removing different percentages of the mammal community, and when adjusting the weighted probabilities of different species entering the simulated fossil record. **My approach therefore allows users to directly test whether a measured fossil diversity gradient might be reflective of biological reality versus fossil record bias.** Direct comparisons between modern and fossil mammal diversity gradients can be made by “fossilizing” modern mammals using the exact distribution of fossil localities or by fitting frequency distributions as done here from each time period of interest (removing varying percentages of species from the simulated fossil record) and comparing the simulation results to the estimated fossil gradient using methods such as the single sample t-test. My simulated fossil approach is therefore a significant step toward increasing the rigor with which diversity of fossil taxa is being studied.

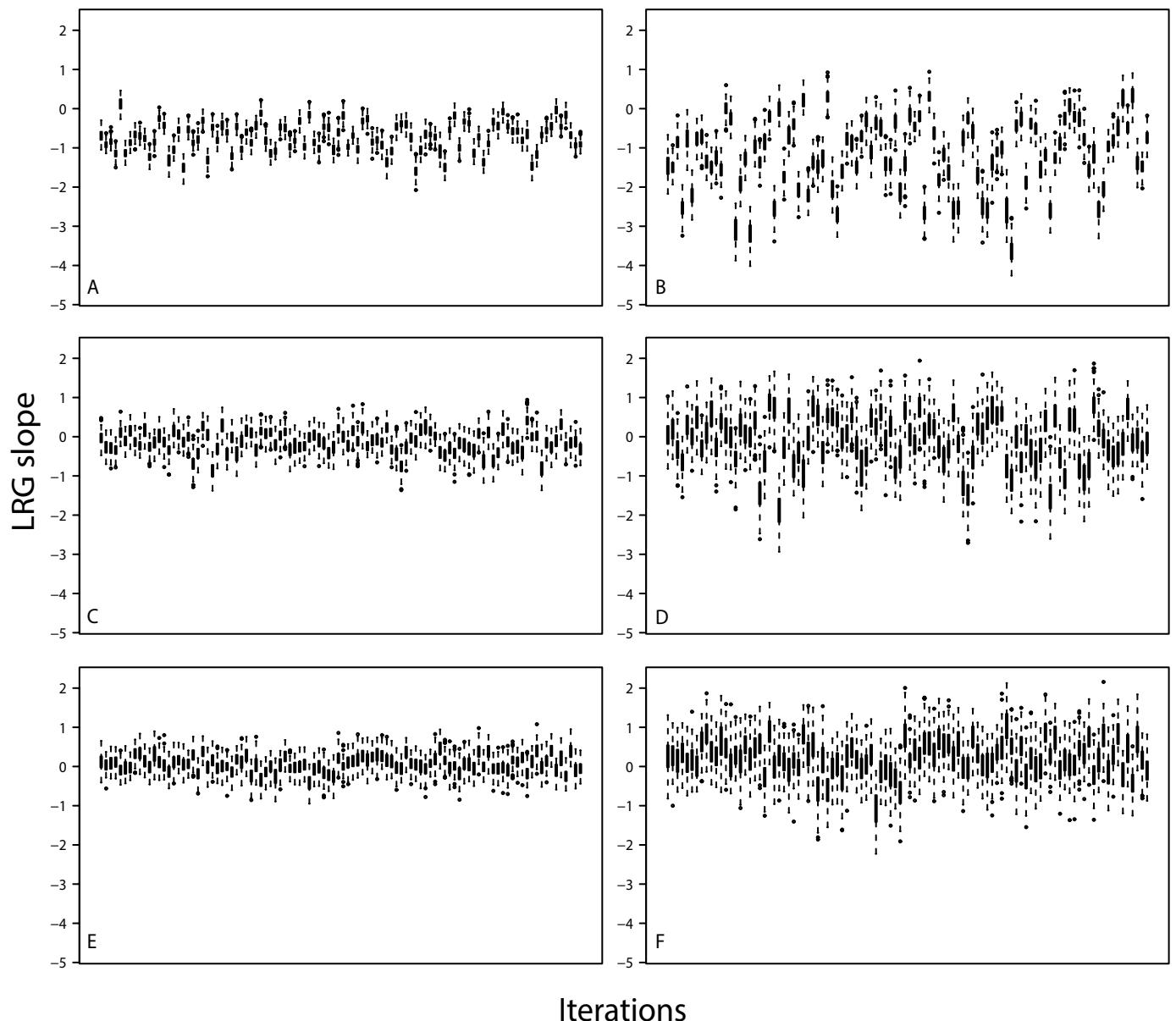


Fig. S2.1 Box plots of latitudinal richness gradient (LRG) slope estimates from an unbiased simulated fossil record when richness is calculated at individual localities. Each box plot summarizes LRG slopes estimated from a single set of simulated fossil localities. Variation within each iteration results from different species being lost from the simulated fossil record. (A) 75% without rarefaction, (B) 75% with rarefaction, (C) 50% without rarefaction, (D) 50% with rarefaction, (E) 25% without rarefaction, (F) 25% with rarefaction sampling rates when bats are included. Patterns are the same when bats are excluded.

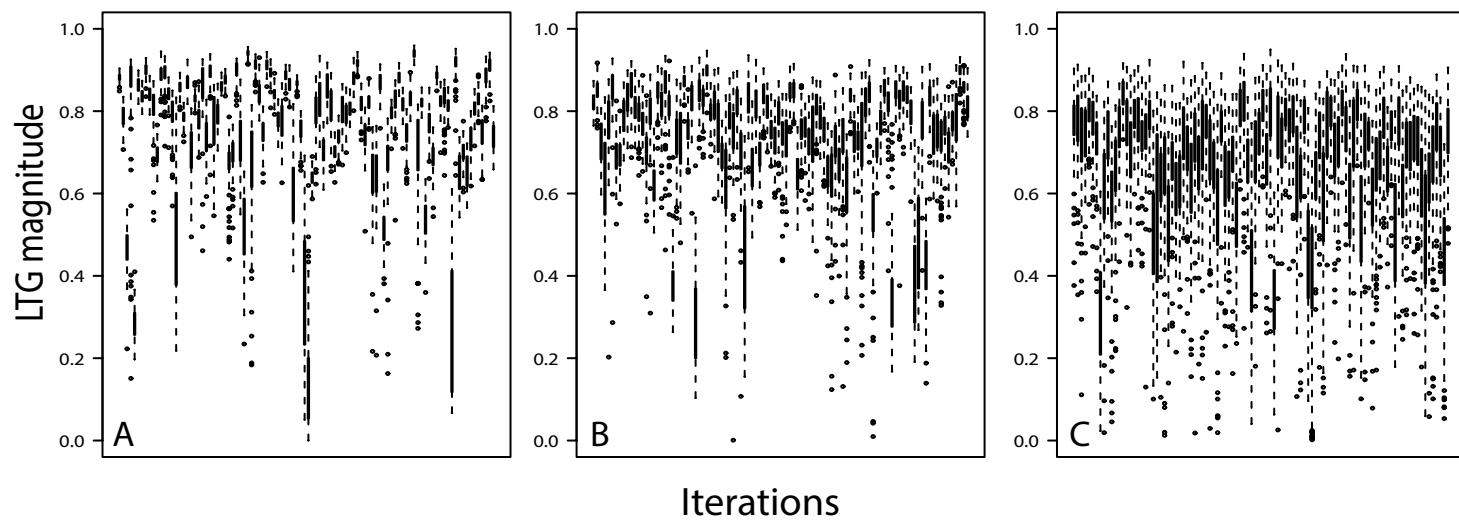


Fig. S2.2 Box plots of latitudinal turnover gradient magnitude (LTG) estimates from an unbiased simulated fossil record. Each box plot summarizes LTG magnitudes estimated from a single set of simulated fossil localities. Variation within each iteration results from different species being lost from the simulated fossil record. (A) 75%, (B) 50%, and (C) 25% sampling rates when bats are included. Patterns are the same when bats are excluded.

3 Chapter: Mean annual precipitation explains spatiotemporal patterns of Cenozoic mammal beta diversity and latitudinal gradients in North America

3.1 Abstract

Spatial diversity patterns are thought to be driven by climate-mediated processes. However, temporal patterns of community composition remain poorly studied. We provide two complementary analyses of North American mammal diversity, using (i) a paleontological dataset (2077 localities with 2493 taxon occurrences) spanning 21 discrete subdivisions of the Cenozoic based on North American Land Mammal Ages (36 Ma – present), and (ii) climate space model predictions for 744 extant mammals under eight scenarios of future climate change. Spatial variation in fossil mammal community structure (β diversity) is highest at intermediate values of continental mean annual precipitation (MAP) estimated from paleosols (~450 mm/year) and declines under both wetter and drier conditions, reflecting diversity patterns of modern mammals. Latitudinal gradients in community change (latitudinal turnover gradients, aka LTGs) increase in strength through the Cenozoic, but also show a cyclical pattern that is significantly explained by MAP. In general, LTGs are weakest when continental MAP is highest, similar to modern tropical ecosystems in which latitudinal diversity gradients are weak or undetectable. Projections under modeled climate change show no substantial change in β diversity or LTG strength for North American mammals. Our results suggest that similar climate-mediated mechanisms might drive spatial and temporal patterns of community composition in both fossil and extant mammals. We also provide empirical evidence that the ecological processes on which climate space models are based are insufficient for

accurately forecasting long-term mammalian response to anthropogenic climate change and inclusion of historical parameters may be essential.

3.2 **Introduction**

Terrestrial species from all major taxonomic groups show dramatic changes in richness and diversity across the landscape (Hawkins et al. 2003). One of the fundamental goals in ecology is therefore to ascertain why there are more species in some places than in others. A satisfactory answer would identify and disentangle the drivers of biodiversity at all spatial scales, from the microhabitat to the globe, as well as explain changes through time. Attempts to provide such an answer have produced many studies of species richness patterns and community composition in extant organisms (Currie and Fritz 1993; Currie et al. 1999; Engle and Summers 1999; Condit et al. 2002; Hawkins et al. 2003; Qian et al. 2009; Baselga et al. 2012; Condamine et al. 2012). Prime examples are the numerous studies of latitudinal richness gradients (LRGs), which have been observed in many terrestrial groups including angiosperms, birds, mammals, insects and other invertebrates. The best supported hypotheses show that richness declines toward the poles in correlation with reductions in precipitation, temperature, and net primary productivity (Mittelbach et al. 2007). Correlation of global climate with animal richness over the past 65 Ma, specifically a decline in richness as climates cooled, similarly supports a link between diversity and climate (Sepkoski 1998; Figueirido et al. 2012; Mayhew et al. 2012). However, of the spatial and temporal dimensions of diversity, spatial patterns of community differences (“ β diversity”) are infrequently studied despite considerable variation on both local and regional scales (Legendre et al. 2005; Qian et al.

2009; Kent et al. 2011) and their influential role in the structuring of continental-scale richness patterns including LRGs (Condit et al. 2002; Baselga et al. 2012).

β diversity has been defined most broadly as the differentiation in community composition (i.e. the species that make up the community) among regions or along environmental gradients (Whittaker et al. 2001). Similar to LRGs, β diversity generally declines from the tropics to the poles in correlation with climate (Qian et al. 2009). However, temporal changes in β diversity remain poorly studied despite their potential power for illuminating the drivers of past and present richness patterns and importance in modern conservation (Soininen 2010; Hassall et al. 2012; Dornelas et al. 2014). This study therefore tests the hypothesis that climatic influences on mammalian β diversity apply equally to temporal patterns, i.e. that the underlying ecological processes are “ergodic” (dynamic processes that are the same in both time and space).

The mid to late Cenozoic (36 Ma to present) has been a time of dramatic mammalian diversity change, shaped in part by the transition from the productive ice-free ecosystems of the early to mid Cenozoic to the more temperate glaciated ecosystems of the late Cenozoic. Under these changing climatic conditions, mammalian communities show dramatic reductions in richness, changes in community composition, and morphology (Janis et al. 2000; Barnosky et al. 2003; Barnosky 2005; Davis 2005; Finarelli and Badgley 2010; Atwater and Davis 2011; Figueirido et al. 2012). The most dramatic changes occurred at high latitudes, where ecosystems transitioned from *Metasequoia* forests during the early to mid Cenozoic (Eberle et al. 2009; Eberle et al. 2010) to boreal-type forests during the later Cenozoic and to modern tundra (Polyak et al. 2010). Associated with Cenozoic climate change, were changes in latitudinal climate

gradients; overall, the intensity of latitudinal climate gradients increased toward the present, reflecting disproportionate polar cooling due to the formation of permanent Arctic glaciation (Micheels et al. 2009; Clementz and Sewall 2011). We therefore predict that latitudinal diversity gradients increased in strength under cooler, less productive environmental conditions just as modern LRGs are steeper in temperate than in tropical regions. Further, we predict that β diversity declined under cooler, less productive environmental conditions just as modern β diversity declines toward the poles (Currie and Fritz 1993; Qian et al. 2009).

Quaternary (2.6 Ma to present) climates have been cool relative to the majority of the late Cenozoic. Recently, however, high latitudes have experienced disproportionate increases in annual temperature (up to 2°C to date), increases in plant primary productivity, and loss of large areas of perennial ice under anthropogenic global warming (Post et al. 2009). Flora and fauna have responded through shifts in phenology (Primack et al. 2009), *in situ* evolution (Bradshaw and Holzapfel 2006), and, in some cases, extinction (Parmesan 2006). However, perhaps the most often recorded response is the climatically-correlated pattern of extirpations and colonization that manifest as shifts in the location of a species' geographic range. Distributional studies over ecological timescales (<100 yrs) have recorded dramatic pole-ward range shifts and expansions for a wide range of terrestrial taxa in response to northern warming (Parmesan and Yohe 2003; Chen et al. 2011). Projections (i.e. Special Report on Emissions Scenarios) for the next 100 years predict levels of global warming similar to the middle Miocene (+ 6°C) – a time of reduced or absent perennial Arctic glaciation (Foster et al. 2009; Foster et al. 2012) – or warmer (+ 11°C for the most extreme case; Table S3.1). We therefore expect

continued range expansion, extinction, evolution, and community level changes among North American animals and plants.

A common approach to predicting the long-term outcomes of climate change for terrestrial organisms is climate space modeling (CSM). CSMs use distributional information and climate data to project species ranges into the future, usually under the assumption of no evolution and without adjustment for dispersal differences among species (Lawler et al. 2006; Hoffmann and Sgró 2011; Thuiller et al. 2013). Rapid evolutionary changes on very short timescales and high degrees of variation in dispersal ability under climate change have been observed across a wide range of organisms (Lavergne et al. 2010; Chen et al. 2011; Hoffmann and Sgró 2011), therefore CSMs are unlikely to generate accurate forecasts of climate change response. The fossil record, which encompasses many disparate environments and climates, might serve as record of a natural experiment by which ecological hypotheses can be tested in the temporal dimension. Fossil collections are a rich historical record of response to various climatic events that can be incorporated into predictive models, and mammals, in particular, are an excellent group for testing the generality of ecological hypotheses because they have an extensive Cenozoic fossil record. However, studies of extinct organisms have focused largely on richness (Sepkoski 1997; Barnosky et al. 2003; Davis 2005; Rose et al. 2011; Mayhew et al. 2012) or morphology (Secord et al. 2012), with limited focus on community composition (Davis 2005; Atwater and Davis 2011). Because changes in biological communities are not always associated with changes in richness,

spatiotemporal patterns of community composition may be better indicators of climate change response (Kent et al. 2011; Dornelas et al. 2014).

We propose that integrating the study of fossil, modern, and projected spatiotemporal patterns of community composition i) allows for the testing of ecological principles in the temporal dimension, ii) provides the most complete picture of diversity responses to climate change, and iii) enables evaluation of the performance of commonly employed CSMs. Our approach of combining the study of fossil, modern, and projected diversity patterns provides novel insights into the ecological and evolutionary processes that drive continental patterns of biodiversity in space and time.

3.3 Materials and Methods

3.3.1 Data collection and preparation

We downloaded occurrences for modern North American mammals from NatureServe Canada. The extant mammal dataset included 744 species after the exclusion of a small number of unreadable or corrupted files (Patterson et al. 2007). We restricted our study of fossil mammals to the late Eocene through Pleistocene, thus avoiding the confounding effects of the early Paleogene mammal radiation. We partitioned the fossil mammal occurrence data by North American Land Mammal Age (NALMA) subdivisions because they delineate relatively temporally stable community assemblages and allowed us to obtain a nearly continuous sequence of mammal community change without large intervening gaps. Using NALMA subdivisions leads to time averaging of mammal communities and to differences in sampling (i.e. intensity, geographic coverage etc.) among time periods. However, we use a statistical approach to reduce these biases, described below. We based the dates for all NALMA subdivisions on Woodburne (2004).

Further, we combined data for the entire Clarendonian and excluded for the Whitneyan, late Late Hemphillian, and early Chadronian due to poor sampling (Table 3.1).

Table 3.1 Summary of sampled North American Land Mammal Age (NALMA) subdivisions.

Epoch	NALMA subdivision	Age Range (Ma)	Midpoint Age (Ma)	Number of species	Number of fossil localities	Area (km ²)
Pleistocene	Rancholabrean	0.25-0.011	0.1305	222	180	176615.9
Pliocene	Irvingtonian II	0.85-0.25	0.55	189	94	144745.5
Pliocene	Irvingtonian I	1.72-0.85	1.285	102	37	60361.4
Pliocene	Blancan V	2.5-1.72	2.11	165	130	125042.6
Pliocene	Blancan III	4.1-2.5	3.3	183	163	122839.5
Pliocene	Blancan I	4.9-4.1	4.5	85	66	140433.4
Miocene	Early late Hemphillian	6.7-5.9	6.3	68	46	20108.2
Miocene	Late early Hemphillian	7.5-6.7	7.1	63	55	29446.7
Miocene	Early early Hemphillian	9.7-5	8.25	65	47	31455.8
Miocene	Clarendonian	12.5-9	10.75	104	90	36139.8
Miocene	Late Barstovian	14.8-12.5	13.6	195	194	33789.1
Miocene	Early Barstovian	15.9-14.8	15.5	150	168	51753.3
Miocene	Late Hemingfordian	17.5-15.9	16.7	100	83	25478.4
Miocene	Early Hemingfordian	18.8-17.5	18.15	107	105	45531.3
Miocene	Late late Arikareean	19.5-18.8	19.15	108	123	38307.2
Oligocene/Miocene	Early late Arikareean	23.8-19.5	21.65	71	67	37892.2
Oligocene	Late early Arikareean	27.9-23.8	25.85	95	65	20927.8
Oligocene	Early early Arikareean	30-27.9	28.95	116	124	15382.3
Oligocene	Late Orellan	33.1-32	32.55	38	36	17725.7
Oligocene	Early Orellan	33.7-33.1	33.4	88	130	5579.8
Eocene	Middle Chadronian	35.7-34.7	35.3	88	37	10349.7

We downloaded fossil mammal occurrence data for the Eocene, Oligocene, Pliocene, and Pleistocene from the the Paleobiology Database using the Fossilworks Gateway (fossilworks.org) in July and August, 2012, using the group name 'mammalia' and the following parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial (primary contributor: John Alroy; literature sources summarized in Appendix D). We downloaded Miocene mammal occurrence data from the Miocene Mammal Mapping Project in March 2011 (Carrasco et al. 2005) using the NALMA subdivision as our search criterion. For all analyses, with the exception of the Miocene, we used paleolatitudes and paleolongitudes. We chose to use MIOMAP for the Miocene data because it is the most complete Miocene dataset. However, MIOMAP does not provide paleo-coordinates. Fortunately, there are only small differences between modern and Miocene latitudes for the downloaded localities. We removed all taxa with equivocal species identifications (e.g. *Equus* sp.) unless they were the only occurrence for a genus. We assumed all occurrences of open nomenclature (e.g. *Equus* cf. *simplicidens*) were correct identifications.

We did not use latitudinal grids for fossil or extant mammals as in previous studies of latitudinal richness gradients (McCoy and Connor 1980; Hawkins et al. 2003) because our study is focused on community composition. We therefore do not need to clump localities by spatial proximity to employ rarefaction methods. In addition, the uneven spatial distribution of fossil localities makes the use of a grid method impractical. Instead, we created taxon-by-locality occurrence matrices for extant and fossil mammals at the species taxonomic level excluding *Homo sapiens* (Davis 2005; Atwater and Davis

2011). In all cases, taxa and localities with fewer than two occurrences were removed from the dataset. Final numbers of localities and species are summarized in Table 3.1.

To make direct comparisons with modern mammals, we created occurrence matrices for extant mammals by pseudo fossil localities, which were generated using an iterative procedure in R with the maptools, sp, gpclib, ggplot2, rgeos, and MASS packages (Venables and Ripley 2002; Pebesma and Bivand 2005; Peng 2007; Bivand et al. 2008; Lewin-Koh and Bivand 2008; Wickham 2009; Bivand and Rundel 2012). To generate pseudo fossil localities and to ensure that we created pseudo fossil localities with the same spatial distributions as the fossil localities, we fit frequency distributions (normal, gamma, or β) to fossil localities for each NALMA subdivision (Appendix A). We then generated point samples based on the frequency distributions and the number of fossil localities from which we created occurrence matrices (taxon-by-pseudo locality), repeating the procedure 100 times for each NALMA sub-age for a total of 2100 occurrence matrices. Fossil localities do not record the entire community and so show reduced richness compared to the actual communities (however, note that time averaging also increases richness at fossil localities). Further, most fossil localities, unless intensively screen washed, are biased against small species. Therefore, we also intentionally tested for the effects of sampling bias by removing 25%, 50%, and 75% of species from the extant mammal occurrence matrices for a total of 6300 occurrence

matrices. Further, we tested for the effects of body mass bias by 25%, 50%, and 75% of species smaller than 5 kg for a total of 6300 occurrence matrices.

3.3.2 Climate space models

To create climate space models, we sampled the ranges of extant North and South American mammals at a series of 5066 points corresponding to a 1° grid (which we only used to project mammal occurrences under climate change models, but not to calculate biodiversity). Due to the focus on North America, we omitted any species with southern hemisphere ranges that did not cross the equator (n=602; Appendix B). We also excluded rare species (present in <20 cells) for which accurate species distribution models could not be generated (n=361), leaving 706 species for the climate change projections. We extracted mean annual and winter (December, January, February) temperature and mean annual precipitation data from Climate Wizard (www.climatewizard.org) for the period of 1951-2006 and the following SRES scenarios and time periods: B1 2050s, A1b 2050s, A1b 2080s, A2 2050s, and A2 2080s (Nakicenovic and Swart 2000) (Table S3.1). Each of these projections is based on an ensemble of 16 global circulation models (Girvetz et al. 2009). However, to ensure that we sampled a range of potential warming, we also extracted the ensemble lowest B1 2050s projection (hereafter "B1 2050s low") and the ensemble highest A2 2080s projection (hereafter "A2 2080s high"). This gave a range of warming in North America from 1.49 °C (B1 2050s low) to 6.78°C (A2 2080s high, see Table S3.1 for the full range).

We modeled species' ranges with the BIOMOD package in R using generalized linear models, generalized boosted models, classification tree analysis, artificial neural networks, surface range envelopes, flexible discriminant analysis, multiple adaptive

regression splines, and random forests (Thuiller et al. 2012). We then used these models to make consensus forecasts for each of the projections described above, as well as current climate to evaluate the performance of the models. We tested model performance using area under the receiver operating curve (AUC), true skill statistic (TSS), and proportion correct classification (PCC, Fig. S3.1). Species and generic presences were determined across the 1° latitude-longitude grid to give presence or absence in each location at each time and SRES scenario.

Using the projections described above, we created pseudo localities, as before. From this, we created occurrence matrices as described above. We repeated this process 100 times for each projection for a total of 16,800 occurrence matrices.

3.3.3 Latitudinal turnover gradients (LTGs) and β diversity

We calculated β diversity as the change in mammalian communities across the North American landscape using multivariate dispersion and the Jaccard index for each NALMA sub-age, for modern mammals, and for the climate projections (Anderson et al. 2006). We calculated Euclidean distances from the centroid for localities using the R package vegan (Oksanen et al. 2012). Larger distances from the centroid indicate greater spatial community turnover and thus higher β diversity. We did not regress the Jaccard index values against distance, as has been used for modern species (Qian et al. 2009) because we have found such an approach to be highly influenced by species-area relationships.

To estimate ancient, modern, and projected LTG strength for North American mammals, we calculated the amount of community change with latitude using detrended correspondence analysis (DCA; an ordination technique) in the vegan R package

(Oksanen et al. 2012). We used explained variance (R^2 ; how much of the variation in community change is explained by latitude) as a measure of LTG strength (Kent et al. 2011). High values of explained variance indicate strong LTGs (Tuomisto and Ruokolainen 2006). We did not compute latitudinal richness gradients because sampling bias (e.g. loss of taxa, body mass bias) is too great (Chapter 2).

3.3.4 Sampling bias control

Although we have chosen methods that minimize the effects of sampling bias, we still used multiple methods to control for the non-independence of β diversity from the number of localities, the geographic area sampled, and the number of sampled taxa. We used three approaches. Firstly, we used a re-sampling approach wherein we sub-sampled (without replacement) each NALMA 100x using a standardized number of localities (thirty) and limited to localities occurring between 30° and 50° North latitude. We also re-sampled the extant mammal ranges under various conditions of bias (taxonomic bias through the removal of 25%, 50%, 75% of taxa and body mass bias where we removed 25%, 50%, and 75% of species with a body mass lower than 5 kg) as above to test for direct causality of sampling bias. We also used a method of detrending whereby we regressed LTG strength and β diversity against statistically significant sampling bias metrics and further analyzed the residuals from the model. Finally, we used multivariate linear models to simultaneously account for the model variance explained by sampling and biological phenomena. The last multivariate method is similar to (Benson and

Mannion 2012) and (Mannion et al. 2011) (also addressed in (Benton et al. 2011)) who combine the predictive properties of models of biodiversity change and taphonomic bias.

3.3.5 Correlation with climate

We tested for correlations of β diversity and LTG strength with stable oxygen isotopes from benthic foraminifera ($\delta^{18}\text{O}$ ‰) (Zachos et al. 2001; Zachos et al. 2008), mean annual precipitation estimated from paleosols (Retallack 2007), number of localities, sampling area (km^2), number of species, latitudinal range (degrees), and length of the sampled interval (Ma) of the fossil localities using generalized least squares and using an autocorrelation structure of order one (corAR1) to account for temporal autocorrelation in R (Development core team 2012; Dornelas et al. 2013). Best fit models were selected using automated model selection in the MuMIn R package (Bartoń 2013) and the Akaike Information Criterion (ΔAIC).

3.4 Results

Fossil mammal β diversity showed considerable variation with the warmest intervals (late Eocene, mid-late Oligocene, mid Miocene, and mid Pliocene), but showed generally higher β diversity than with cooler intervals (early Oligocene, late Miocene) (Fig. 3.1C). The best fit model includes mean annual precipitation (MAP squared), length of the NALMA subdivision, and number of taxa, which together accounts for 67% of model variance (Table 3.2). β diversity is statistically significant for all three predictors ($p < 0.05$). Residual β diversity is significantly explained by MAP only (Table 3.2; Fig. 3.2B). Re-sampling did not alleviate the effects of sampling bias; re-sampled β diversity is significantly explained by MAP-squared, number of taxa, and NALMA subdivision

length (Table 3.2). The remainder of the manuscript will discuss the results from the analyses of raw and residual β diversity only.

Mammalian latitudinal turnover gradients (LTGs) are weak prior to the late Miocene (Fig. 3.1D). Raw LTG strength (i.e. not detrended) peaks during late Miocene (Hemphillian) and late Pleistocene (Rancholabrean) (Fig. 3.1D). The best fit model includes mean annual precipitation (MAP) (Retallack 2007), number of taxa, area (km^2)

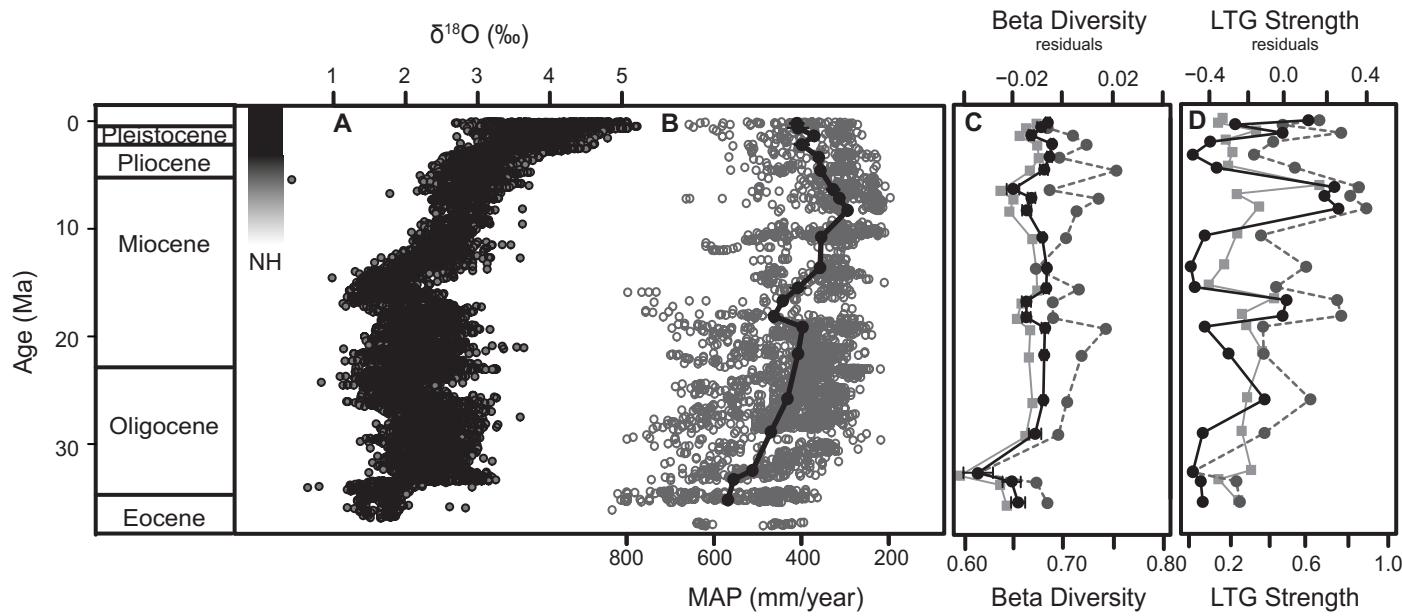


Fig. 3.1 Mid to late Cenozoic trends of (A) $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Zachos et al. 2008), (B) mean annual precipitation estimated from paleosols (Retallack, 2007), (C) β diversity of North American mammal species measured using multivariate dispersion (average distance from the centroid), and (D) strength of latitudinal turnover gradients (LTGs) measured as gradient strength for North American fossil mammals. Black lines are raw values, gray lines are residuals from significant sampling bias predictors, and gray dashed lines are re-sampled. Standard errors for re-sampled data are too small to display.

Table 3.2 Results of best fit generalized least squares models relating β diversity and latitudinal turnover gradient (LTG) strength to mean annual precipitation from paleosols (Retallack, 2007), $\delta^{18}\text{O}$ (%) from benthic forams (mm/year; Zachos et al. 2001; 2008), length of North American Land Mammal Age subdivision, number of taxa sampled, sampling area (km²), and number of fossil localities.

Dependent Variable	Parameters of Best Fit Model	Variance explained by model (%)	t value	p
Beta Diversity	Mean annual precipitation (quadratic)	66.51	-3.25	0.005
	Length of NALMA subdivision		2.43	0.027
	Number of taxa	5.30	< 0.001	
Beta Diversity Residuals	Mean annual precipitation (quadratic)	26.48	-3.50	0.002
	Mean annual precipitation (quadratic)	66.04	-2.39	0.029
	Length of NALMA subdivision		2.51	0.023
Latitudinal Turnover Gradient Strength (LTGs)	Number of taxa	5.47	< 0.001	
	Mean annual precipitation (quadratic)	46.76	-5.65	< 0.001
	Area		-4.62	< 0.001
LTG Resampled	Number of taxa		-4.36	< 0.001
	Area : Number of taxa	4.85	< 0.001	
	Mean annual precipitation (linear)	37.48	-3.79	0.001
LTG Resampled	Number of taxa	28.59	-2.55	0.020

and an interaction of area and the number of taxa, which explains 47% of the model variance (Table 3.2; Fig. 3.2C). LTG strength of late Cenozoic mammal species is statistically significantly explained by all four metrics ($p < 0.001$; Table 3.2). Residual LTG strength is significantly explained only by MAP ($p < 0.05$; Table 2; Fig. 3.2D). As above, re-sampling did not alleviate the effects of sampling bias on LTG strength (Table 3.2). In other words, even accounting for variables that describe potential sources of bias, a climatic variable (MAP) still explains a significant proportion of the variance.

β diversity is much lower for extant mammals than for extinct mammals (Fig. 3.3A). LTG strength for extant mammals is also greater than for early to mid Cenozoic fossil mammals, but similar to the values for the late Miocene and Pleistocene (Fig. 3.3B). Extant mammal β diversity shows a slight decrease under incomplete sampling and a slight increase under body-mass–bias sampling (Fig. 3.3A), but the change is much smaller than observed for fossil mammals. LTG strength does not appear to be significantly affected by the sample size reduction.

Our forecast models (which showed a strong fit to modern mammalian distributions, see Fig. S3.2A-C) show a slight increase in β diversity for extant mammals (Fig. 3.3C), but no substantial change in LTG strength compared to the present (Fig. 3.3D).

3.5 Discussion

Spatiotemporal patterns of β diversity remain poorly studied despite being potentially very useful in conservation biology (Buckley and Jetz 2008; Hassall et al. 2012; Dornelas et al. 2014) and linkage to well-studied biogeographic phenomena such as latitudinal richness gradients (Baselga et al. 2012). Using an extensive analysis of past

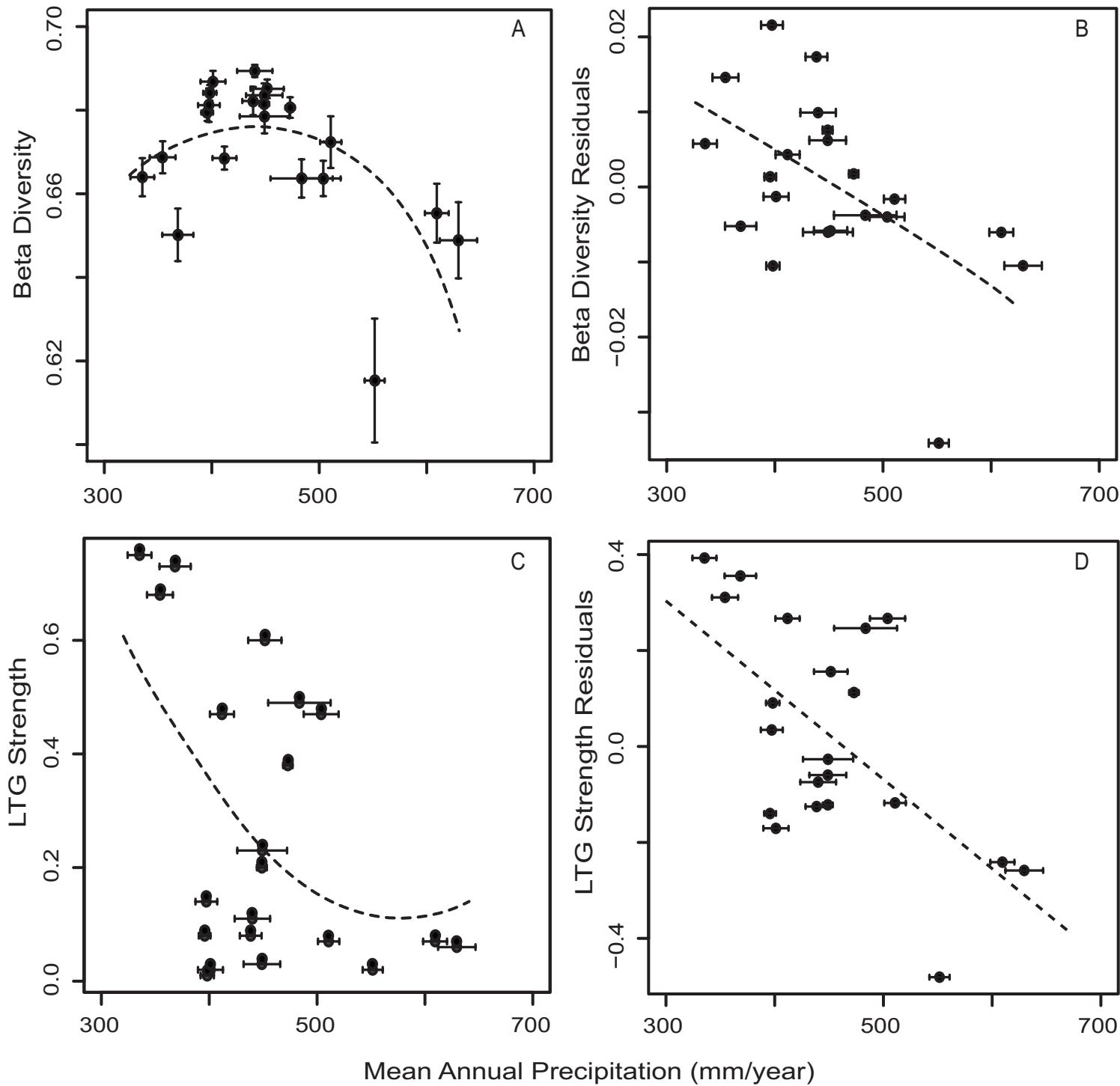


Fig. 3.2 Relationship of mean annual precipitation estimated from paleosols (Retallack, 2007) with North American fossil mammal (A) raw β diversity ($R^2 = 0.43$), (B) residual beta diversity ($R^2 = 0.26$) and (C) raw latitudinal turnover gradient (LTG) strength ($R^2 = 0.25$), and (D) residual LTG strength ($R^2 = 0.37$).

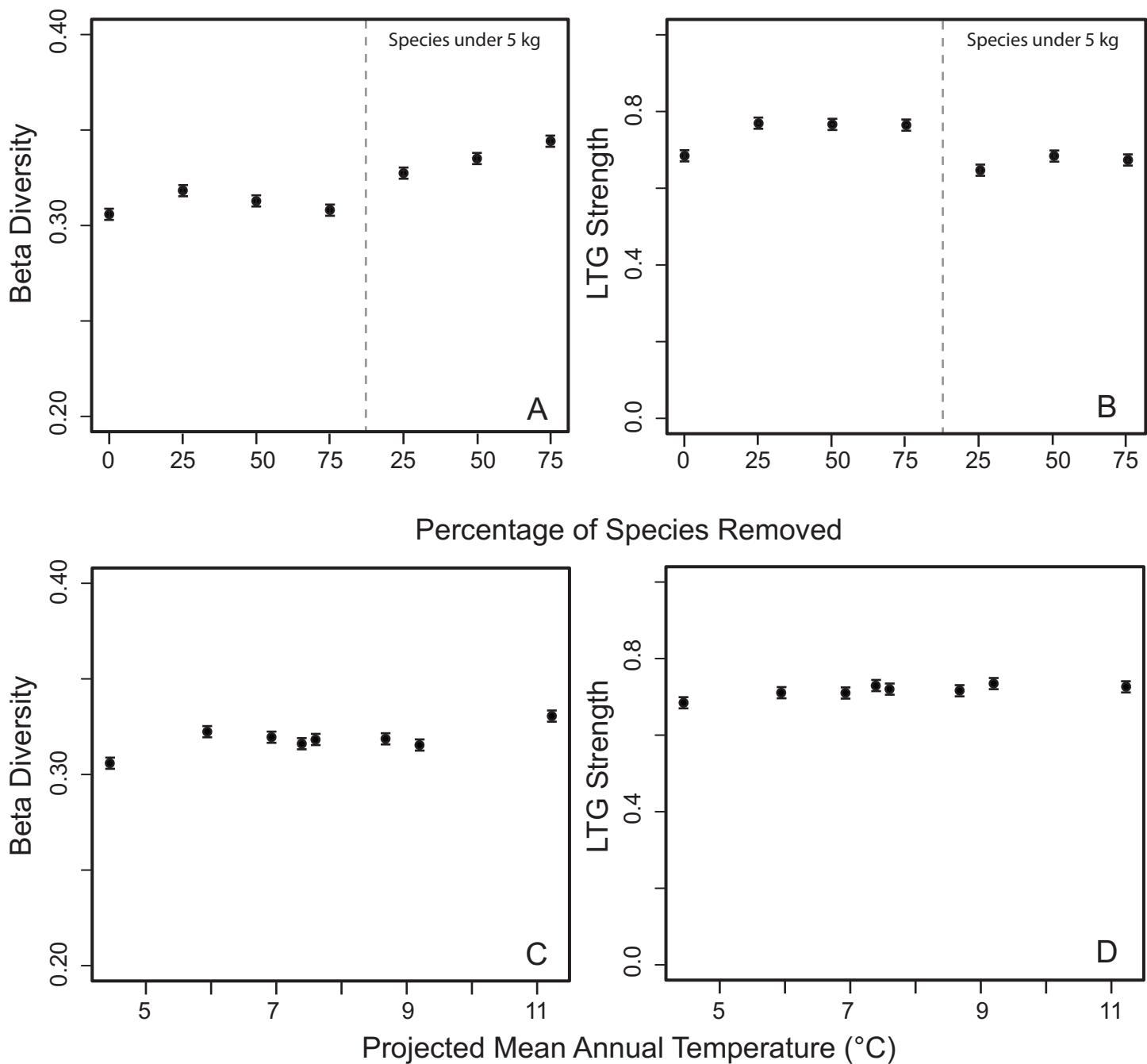


Fig. 3.3 (A) β diversity (distance from centroid) and (B) latitudinal turnover gradients (LTG) strength of extant North American mammals under incomplete taxonomic sampling (removal of 25, 50, and 75% of species in sample) and body mass bias (removal of 25, 50, 75% of species smaller than 5 kg) and (C) β diversity (distance from centroid) and (D) latitudinal turnover gradients (LTG) strength of extant North American mammals under several International Panel on Climate Change scenarios (Special Reports on Emissions Scenarios).

and present mammalian communities, we demonstrate that, over the past 36 Ma, spatiotemporal patterns of mammal community composition have varied by orders of magnitude in North America. Specifically, Cenozoic spatial turnover of mammal communities is explained by continental mean annual precipitation (MAP) (Fig. 3.2A-B), broadly supporting predictions drawn from published studies of modern terrestrial organisms (Currie 1991; Buckley and Jetz 2008; Qian et al. 2009) and our predictions outlined above.

Contemporary ecological theory predicts that mammal diversity either declines monotonically with productivity or shows a unimodal pattern, declining with both low and high productivity (VanderMeulen et al. 2001; Hawkins et al. 2003; Buckley and Jetz 2008; Qian et al. 2009). Further, stronger latitudinal diversity gradients are associated with cooler, less productive environments (Currie 1991) and steeper latitudinal climate gradients (Hawkins et al. 2003; Buckley and Jetz 2008). Both sets of predictions assume that changes in climate, productivity, and seasonality influence rates of origination and extinction (VanderMeulen et al. 2001; Weir and Schluter 2007), niche breadths (Vázquez and Stevens 2004), as well as the carrying capacity of the ecosystem (Buckley et al. 2010), all factors that change the spatial turnover of terrestrial faunas (Buckley and Jetz 2008). Specifically, terrestrial organisms in low latitude, high productivity environments show low rates of speciation and extinction (Weir and Schluter 2007), high β diversity (Qian et al. 2009; Qian and Xiao 2012), and weak or absent latitudinal diversity gradients (Currie 1991). In contrast, high latitude organisms show high rates of speciation and extinction (Weir and Schluter 2007), low β diversity (Qian et al. 2009; Qian and Xiao 2012), and strong latitudinal diversity gradients (Currie 1991). Evolutionary history also

plays a role in determining rates of spatial community turnover. Modern tropical organisms show faster turnover than their temperate counterparts regardless of the rate of environmental change (Buckley and Jetz 2008). Spatial and, by extension, temporal patterns of β diversity are the result of a mosaic of ecological and evolutionary processes.

Cenozoic fossil mammal β diversity peaked at intermediate values of mean annual precipitation and declined under both drier and wetter conditions (MAP; ~450 mm per year; Fig. 2B), showing a similar shape to latitudinal diversity curves for modern mammals (Currie 1991). Mammal β diversity was similarly lowest during periods of relative cooling, including the early Oligocene and late Miocene, coincident with declining atmospheric CO₂ (DeConto et al. 2008; Franks and Beerling 2009; Tripati et al. 2009; Zhang et al. 2013) and, in the latter case, the expansion of ice sheets in the Northern Hemisphere (Foster et al. 2009; Polyak et al. 2010), strengthening of thermohaline circulation (Haywood et al. 2001; Ballantyne et al. 2006; Ballantyne et al. 2010; Polyak et al. 2010; Foster et al. 2012; Yasuhara et al. 2012), and transition from C₃ to C₄ dominated ecosystems at middle latitudes (Retallack 2007; Strömberg and McInerney 2011; Fox et al. 2012). Declining β diversity during the late Miocene is also coincident with increased maximum body mass (Smith et al. 2010), an ecologically relevant characteristic linked to lower ecosystem energy (Blackburn et al. 1999; Freckleton et al. 2003). Water is a key component in photosynthesis and therefore net primary productivity (NPP) and MAP are correlated at a global scale, showing an asymptotic relationship (Del Grosso et al. 2008). Our results therefore suggest that putatively lower energy ecosystems (e.g. early Oligocene, late Miocene) supported more spatially homogenous mammal faunas than putatively higher energy ecosystems (e.g. late

Eocene, mid Miocene, mid Pliocene). Temporal changes in fossil mammal β diversity (this study) are therefore conceptually similar to spatial patterns observed in extant mammals.

Early Oligocene mammals had lower β diversity than expected based on MAP (Fig. 3.1C; Fig. 3.2A). The early Oligocene is associated with rapid global cooling (Zachos et al. 2008) and expansion of open grassy ecosystems (Jacobs et al. 1999), which may have resulted in lower ecosystem energy. However, our taxonomic sample is the poorest for the early Oligocene; number of taxa is a significant predictor of fossil mammal β diversity (Table 3.2), suggesting some variation in preservation of species among NALMA subdivisions. Rarefied diversity also shows little change from the late Eocene to the early Oligocene (Figueirido et al. 2012). However, our incomplete sampling trials show that removing even 75% of species reduces β diversity by a negligible amount (Fig. 3.3A), suggesting that at least some (but not all) of the observed decline in early Oligocene β diversity may have been climatically driven.

The magnitude of the latitudinal turnover gradient (LTG) for fossil mammals shows a temporally cyclic pattern that increases in amplitude during the late Cenozoic as well as a general trend toward stronger LTGs (Fig. 1D), coincident with the formation of ice on Svalbard at \sim 15 Ma and perennial Arctic sea ice at \sim 14 Ma, declining atmospheric CO₂ (Foster et al. 2012), and declining terrestrial MAP (Fig. 3.2B). Specifically, LTGs are strongest when precipitation is lowest (putatively lower productivity environments) and weakest at when precipitation is highest (putatively high productivity environments; Fig. 3.2B), similar to modern mammals that show weak or absent latitudinal diversity gradients in the tropics and strong diversity gradients at mid to high latitudes (Currie

1991). Climate gradients are steeper at mid to high latitudes in North America due to the albedo of high latitude glaciation. Northern glaciation is an important means by which solar radiation is reflected from high latitudes, resulting in cool, low productivity Arctic environments (Holland and Bitz 2003; Alexeev et al. 2005). Mammal communities are sorted along a latitudinal axis according to their climatic tolerances and the process of abiotic filtering, whereby taxa meet the limits of their environmental tolerances and are excluded from communities farther north (Soininen et al. 2007). Although late Miocene sea and land ice thickness and extent were reduced compared to the modern, increasing northern albedo and strengthening of thermohaline circulation are coincident with that strengthening of mammal LTGs during the late Miocene (25-60% stronger than for any preceding NALMA; Fig. 3.1D) (Haywood et al. 2001; Ballantyne et al. 2006; Ballantyne et al. 2010; Polyak et al. 2010; Yasuhara et al. 2012).

At first glance, the Pliocene appears to be anomalous because the magnitude of the mammalian LTG declines dramatically (60-70% reduction in the magnitude of the LTG; Fig. 3.1D). However, evidence from fossil deposits on Ellesmere Island show that approximately 3.5 Ma the Pliocene Arctic was ~14-22°C warmer than present (Ballantyne et al. 2010; Csank et al. 2011; Rybczynski et al. 2013) with an associated reduced volume of Arctic sea ice (Haywood et al. 2001; Polyak et al. 2010). Pliocene Arctic warming is similarly coincident with reduced richness gradients of marine zooplankton (Yasuhara et al. 2012). The Pliocene might therefore be the “exception” that proves the rule.

Under modern global warming, Arctic winter temperatures have increased at a greater rate than at southern latitudes (Kaplan et al. 2003). Long-term projections suggest

boosts in high latitude net primary productivity due to increasing nitrogen fertilization and increases in mean annual precipitation of 100-150 mm per year or 5-20% at middle to high latitudes (Oechel and Vourlitis 1994). From our analyses of fossil North American mammals and published studies of beta diversity (Dornelas et al. 2014), we therefore expect weakened climate gradients and thus weakened LTGs due to northward range shifting, and, in the long-term, declining β diversity under the influence of modern anthropogenic climate change. β diversity decline may be facilitated by the homogenization of communities due to any of the following (note the lack of mutual exclusivity): i) extinction of species with small geographic ranges and replacement with wide-ranging species, ii) evolution toward larger range sizes within species, and, iii) invasion by wide-ranging species even without the extinction of residents (Dornelas et al. 2014). However, our climate space models that are based on SRES scenarios corresponding to absolute mean annual temperatures of 4.4 – 11.2°C (averaged across North and South America) did not show changes in mammal LTGs or β diversity (Fig. 3.3C-D). We suggest that climate space models (CSMs) are unlikely to accurately forecast the outcomes of anthropogenic climate change for modern mammals because current CSM algorithms do not incorporate microevolutionary, macroevolutionary, or ecological processes, such as niche shifts, niche creation, and differences in dispersal abilities that are inherent in the response of animals to climate change. However, even on modern ecological timescales, rapid evolutionary changes and niche shifts have been observed in native and invasive populations (Lavergne et al. 2010), and this local adaptation complicates the prediction of range shifts. On longer timescales, taxa adapt to new climates and the processes of speciation and extinction help form new terrestrial

communities. Without the explicit inclusion of evolutionary parameters and historical data for the taxa of interest, we are unlikely to accurately predict long-term changes in terrestrial biodiversity patterns.

We have shown here that macroecological patterns of North American mammal community composition varied considerably over the past 35 million years in response to changes in global climate change and Arctic glaciation (Fig. 3.1C-D). Furthermore, our comparison of fossil evidence with climate-space forecast models (CSMs) suggests that CSMs (in which species are modeled to simply track climate variables) may distort the degree of community composition change we should expect in the future. A unifying ecological theory relating diversity to climate must address both the spatial and temporal dimensions of diversity, as well as both richness and community composition. However, studies of organismal richness are far more common than studies of community composition (β diversity), despite the importance of the latter in conservation and their vast potential for contributing to our understanding of the processes underlying modern biodiversity. Studying the community composition of fossil animals represents a new frontier in paleontological research with potential to truly inform modern conservation.

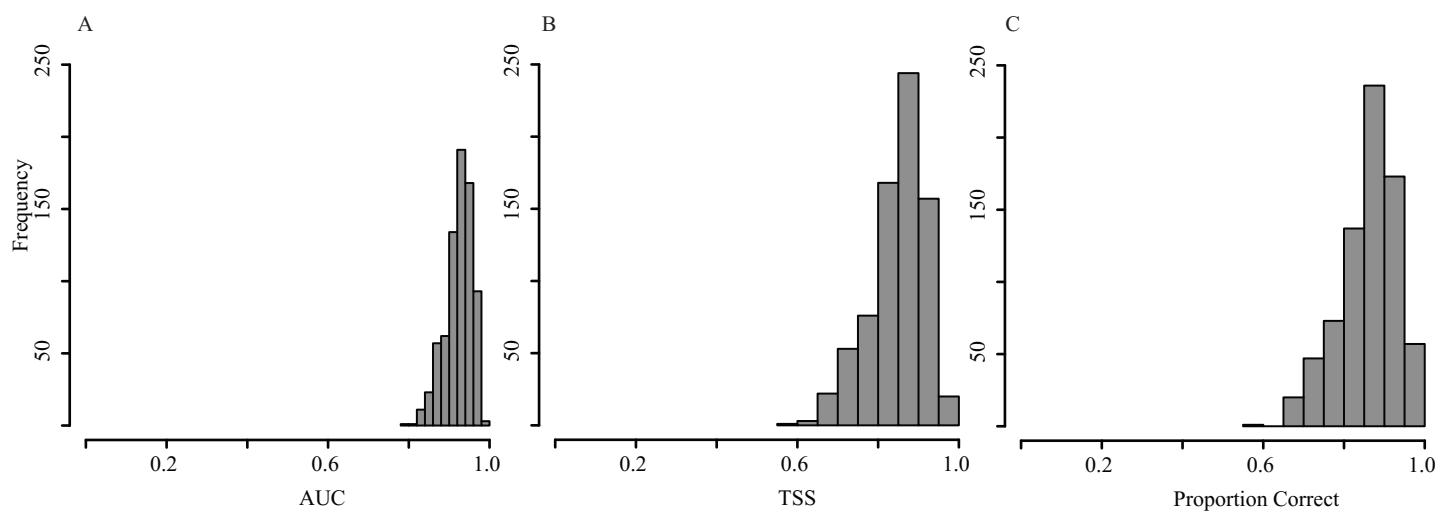


Fig. S3.1 Model fit statistics for climate space models of extant North American mammals. Model performance was tested using area under the operating curve (A; AUC), the true skill statistics (B; TSS), and the proportion of correct classification (C).

Table S3.1. Summary of Special Emissions Report Scenarios (SERs) to which we fit climate models for extant mammalian species.

Scenario	year	Mean Annual Temperature (°C)	Standard Deviation	Standard Error
	Present	4.447	15.850	0.057
B1_low	2050s	5.941	15.540	0.056
B1	2050s	6.926	15.420	0.056
A1b	2050s	7.602	15.336	0.056
A2	2050s	8.674	15.163	0.055
A1b	2080s	7.390	15.444	0.056
A2	2080s	9.196	15.198	0.055
A2_top	2080s	11.225	14.721	0.053

4 Chapter: Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals

4.1 Abstract

Animal richness, community composition, and phylogenetic community structure (PCS) vary across the modern landscape. Animal communities vary from phylogenetically clustered (i.e. higher relatedness amongst co-occurring species than is expected by chance) to phylogenetically even (i.e. co-occurring taxa are more distantly related than expected by chance), which is explained by abiotic or climatic filtering and competitive exclusion, respectively. Under this model, the contribution of historical origination and extinction events to modern animal PCS remain relatively unknown. Because origination and extinction determine the makeup of the terrestrial community, the study of historical changes in animal PCS is tantamount to understanding formation of modern communities. We test the effects of macroevolution and climate changes on “hoofed mammal” (i.e. perissodactyl and artiodactyl) PCS from the late Cenozoic of North America because they experience large, phylogenetically dispersed extinctions of browsing species and phylogenetically dispersed originations of grazing species associated with the evolution of grassland ecosystems during the late Miocene. We show that the loss of numerically dominant non-hypsodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale that is well explained by global climate changes. Phylogenetic

evenness and reduced richness during the late Cenozoic may have facilitated reduced niche overlap among co-occurring hoofed mammal species as global climates cooled.

4.2 **Introduction**

The richness and composition of modern animal communities changes vastly across space, a phenomenon that is attributed to geographic variation in climate and topography (Rosenzweig 1995). Spatial diversity patterns are also associated with changes in phylogenetic composition of communities; animal communities vary across the landscape in the degree of relatedness among species (Buckley and Jetz 2008; Qian et al. 2013). Studying the phylogenetic structure of modern communities is revealing the proximate factors driving geographic diversity patterns (Hardy and Senterre 2007; Kraft et al. 2007; Emerson and Gillespie 2008; Vamosi et al. 2009; Swenson et al. 2012). Most studies of modern phylogenetic community structure (PCS) invoke contemporary drivers such as abiotic or climatic filtering and competition (Vamosi et al. 2009) to the exclusion of historical macroevolutionary events. Understanding the contribution of macroevolution and historical factors to community assembly is required for testing hypotheses on the formation of modern communities. Studying trends in PCS through time using the fossil record might reveal the effects of macroevolutionary processes on PCS, as well as the role of long-term climate changes in the formation of modern communities.

Modern species assemblages are comprised of populations of species drawn from the regional source pool, i.e. from the entire complement of species in a region. The identity and relatedness of species in a local assemblage are determined by a variety of factors, including but not limited to abiotic filtering, dispersal, and competition (Webb et

al. 2002; Kraft et al. 2007; Emerson and Gillespie 2008). Abiotic filtering is a process whereby species with different environmental tolerances are filtered out of terrestrial communities along environmental gradients (Swenson et al. 2012). Assuming niche conservatism (closely related species share similar niches), low rates of dispersal and abiotic filtering are associated with high phylogenetic relatedness among species or phylogenetic clustering. Conversely, competitive exclusion and high rates of dispersal can lead to phylogenetic evenness or species being less phylogenetically related than expected by chance (Cavender-Bares et al. 2004; Losos 2008). Thus, local species assemblages occupy a point on a spectrum between phylogenetically clustered and even. Note that myriad conditions such as low rates of phylogenetic niche conservatism and trait convergence can result in communities that show every condition from phylogenetic evenness to phylogenetic clustering (Cavender-Bares et al. 2004; Kraft et al. 2007). However, the theoretical framework outlined above generally excludes the fossil record and thus excludes the contribution of historical factors such as extinction events.

On long time scales of thousands to millions of years, origination and extinction are two of the dominant processes driving changes in organismal diversity (Benton and Pearson 2001; Blois and Hadly 2009; Dobrovolski et al. 2012; Mayhew et al. 2012; Price et al. 2012). The composition of regional species pools and local assemblages through time are likely dependent upon numerous factors, including history of clades (e.g. species composition in preceding time intervals), patterns of origination and extinction across the phylogenetic tree (e.g. whether they are phylogenetically clumped or dispersed), climate, and tectonic changes. Whether extinction and origination are phylogenetically clumped or dispersed will largely depend on the distribution of ecologically relevant traits across

the phylogenetic tree (i.e. whether those traits are conserved or convergent) (Green et al. 2011). Thus both phylogenetically clumped and dispersed patterns of extinction and origination can result from abiotic filtering (Janis et al. 2000; Janis et al. 2004; Barnosky 2005; Green et al. 2011; Figueirido et al. 2012). However, phylogenetically dispersed extinction should result in a trend of increasing phylogenetic evenness through time as the average phylogenetic distance among surviving taxa increases. Conversely, if extinction is phylogenetically clumped, there should be a trend of increasing phylogenetic clustering through time as the average phylogenetic distance between surviving taxa decreases. The effects of origination on PCS are more complex because they change throughout the history of a clade. For example, under an adaptive radiation model, early in the evolutionary history of a clade, the appearance of new species should result in increasing phylogenetic evenness as new branches are added to the phylogenetic tree. Later in the history of a clade, origination of new species within well-established genera (i.e. adding new “leaves” to the tree) should result in increasing phylogenetic clustering. Through time, local assemblages might mirror the changes in the regional species pool (i.e. follow the same trajectory) or show a different temporal trajectory related to more proximate drivers such as spatial abiotic filtering, dispersal, and competition. Comparison of phylogenetic community structure at regional and local scales might therefore reveal the extent to which local assemblages are influenced by macroevolutionary processes and changes in the regional species pool through time.

Over geological time, the diversity and composition of animal communities has changed dramatically, especially during the transition from the warm equitable climates of the early and mid Cenozoic to the cool temperate climates of the late Cenozoic (Alroy

et al. 2000; Janis et al. 2000; Janis et al. 2004; Mayhew et al. 2008; Mayhew et al. 2012; Fraser et al. 2014a). Therefore, the phylogenetic structure of regional species pools and local species assemblages has likely also been temporally variable. Evolution of late Cenozoic (Miocene through Pleistocene) North American ungulates is marked by a decline in richness, particularly of browsers (feeding on parts of woody plants, not herbaceous plants), associated with the expansion of open grassland habitats (Janis et al. 2000; Fox and Koch 2004; Janis et al. 2004; Fraser and Theodor 2013). Further, ecologically relevant traits such as tooth crown height and body size show significant changes among North American hoofed mammals as ecosystems shifted away from woodland savannahs and primary productivity consequently declined (Janis et al. 2000; Janis et al. 2004; Smith et al. 2010). In this study, we tested for effects of late Cenozoic (15 – 0.01 Ma) extinction and global climate changes on North American “ungulate” PCS at the regional and local-scales.

4.3 Materials and Methods

We downloaded fossil occurrence data for the Miocene, Pliocene, and Pleistocene, which we partitioned by subdivisions of the North American Land Mammal Ages (NALMAs; Table S4.1) because they delineate relatively stable community assemblages. The dates for all NALMA subdivisions are based on Woodburne (2004). Fossil ungulate (Perissodactyla and Artiodactyla) occurrence data for the Pliocene, and Pleistocene were downloaded from the Paleobiology Database (<http://paleodb.org/>) in July and August 2012, using the group name 'mammalia' and the following parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial. Miocene ungulate occurrence data were downloaded from the Miocene Mammal

Mapping Project (Carrasco et al. 2005) in March 2011 using the NALMA subdivision as our search criterion. We then created taxon-by-NALMA subdivision occurrence matrices for perissodactyls and artiodactyls separately at the species level (Davis 2005; Atwater and Davis 2011). We removed all taxa that had equivocal species identifications (e.g. *Equus* sp.) unless they were the only occurrence for a genus. We assumed all occurrences of open nomenclature (e.g. *Equus* cf. *simplicidens*) were correct identifications.

We created composite phylogenies for fossil artiodactyls and perissodactyls primarily using Janis et al. (1998) and Maguire and Stigall (2009). The backbone of the artiodactyl phylogeny is based on Price et al. (2005). For comparison, we created two composite phylogenies each for the artiodactyls and perissodactyls, one better resolved tree based on published hypotheses (Fig. S4.1A-B) and one poorly resolved tree (Fig. S4.2A-B) where we assumed nothing about inter- and intra-generic relationships. For both sets of composite trees, we used taxonomy as a guide (i.e. we assumed species from the same genus were sister taxa with notable exceptions such as *Merychippus*, which is a known polyphyletic genus). Although fossil phylogenies inevitably include many polytomies, they are not problematic (Finarelli, 2010; Raia et al. 2010). As such, our composite phylogenies may contain as of yet unknown polyphyletic genera but reflect the current state of knowledge. Further, all equivocal interfamilial and inter-generic relationships were represented by polytomies, and species that we could not place phylogenetically were removed from the analysis. We created a third set of composite phylogenies for the artiodactyls from which we excluded the Bovidae and Cervidae, which are comprised of Eurasian immigrants. We used first and last occurrences of perissodactyl and artiodactyl taxa from the taxonomic range tool on the Paleobiology

database with North American Land Mammal Ages (NALMA) as our time model and default settings to create dated composite phylogenies using the paleotree R package (Bapst 2012).

We calculated the Net Relatedness Index (NRI), which is a standardized measure of mean pairwise phylogenetic distance among co-occurring species, using the picante R package (Webb 2000; Webb et al. 2002; Kembel et al. 2014). Positive values of NRI indicate that species in an assemblage (i.e. species that co-occur within a specific NALMA) are more closely related than expected by chance. Negative values of NRI indicate that species in an assemblage are more distantly related than expected by chance. NRI values of zero indicate phylogenetic randomness (Webb 2000; Webb et al. 2002; Raia 2010). We calculated NRI for each NALMA subdivision considered in this study (Table S4.1) at both the regional and locality scales. At the regional scale, we used the entire phylogeny (i.e. the total diversity of North American perissodactyls and artiodactyls) as the source pool from which communities (i.e. assemblages of species present in each NALMA subdivision) were drawn (Raia 2010). At the locality scale, we calculated the average NRI for all localities within each NALMA subdivision (i.e. assemblages of species present at each locality in each NALMA subdivision). Critically, we used a time slicing approach when analyzing locality scale NRI using the paleotree R package (Bapst 2012). The time slice approach involves shortening the branch lengths to the youngest boundary for each NALMA subdivision in order to preclude overestimation

of phylogenetic distance and thus to exclude species with temporal ranges outside the selected time interval.

To evaluate the relationship between dietary traits and extinction, we used stochastic character mapping to visualize the distribution of tooth crown traits (hypodont, mesodont, submesodont, and brachydont) across the artiodactyl and perissodactyl composite phylogenies (Huelsenbeck et al., 2003; Paradis et al., 2004; Bollback, 2006; Revell, 2011). We assigned tooth crown types to fossil taxa using published sources (Janis, Damuth, & Theodor, 2004; Mihlbachler et al., 2011). Where tooth crown types were unknown, we assumed similarity within genera. However, taxa for which tooth crown type is equivocal were excluded.

We tested for significant temporal trends in artiodactyl and perissodactyl NRI by regressing NRI against the midpoint age of each NALMA subdivision using generalized least squares (gls) regression in R (Development core team 2012; Dornelas et al. 2013). We also tested for a climatic filter by regressing NRI for both groups of hoofed mammals against stable oxygen isotopes from benthic foraminifera ($\delta^{18}\text{O}$ ‰) (Zachos et al. 2008), atmospheric carbon dioxide (CO₂; Zhang et al. 2013), and mean annual precipitation estimated from paleosols (inferred from degree of weathering and depth of carbonate nodules; Retallack, 2007) using the gls approach. We also included several proxies for sampling bias in our gls models, including number of localities, number of species, and length of the sampled interval (Ma) of the fossil localities. Number of localities broadly correlates with amount of available rock record and sampling effort. Similarly, number of species accounts for sampling effort but may also represent true changes in richness (Benton et al., 2011). The length of NALMA subdivisions is a metric for the amount of

time averaging in each sample; sample species richness should tend to increase with higher time averaging. Best fit models were selected using an information theoretic approach in the MuMIn R package (Bartoń 2013), which is superior to the commonly employed step-wise regression approach (Whittingham et al. 2006). Further, the multivariate approach used here allows for the combination of climate proxies and taphonomic biases into a single model, thereby partitioning their explanatory power (Mannion et al. 2011; Benson and Mannion 2012; Dornelas et al. 2013). We did not use de-trending methods such as first differences or extraction of residuals, because the gls method simultaneously deals with both temporal autocorrelation and bias.

4.4 Results

Both artiodactyls and perissodactyls show phylogenetically dispersed extinction and origination through time (Fig. S4.1A-B; Fig. S4.2A-B). Both clades also show dietary trait convergence (Fig. S4.3A-B). Further, our composite phylogenies reflect declining browser (black) and mixed feeder (green and blue) diversity through time, in agreement with Janis et al. (2000; 2004) (Fig. S4.3A-B).

At the regional scale, both artiodactyls and perissodactyls show significant increases in phylogenetic evenness or decreases in the Net Relatedness Index (NRI) through time when using both poorly resolved and better resolved composite phylogenies (Fig. 4.1B; Fig. S4.4B; Table 4.1). Artiodactyl NRI shows a significant correlation with $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Fig. 4.2A-B; Table 4.2). Perissodactyl NRI is best

fit by models of North American Land Mammal Age (NALMA) length and $\delta^{18}\text{O}$ (‰) from foraminifera (Fig. 4.2C-D; Table 4.2).

Locality-scale NRI also shows a significant increase in phylogenetic evenness through time for artiodactyls (Fig. 4.1C; Table 4.1), but shows strong dependence on the number of taxa in the sample when using both composite phylogenies (Table 4.2). Perissodactyl locality-scale NRI varies between phylogenetically even and clumped

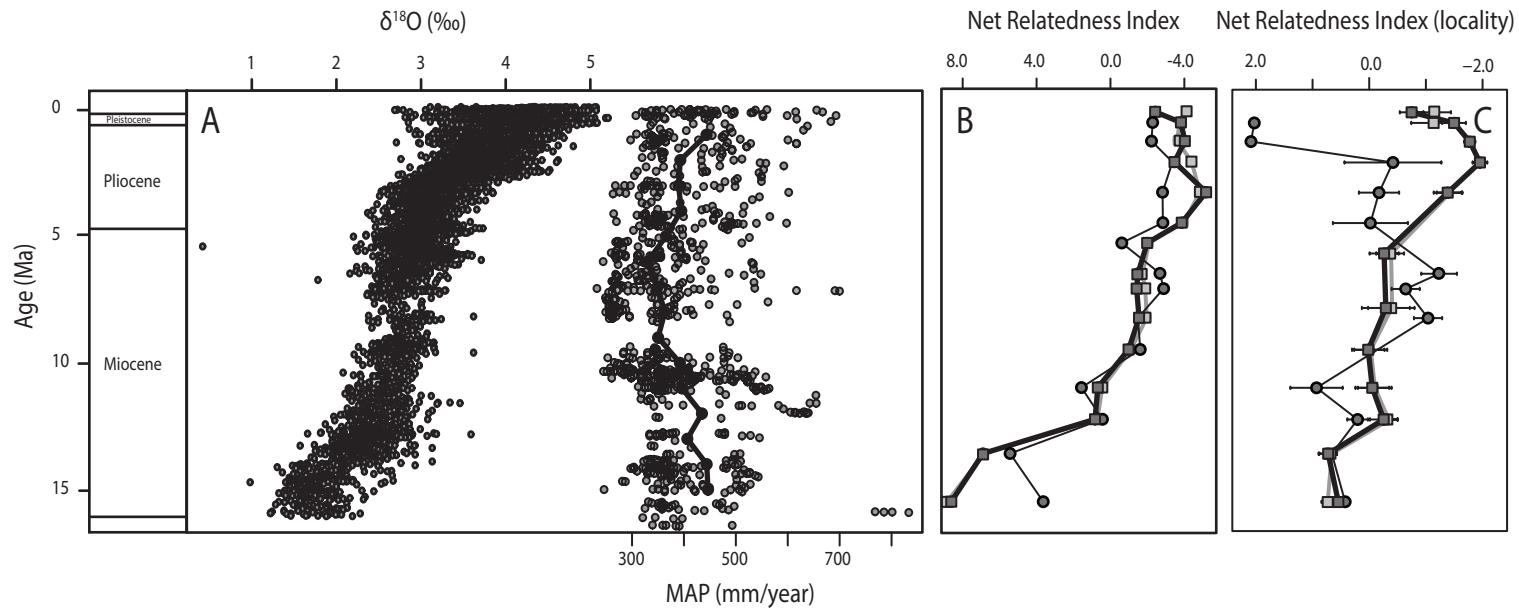


Fig. 4.1 Relationships of artiodactyl (squares; black with immigrants and gray without immigrants) and perissodactyl (circles) PCS (NRI) with (A) $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Zachos et al., 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the well resolved artiodactyl and perissodactyl phylogenies. PCS = phylogenetic community structure; NRI = net relatedness index.

Table 4.1. Generalized least squares regression of phylogenetic community structure against North American Land Mammal Age subdivision midpoint age.

Order	Dependent Variable	t value	p value
Artiodactyla	Net Relatedness Index (resolved)	4.98	< 0.001
	Net Relatedness Index (unresolved)	2.63	0.020
	Net Relatedness Index without immigrants (resolved)	3.60	0.003
	Net Relatedness Index without immigrants (unresolved)	3.38	0.005
	NRI local scale (resolved)	3.29	0.008
	NRI local scale (unresolved)	3.23	0.009
	NRI local scale without immigrants (resolved)	5.50	< 0.001
	NRI local scale without immigrants (unresolved)	7.29	< 0.001
	Net Relatedness Index (resolved)	4.06	0.001
	Net Relatedness Index (unresolved)	4.23	0.001
Perissodactyla	NRI local scale (resolved)	-0.59	0.570
	NRI local scale (unresolved)	-0.35	0.730

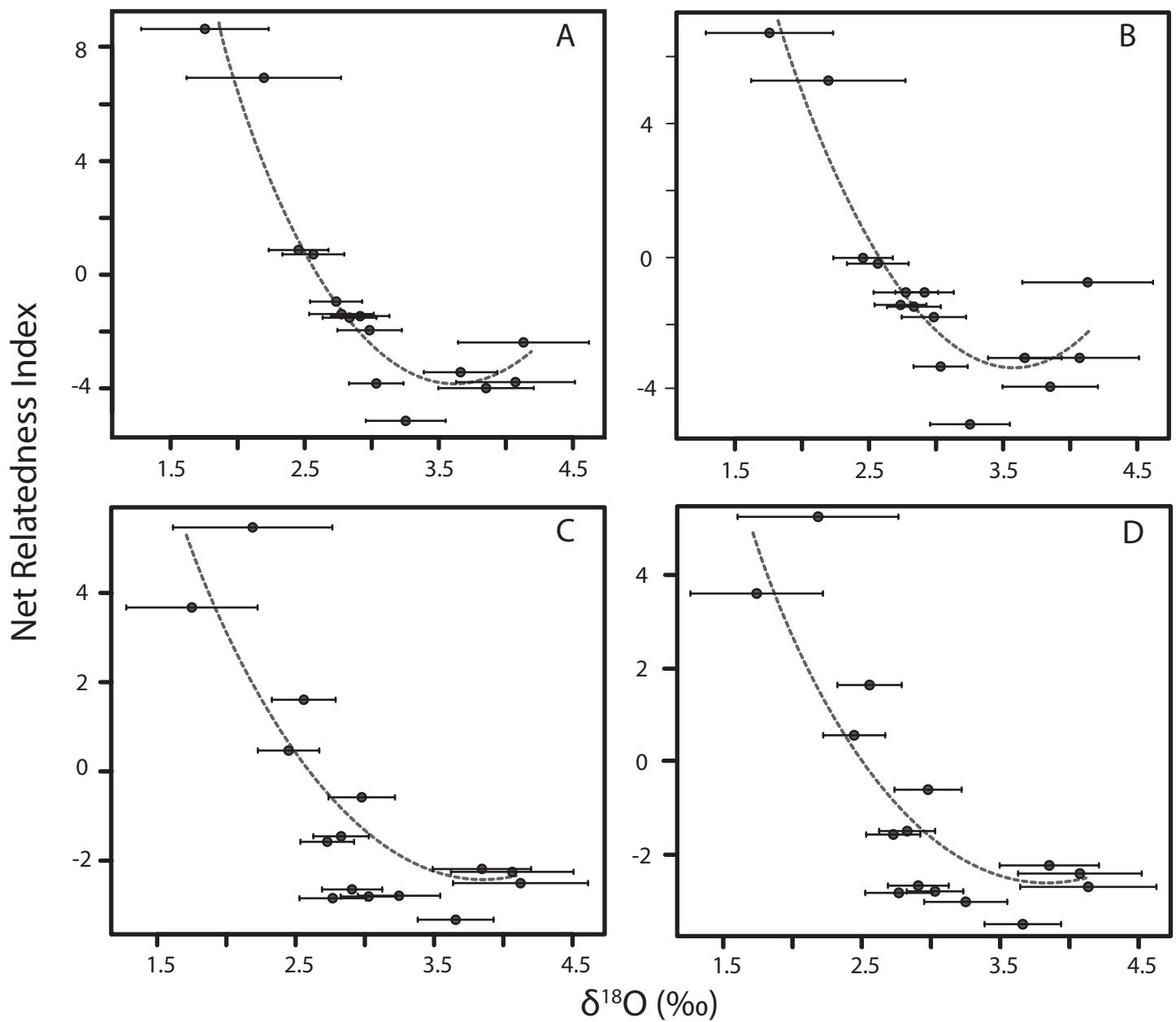


Fig. 4.2 Relationship of $\delta^{18}\text{O}$ (‰) from benthic foraminifera with (A) artiodactyl regional PCS (NRI) calculated from the resolved, (B) un-resolved composite phylogeny, (C) perissodactyl regional NRI calculated from the resolved, and (D) un-resolved composite phylogeny. PCS = phylogenetic community structure; NRI = net relatedness index.

Table 4.2 Results of best fit generalized linear models relating phylogenetic community structure to mean annual precipitation (MAP) from paleosols (Retallack, 2007), $\delta^{18}\text{O}$ (‰) from benthic forams (mm/year; Zachos et al. 2008), length of North American Land Mammal Age subdivision, number of taxa sampled, and number of fossil localities.

Order	Dependent Variable	Best Fitted Model	Pseudo R ²	Independent Variable	t value	p value
Artiodactyla	Net Relatedness Index (resolved)	$\delta^{18}\text{O}$ (‰) (polynomial)	0.93	$\delta^{18}\text{O}^2$ $\delta^{18}\text{O}$	6.11 -7.43	< 0.001 < 0.001
	Net Relatedness Index (unresolved)	δO (‰) (polynomial)	0.88	$\delta^{18}\text{O}^2$ $\delta^{18}\text{O}$	4.99 -6.02	< 0.001 < 0.001
NRI local scale (resolved)	Number of taxa	0.43	-	-	3.33	0.008
NRI local scale (unresolved)	Number of taxa	0.51	-	-	3.23	0.009
Perissodactyla	Net Relatedness Index (resolved)	δO (‰) (polynomial), Length of NALMA subdivision	0.88	$\delta^{18}\text{O}^2$ $\delta^{18}\text{O}$	3.57 -4.18	0.002 0.004
	Net Relatedness Index (unresolved)	δO (‰) (polynomial), Length of NALMA subdivision	0.87	Length of NALMA	4.53	0.001
NRI local scale (resolved)	Null	-	Intercept	0.68	0.51	
NRI local scale (unresolved)	Null	-	Intercept	2.21	0.049	

(Fig. 4.1C). There were no significant regression coefficients for perissodactyl locality-scale NRI (Table 4.1; Table 4.2).

At the regional and local scales, artiodactyls still show increasing phylogenetic evenness through time after the removal immigrant taxa; with and without immigrant taxa artiodactyl PCS show a nearly identical trend (Fig. 4.1B; Fig. S4.4B). We have not further analyzed these data due to model non-convergence, but are confident that our interpretations will be unaffected.

4.5 Discussion

Neontological studies of phylogenetic community structure (PCS) often invoke the proximate processes of abiotic filtering and competition to explain phylogenetic clustering and evenness, respectively (Webb 2000; Losos 2008; Vamosi et al. 2009). However, there has been limited focus on how historical events have influenced the PCS of modern communities, even though macroevolutionary events determine the number and identity of taxa in regional source pools from which local assemblages are drawn (McPeek 2008). We therefore specifically test for the effects of North American “ungulate” macroevolution on PCS because ungulate extinction rates are high after the warm mid Miocene climatic optimum (Janis et al. 2000; Janis et al. 2004).

At the regional scale, assemblages of species emerge from the cumulative effects of origination, extinction, immigration, and emigration (McPeek 2008). Thus, climatic filtering, insofar as climate influences patterns and rates of extinction and origination (Mayhew et al. 2008), are more likely to explain long-term temporal changes in the regional pool than competition. We made two predictions about the PCS of regional species pools based on the distribution of extinction events throughout the phylogenetic

tree, i) phylogenetically dispersed extinction and origination should result in a trend toward phylogenetic evenness and ii) phylogenetically clumped extinction and origination should lead to increased phylogenetic clustering through time. We also suggest that iii) local assemblages might follow the same trajectory as the regional species pool if they are drawn at random from the regional pool or, alternatively, that changes in local assemblages might diverge from the regional pattern due to other proximate mechanisms (e.g. abiotic filtering, dispersal, competition).

The evolution of late Cenozoic North American ungulates is typified by both a dramatic decline in richness and a dramatic loss of browsing species (i.e. woody plant specialists) within both the artiodactyl and perissodactyl clades (Janis et al. 2000; Janis et al. 2004). Large, dominant clades of browsers were replaced by comparatively depauperate faunas comprised primarily of larger bodied grazers and mixed feeders (Janis et al. 2004). One of the drivers of declining browser richness may have been the mid latitude transition from productive woodland savannah during the mid Miocene to grassland savannah from the latest Miocene through the Pliocene that was facilitated by climatic cooling and declining atmospheric CO₂ (Jacobs et al. 1999; Janis et al. 2000; Janis et al. 2004; McInerney et al. 2011; Strömberg and McInerney 2011; Fox et al. 2012; Fraser and Theodor 2013; Zhang et al. 2013). We showed that, contemporaneous with declining browser richness, regional ungulate PCS increased in phylogenetic evenness through time (Fig. 4.1B). At the regional scale, artiodactyls and perissodactyls show significant decreases in the Net Relatedness Index (NRI) when using the poorly resolved and better resolved phylogenies (Table 4.1; Fig. 4.1B). Declining ungulate NRI is well explained by changes in global temperatures ($\delta^{18}\text{O}$ from benthic foraminifera) (Fig. 4.2A-

D; Table 4.2). However, perissodactyl NRI does show dependence on the length of the North American Land Mammal Age (NALMA) subdivision (Table 4.2), which might reflect a lack of precision in first and last occurrence dates used to timescale the composite phylogeny; some first and last occurrences correspond to NALMA boundaries in the absence of chemical dating.

Among North American ungulates, increased tooth crown height (i.e. hypsodonty) or a tendency toward open habitat living and consumption of herbaceous plants has evolved multiple times (Fig. S4.3A-B), i.e. feeding specialization is phylogenetically dispersed. We show that the loss of numerically dominant non-hypsodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale. Strong correlation with global climate proxies ($\delta^{18}\text{O}$ from benthic foraminifera and mean annual precipitation; Table 4.2; Fig. 4.2A-D) is likely indirectly driven by the effects of declining global temperatures and possibly declining atmospheric CO₂ on the evolution of grassland ecosystems (Zachos et al. 2001; Zachos et al. 2008), consistent with the proposition of Janis et al. (2000; 2004). Our analysis therefore adds a phylogenetic component to the findings of Janis et al. (2000; 2004), revealing that loss of diversity during the late Miocene resulted in phylogenetic evenness and probably reduced niche overlap, as they had suggested.

At the local scale, trends in artiodactyl and perissodactyl phylogenetic community structures are divergent (Fig. 4.1C). Artiodactyl PCS shows a similar, albeit damped, increase in phylogenetic evenness as at the regional scale (Table 4.1; Fig. 4.1C), suggesting that local assemblages are partly reflecting macroevolutionary dynamics

rather than other proximate processes, e.g. competition and dispersal limitation (Raia et al. 2012), at least at this scale of analysis. However, local artiodactyl PCS is not well explained by global climate ($\delta^{18}\text{O}$ from benthic foraminifera) (Table 4.2), but rather by the number of taxa in the sample. Artiodactyl local-scale PCS might therefore reflect the combined effects of phylogenetically dispersed extinctions and originations as well as sampling effort. Even with the possible influence of sampling bias, our result is significant because we show that the extinctions noted by Janis et al. (2000; 2004) resulted in larger phylogenetic distances amongst surviving species, lending circumstantial support to their model of reduced niche overlap among late Cenozoic ungulates.

Perissodactyl locality-scale PCS shows a contrasting pattern to the regional-scale, cycling between phylogenetic clustering and evenness throughout the late Cenozoic (Fig. 4.1C). There are two periods of large PCS changes among late Cenozoic perissodactyls: late Miocene and late Pliocene (Fig. 4.1C; Fig. S4.4C; circles). The late Miocene increase in phylogenetic evenness (i.e. decrease in NRI) is coincident with the loss of small-bodied, non-grazing species from within *Merychippus*, *Archaeohippus*, and *Hypohippus* (Fig. S4.3B) associated with the opening of grassland ecosystems and loss of woodland savannah in North America (Janis et al. 2000; Janis et al. 2004). The late Pliocene increase in phylogenetic clustering is coincident with a loss of most perissodactyl diversity in North America with the exception of a few grazing equid genera including *Equus* and *Nannippus* as well as *Tapirus* (Fig. S4.3B). Changes in perissodactyl locality-scale PCS therefore appear to have resulted from stepped extinction and origination events that were coincident with the closure of the Panama seaway, with consequent

changes in the distribution of oceanic heat, declining atmospheric CO₂ and the intensification of Northern Hemispheric glaciation (Zachos et al. 2001; Ballantyne et al. 2006; Zachos et al. 2008; Ballantyne et al. 2010; Csank et al. 2011; Zhang et al. 2013).

4.5.1 Conclusions

The role of macroevolution in shaping the phylogenetic structure of animal communities is poorly known. We show that North American perissodactyl and artiodactyl communities increased in phylogenetic evenness at the regional scale, coincident with large extinctions of woody dicot specialists or browsers and their replacement by depauperate faunas of grazers and mixed feeders following the mid Miocene climatic optimum. We suggest that the phylogenetic community structure of both clades reflects the loss of speciose non-grazing clades due to climatic filtering resulting from global cooling trends and the encroachment of grasslands during the late Cenozoic of North America. Artiodactyl phylogenetic community structure following the mid Miocene climatic optimum is also explained by phylogenetically dispersed origination of large bodied, grazing species. Patterns of perrissodactyl community structure diverge, particularly at the locality scale, because origination is confined primarily to *Equus* during the late Cenozoic. Our results lend further support to studies of North American hoofed mammal richness, showing the effects of climatic filtering on ungulate phylogenetic community structure in North America.

Table S4.1 Summary of North American Land Mammal Age subdivisions and associated sample sizes.

Epoch	NALMA Subdivision	Midpoint age	Artiodactyl taxa	Perissodactyl taxa
Miocene	Early Barstovian	15.50	67	42
	Late Barstovian	13.60	55	50
	Early Clarendonian	12.25	15	24
	Middle Clarendonian	11.00	20	18
	Late Clarendonian	9.50	8	17
	Early early Hemphillian	8.25	22	22
	Late early Hemphillian	7.10	26	30
	Early late Hemphillian	6.50	11	13
	Late late Hemphillian	5.30	9	6
Pliocene	Blancan I	4.50	16	15
	Blancan III	3.30	28	16
	Blancan V	2.11	27	16
	Irvingtonian I	1.29	14	13
	Irvingtonian II	0.55	32	17
Pleistocene	Rancholabrean	0.13	38	18

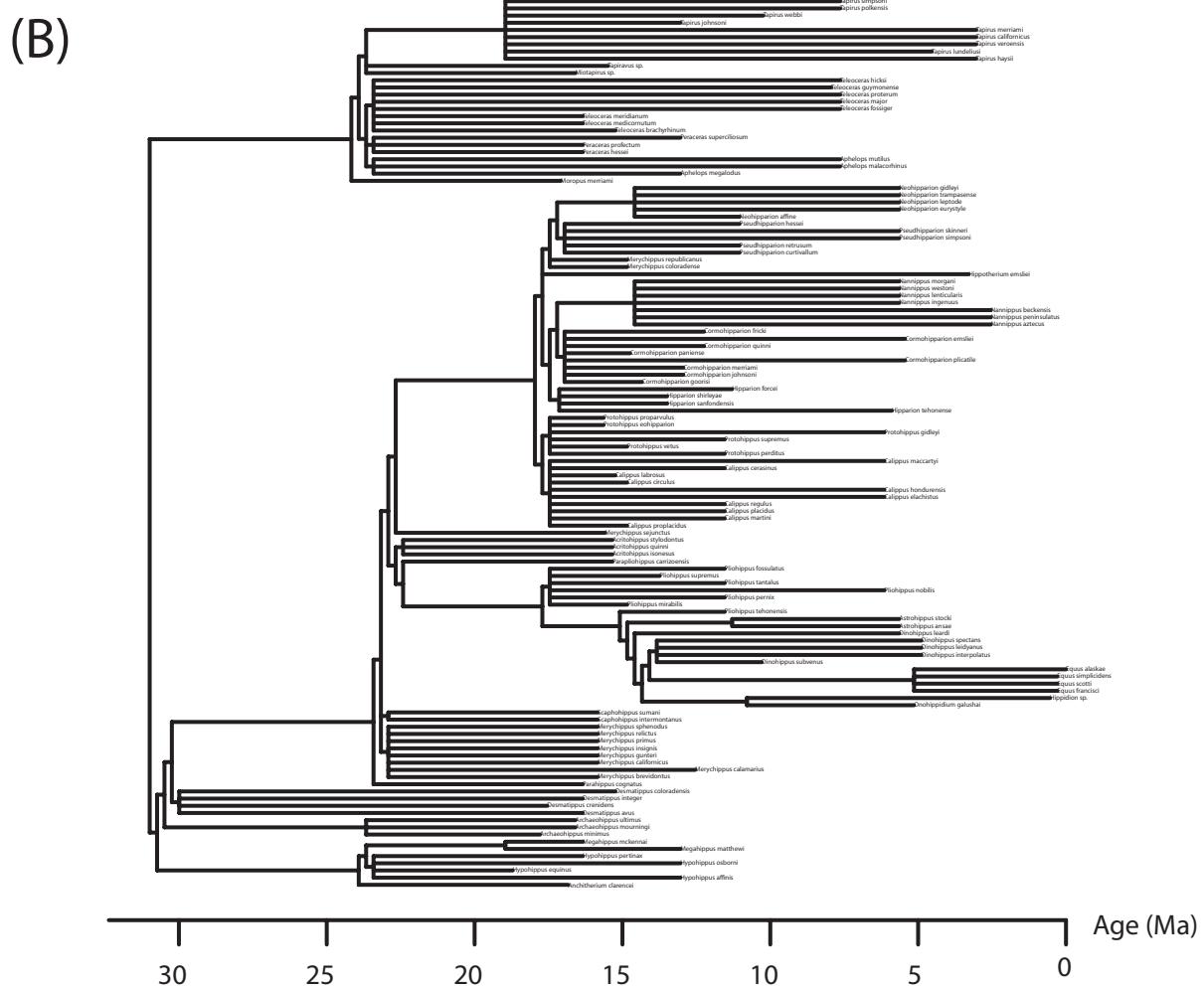
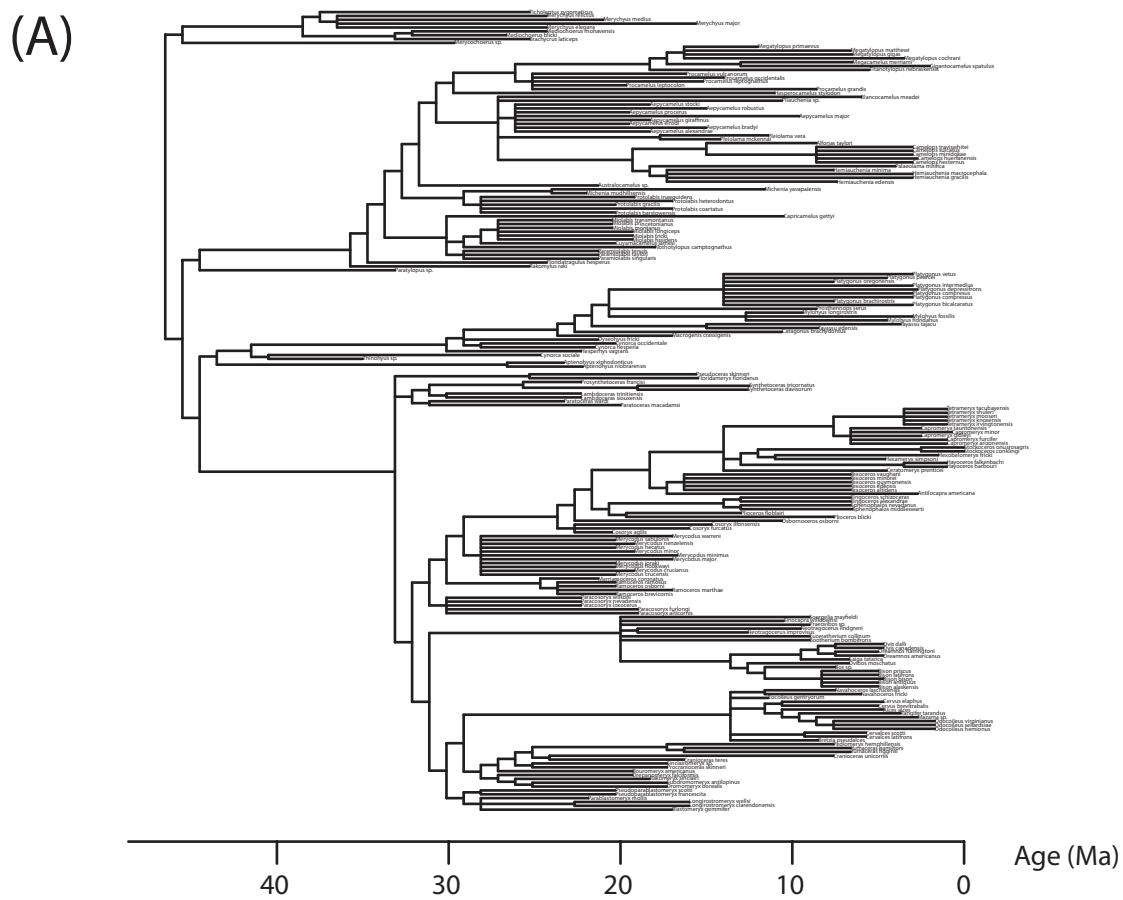


Fig. S4.1 Well-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

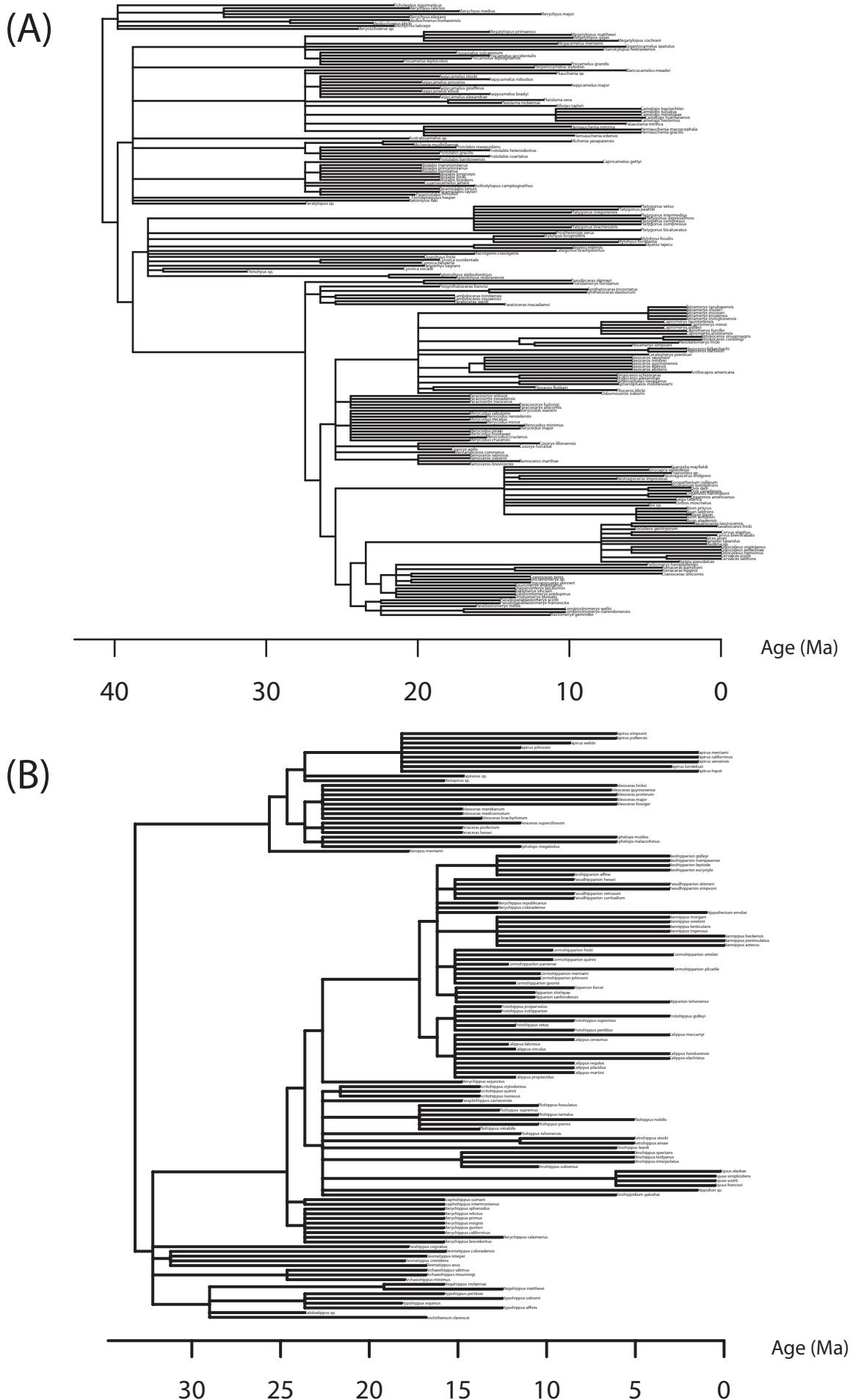


Fig. S4.2 Poorly-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

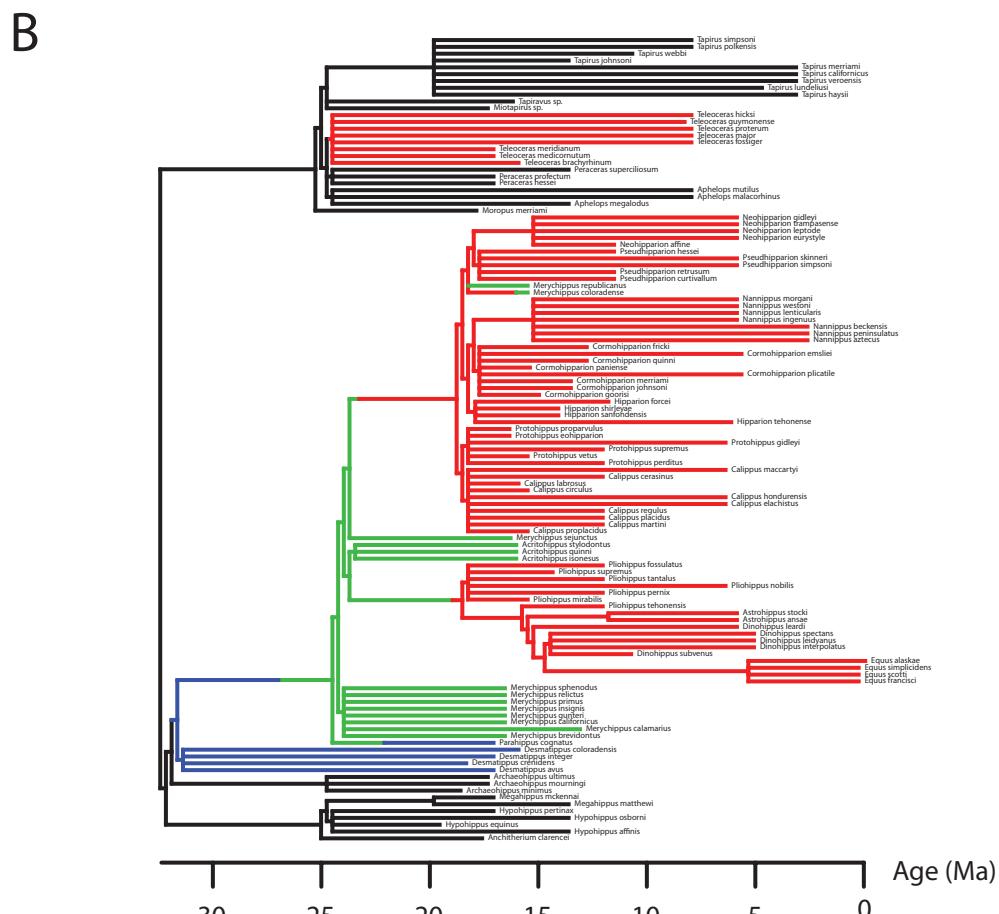
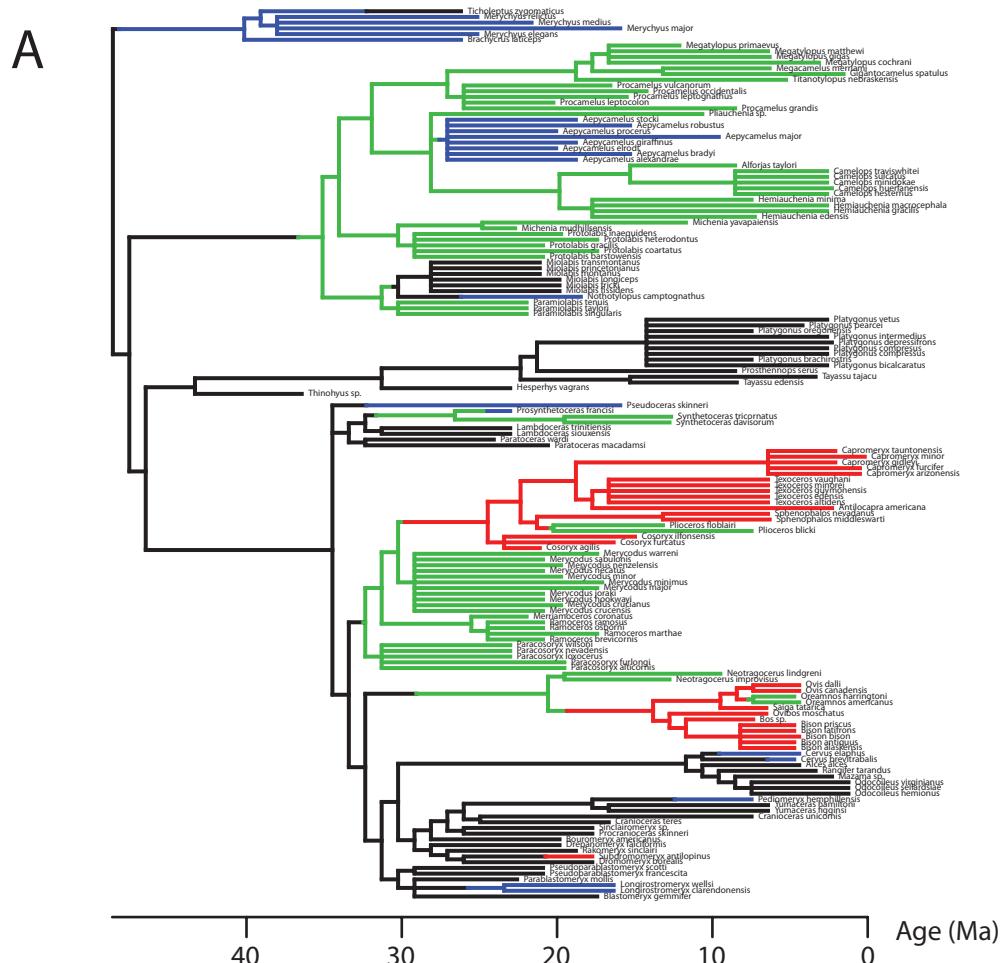


Fig. S4.3 Character maps of tooth crown height conditions in North American (A) Artiodactyla and (B) Perissodactyla. Black lines show the brachydont or low crowned tooth conditions, green shows the mesodont condition, blue shows the submesodont condition, and red shows the hypsodont or high crowned tooth condition.

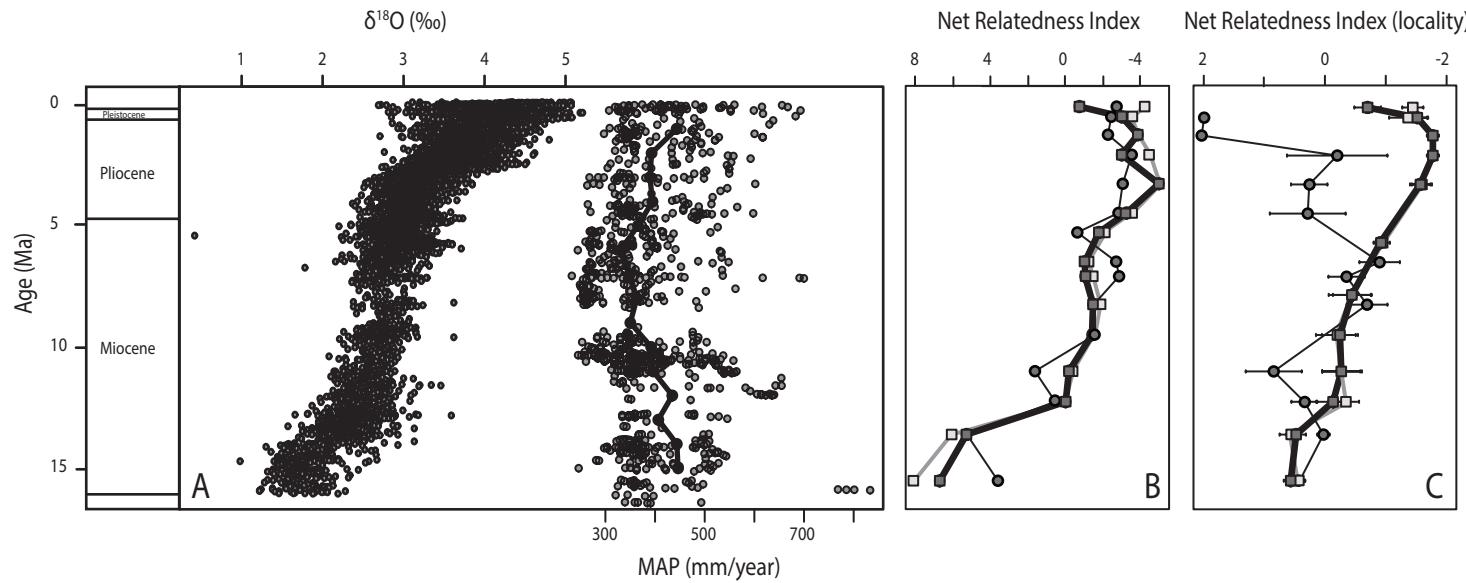


Fig. S4.4 Relationships of artiodactyl (squares) and perissodactyl (circles) PCS (NRI) with (A) $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Zachos et al., 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the poorly resolved artiodactyl and perissodactyl phylogenies. PCS = phylogenetic community structure; NRI = net relatedness index.

5 Chapter: Seasonality in pronghorn (*Antilocapra americana*) enamel oxygen isotope values reflect meteoric water: palaeoclimate implications

5.1 Abstract

Vertebrate tooth enamel stable oxygen isotope compositions are commonly used as biogeochemical indicators for paleoclimate reconstructions. However, the utility of enamel isotopic values across species varies due to differences in rates of enamel deposition and mineralization as well as sources of ingested water. We evaluate the use of stable oxygen isotope compositions from pronghorn (*Antilocapra americana* Gray, 1866) enamel for the reconstruction of terrestrial paleoclimate seasonality. We serially sampled the third lower molars of pronghorn from Wyoming for oxygen isotope composition in phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) and compared patterns to: (1) interpolated and (2) measured yearly variation in central Wyoming environmental waters ($\delta^{18}\text{O}_w$) as well as to (3) $\delta^{18}\text{O}$ values from sagebrush leaves in the same region. Pronghorn $\delta^{18}\text{O}_{\text{PO}_4}$ values from enamel are consistently enriched in ^{18}O relative to expected phosphate oxygen isotope values if body water was a direct reflection of $\delta^{18}\text{O}_w$. Pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values are less offset from ^{18}O of sagebrush leaves, suggesting that pronghorn obtain at least some of their water from evaporatively plants. Sinusoidal patterns in $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel correspond to modern $\delta^{18}\text{O}_w$ values from across Wyoming. Modeling of source body water $\delta^{18}\text{O}$ values show amplitudes between 70% and 95% of seasonal variation from Wyoming $\delta^{18}\text{O}_w$ values. We also show a relationship between temperature and carbonate-phosphate $\delta^{18}\text{O}$ spacing, suggesting temperature dependent disequilibrium of $\delta^{18}\text{O}_{\text{CO}_3}$ - $\delta^{18}\text{O}_{\text{PO}_4}$ incorporation. Collectively, our findings establish that modern

seasonality in source water is reliably reflected in modern pronghorn enamel providing the basis for exploring ancient climates using archived tooth collections.

5.2 Introduction

Terrestrial climates, which are recorded by modern precipitation ($\delta^{18}\text{O}/\delta^2\text{H}$) isotope ratios (Vachon et al. 2010a; Welker 2012) and other climate proxies (Liu et al. 2014), are spatially and temporally heterogeneous. In order to accurately reconstruct palaeoclimates, proxies that record climate with high fidelity at a range of spatial and temporal scales are required. A wide variety of indicators are used in paleoclimate reconstructions, including stable isotope ($\delta^{18}\text{O}$, $\delta^2\text{H}$, $\delta^{13}\text{C}$) compositions of animal hard tissues (Fox and Fisher 2001; Feranec and Macfadden 2006; MacFadden 2008), leaf margin analysis (Wilf 1997; Wilf 1998), paleosol morphology and isotopes (Fortelius et al. 2002; Fox and Koch 2004; Retallack 2009; Stevenson et al. 2010; Fox et al. 2012; Winnick et al. 2013), as well as mammalian community structure (Fortelius et al. 2002; Eronen et al. 2010; Fraser and Theodor 2013). Stable isotope analysis of fossil mammal hard tissues is popular in terrestrial paleoclimatology because their fossil record is temporally and spatially extensive among terrestrial vertebrates, their constant body temperature means stable isotope values from enamel can be interpreted as reflecting the external environment (Koch 2007), and their pattern of enamel formation, mineralization, and tooth replacement means that mammals can record climatic variations on yearly, monthly, and even daily scales (Koch et al. 1989; Koch 1998; Hoppe et al. 2004a; Feranec et al. 2010).

Enamel stable isotope analysis has been applied to the study of dietary ecology and climate reconstruction using nearly every major terrestrial mammal taxon including

but not limited to ungulates (i.e., perissodactyls, terrestrial cetartiodactyls, and proboscideans), rodents, carnivores, and lagomorphs (MacFadden and Cerling 1994; Fox and Fisher 2001; Larson et al. 2001; Passey et al. 2002; Feranec and Macfadden 2006; MacFadden 2008; DeSantis et al. 2009; Feranec et al. 2010; Domingo et al. 2012).

However, the spatial and temporal resolution of climate indicators preserved in mammalian hard tissues varies due to interspecific differences in internal (e.g., enamel mineralization, tooth development, and physiology) (Passey and Cerling 2002; Hoppe et al. 2004a), and external (e.g., water sources, home range sizes) (Luz et al. 1990; Cerling and Harris 1999; Levin et al. 2006) factors. The fidelity with which daily, seasonal, and yearly changes in climate are detectable using mammalian hard tissues is determined by sampling technique (e.g., serial sampling or bulk sampling), rates of enamel amelogenesis and mineralization, the sources from which individuals obtain their body water, and the space over which individuals integrate their external environment (Passey and Cerling 2002; Levin et al. 2006; Zazzo et al. 2012; Blumenthal et al. 2014). Choice of paleoclimate indicator taxa and sampling approach should therefore reflect the desired spatial and temporal scale of paleoclimate reconstructions. In general, ideal mammalian terrestrial paleoclimate indicators should: i) be abundant in the fossil record, ii) have a geographic and temporal range appropriate for the scale of the study, and iii) record their external environment (e.g., temperature, rainfall, local vegetation) with high fidelity.

Antilocaprids (pronghorn and their extinct relatives) have a temporally and spatially rich fossil record. The geographic range of the only remaining modern species *Antilocapra americana* (Gray, 1866) is extensive, encompassing parts of northern Mexico, extending through much of the central and western United States and as far

north as the Canadian provinces of Alberta and Saskatchewan. Furthermore, their modern range is centered on the Great Basin of the intermountain western US, a region which is poorly covered by other extant bovids and cervids, but used today extensively by livestock. Individuals also have geographically limited home ranges, travelling 100-200 km during their seasonal migrations meaning that pronghorn may be ideal for reconstructing spatial patterns of climate (Sawyer et al. 2005). Moreover, antilocaprids have persisted in the same regions throughout their evolutionary history, which is not true of many mammalian taxa (e.g., equids, rhinocerotids, proboscideans).

In this study, we have examined the modern oxygen isotope composition from serial samples of pronghorn tooth enamel and asked whether enamel oxygen isotope ratios reflect the seasonal variation in modern meteoric water $\delta^{18}\text{O}$ values. Strong correspondence between modern enamel and modern precipitation isotope values at monthly time steps would then provide a robust means by which to unravel paleoclimate records using archived ancient teeth of pronghorn. If the oxygen isotope compositions of antilocaprid enamel faithfully record the seasonal environmental variation, then antilocaprids are a potentially untapped paleoecological resource that may enable high resolution as well as spatially and temporally expansive seasonality reconstruction in North America for the late Cenozoic. Previously, $\delta^{18}\text{O}$ values from pronghorn incisors were related to local humidity for the Wyoming population (Fenner and Frost 2008).

However, incisors are formed over a shorter time frame so that serial samples cannot provide as long a time series of $\delta^{18}\text{O}$ values.

5.3 Materials and Methods

5.3.1 Stable oxygen isotope composition from mammalian hard tissues

The stable oxygen isotope composition of precipitation ($\delta^{18}\text{O}_w$) is sensitive to surface temperatures and vapor transport (Dansgaard 1964; Koch 1998; Harvey and Welker 2000; Welker 2000; Vachon et al. 2010b; Vachon et al. 2010a). Near shore and low altitude meteoric waters have higher $\delta^{18}\text{O}$ values than meteoric waters from inland, high altitude regions across the US (Welker 2000, Dutton et al. 2005, Vachon et al. 2007, Vachon et al. 2010, Liu et al. 2014). Similarly, seasonal variations in surface temperature result in lower $\delta^{18}\text{O}$ values during cooler months (enhanced fractionation) and higher $\delta^{18}\text{O}$ values (reduced fractionation) during warmer months (Gat 1996; Koch 1998). Meteoric water sources that experience limited evaporation are most representative of $\delta^{18}\text{O}_w$ values while plant leaf water is ^{18}O enriched due to evapotranspiration, the magnitude of which is dependent on local temperatures, humidity, and depth of the roots (Dansgaard 1964; Dongmann et al. 1974; Yakir et al. 1990; Koch 1998; Leffler and Caldwell 2005).

Mammalian hard tissues (i.e., enamel, bone, and dentin) contain a highly substituted form of hydroxyapatite ($\text{Ca}_{10}[\text{PO}_4,\text{CO}_3]_6[\text{OH},\text{CO}_3]_2$), which forms in equilibrium with body water. Hydroxyapatite is thus reflective of the oxygen isotope composition of ingested water but with a constant offset due to physiological mechanisms and variable amounts of time-averaging that depends on a species-specific rate of enamel formation and mineralization (Longinelli 1984; Luz et al. 1984; Bryant et al. 1994;

Bryant and Froelich 1995; Passey and Cerling 2002; Passey et al. 2005). Tooth enamel mineralizes from the crown to the root, thus preserving a time series of body water isotopic composition. Hypsodont or high crown teeth record 1-4 years of body water isotope composition and, in turn, changes in the oxygen isotope composition of consumed environmental waters throughout (Fricke et al. 1998; Kohn et al. 1998; Balasse 2002; Passey and Cerling 2002; Zazzo et al. 2012).

Antilocapra americana is the only extant species in the family Antilocapridae. They are hypsodont and the enamel of the third lower molar is laid down from crown to root after 180 days of age and before 2 years (Dow, 1962). Enamel formation for pronghorn occurs in about half the time as *Equus*, so we assume an enamel maturation time similar to extant bovids such as *Bison bison* (i.e., 2 months) (Fricke and O'Neil 1996; Higgins and MacFadden 2004). We therefore estimate a rate of enamel formation of ~40 mm/ year (Fricke and O'Neil 1996).

5.3.2 Sampling and preparation

Pronghorn specimens were acquired from the University of Wyoming Anthropology museum (Appendix E). All specimens were collected from wild populations in Wyoming during 1970-1972 and 2010 following deaths that were unconnected to this study. Because the third molar is one of the last to complete enamel mineralization and erupt in hoofed mammals (Dow and Wright 1962), we included only individuals with erupted third lower molars. To recover the most complete isotopic time series, we included only individuals showing no or little wear of the third lower molar. We also excluded individuals with abscesses or obvious abnormalities of the dentition or jaw bone. We extracted lower third molars using a Dremel diamond cutting wheel and

serially sampled the enamel at approximately 2 mm intervals using a Dremel tool with a diamond taper point bit (part #7144). We collected 2-3 mg of powdered enamel for each serial sample. Further, we took bulk samples (~4-6 mg) of bone from the mandibular angle just posterior to third lower molar for each individual.

To analyze the oxygen isotope composition of phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$), we weighed 1.5-2 mg of enamel and 3-4 mg of bone from each specimen. Preparation procedures are after Bassett et al. (2007) and Weidemann-Bidlack et al. (2008). We pre-treated all samples with 300 μl of 2.5% NaOCl for approximately 20 hours to remove organics. Bone samples were usually pre-treated twice to ensure complete organic removal (or more if there was continued gas production). Samples were then rinsed with deionized (DI) water 5 times and dried overnight at 50°C. We then dissolved the remaining powder in 100 μl of 0.5M HNO₃ overnight. To neutralize the solution and precipitate CaF₂, 75 μl of 0.5 M KOH and 200 μl of 0.36 M KF were added. Samples were centrifuged to pellet the CaF₂ and the supernatant was transferred from the vials to reaction vessels. We precipitated silver phosphate with 250 μl of silver amine solution (0.2M AgNO₃, 0.35M NH₄NO₃, 0.74M NH₄OH) plus 3-6 drops of 0.1M AgNO₃ to initiate the precipitation. Samples were placed in a heat block at 50°C overnight in a fume hood to allow for maximum crystal growth. The silver phosphate crystals were rinsed five times with ~2mL of DI water to remove the residual silver amine solution. After the samples dried overnight at 50°C, 200 – 300 μg were weighed into pressed silver capsules and stored in an oven flushed with N₂ until isotopic analysis.

The $\delta^{18}\text{O}$ value of silver phosphate was measured after conversion to CO in a Temperature Conversion Elemental Analyzer (TC/EA, Thermo Scientific) coupled with a

Conflo IV (Thermo Scientific) to a continuous flow isotope ratio mass spectrometer (CF-IRMS, Thermo Scientific Delta V). Three in-house reference materials (two silver phosphate and one benzoic acid) were used to normalize isotopic values and check the effectiveness of pyrolysis within and between runs (ARCOS [N=4 per run], 21UWSIF [N=5 per run], 33UWSIF [N=6 per run]). Variation in $\delta^{18}\text{O}$ values exhibited by these reference materials was $< 0.3\text{\textperthousand}$. In addition, we monitored the potential isotopic alteration during sample preparation by precipitating silver phosphate from a synthetic hydroxyapatite and NBS120c (N=3 and 3 with $1\sigma < 0.3\text{\textperthousand}$). All $\delta^{18}\text{O}_{\text{PO}_4}$ values are reported relative to the standard V-SMOW. Isotope ratios are expressed using δ notation, where:

$$\delta^h X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

X is the element of interest (O), h is the high mass number, and R is the high mass-to-low mass ratio. Units are parts per thousand (\textperthousand) deviations from a standard. All samples were analyzed in triplicate.

To check the carbonate-phosphate spacing, we also analyzed a subset of enamel samples for carbonate $\delta^{18}\text{O}$ values (Kohn and Cerling 2002; Lécuyer et al. 2010). We weighed 1 mg of enamel and 5 mg of bone for each sample analysis of $\delta^{18}\text{O}_{\text{CO}_3}$ values. To remove organic matter from the bone samples, we used 2-3% H_2O_2 at a ratio of 1 ml per 25mg of sample, leaving the caps of the microcentrifuge tubes open to allow the escape of gas for 24 hours. We did not pre-treat the enamel samples to remove organic matter due to the minimal organic content of enamel. Similar to the phosphate preparation, pre-treatment was repeated until gas production ceased. We rinsed the bone samples 5 times with DI water to remove H_2O_2 from solution. We then added 1M

CH_3COOH with Ca acetate buffer ($\text{pH}=4.5$) to remove non-lattice bound carbonates using the same ratio as the preceding step. Samples were rinsed five times with DI water, dried for 24 hours in a freeze drier, and ~ 1 mg weighed into exetainer tubes for isotopic analysis. Once all samples and reference materials were weighed into exetainer tubes, they were dried overnight at 50°C , the headspace flushed with He, and $100\text{-}200 \mu\text{L}$ of $>100\%$ H_3PO_4 was added to react for 24 hours. The CO_2 within the headspace was sampled for isotopic composition measurement using a gas bench (Thermo Scientific) coupled to a CF-IRMS (Thermo Scientific Delta Plus). Three in-house CaCO_3 reference materials were used to normalize isotopic values and check for variation within and between runs (UWSIF18 [$N=4$ per run], UWSIF06 [$N=4$ per run], UWSIF17 [$N=4$ per run]). Variation in $\delta^{18}\text{O}_{\text{CO}_3}$ values of these reference materials was $< 0.2\text{\textperthousand}$. In addition, we monitored the potential isotopic alteration during sample preparation with one lab bioapatite ($N=1$ per run). All $\delta^{18}\text{O}_{\text{CO}_3}$ values are reported relative to the standard V-SMOW.

5.3.3 Modelling and comparison to environmental waters

To recover the oxygen isotope values of source body water ($\delta^{18}\text{O}_{\text{body}}$) from our pronghorn tooth isotopic time series, we used the mathematical models from Passey and Cerling (2002) and Passey *et al.* (2005) as a transfer function. The Passey and Cerling (2002) model reconstructs primary isotope series (i.e., body water) using measured $\delta^{18}\text{O}$ values from tooth enamel as input parameters while also accounting for time averaging due to amelogenesis and variation in enamel maturation from the crown to the root. The Passey *et al.* (2005) method incorporates the Passey and Cerling (2002) time-averaging model and uses an inverse linear system to recover the input signals or body water values

from enamel isotopic time series (see Matlab code associated with Passey *et al.*, 2005).

The input variables for the Passey and Cerling (2002) and Passey *et al.* (2005) models are l_a and l_m , which are the length of apposition (distance along the tooth from where a new enamel layer contacts the enamel-dentine junction and the external layer of the tooth; 0.4 mm) and length of maturation (the length of the tooth that is mineralizing at a given time; 3.8 mm), respectively. We used a constant sample depth (l_s) of 75% of enamel thickness because we drilled through approximately 75% of the enamel when serial sampling. We calculated the length of maturation assuming a two-month period of enamel maturation as in *Bison bison*. The Passey and Cerling (2002) and Passey *et al.* (2005) models were run in MATLAB version 7.10.

To compare pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values to environmental waters, we downloaded interpolated monthly average isotope values for precipitation from central Wyoming (43°N, 107.5 °W at 6,700 ft of elevation) from waterisotopes.org (Bowen *et al.* 2005; Bowen 2014). These interpolations for the entire US are based in large part on Welker's USNIP (United States Network for Isotopes in Precipitation-Welker 2000, 2012) for the years 1989-1994 and scarce IAEA GNIP (Global Network for Isotopes in Precipitation) data from a few years in 1960's for 6 sites across the US (Rozanski *et al.* 1993). Environmental water $\delta^{18}\text{O}_w$ values were converted into expected phosphate values using the following equation from Kohn and Cerling (2002)

$$\delta^{18}\text{O}_{\text{PO}_4} = (0.9 \times \delta^{18}\text{O}_w) + 23 \quad (2)$$

To compare $\delta^{18}\text{O}$ values from environmental waters and enamel we aligned the data assuming a birth month of May to June for all pronghorn specimens. We used ordinary least squares regression to test for a relationship between environmental water

$\delta^{18}\text{O}_w$ and pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values. The generalized least squares models are preferable to generalized linear models because they account for temporal autocorrelation between successive data points.

To validate the interpolated $\delta^{18}\text{O}_w$ values we used 1000+ measured $\delta^{18}\text{O}$ values from precipitation at 9 sites in Wyoming (Appendix F) from USNIP for the entire USNIP record 1989-2006 (Welker 2000; Vachon et al. 2010b; Welker 2012). We made comparisons between the interpolated $\delta^{18}\text{O}_w$ values and measured values using monthly averages across all sample sites and at the site closest to the Laramie and Rawlins region (Albany site), the site closest to the area where our modern pronghorn teeth were collected. All statistical analysis used R version 3.1.1 (R Development Core Team, 2014).

We also obtained published $\delta^{18}\text{O}$ values for sagebrush leaves and stems, rabbitbrush leaves, and pronghorn incisor enamel from Fenner and Frost (2008) for comparison to $\delta^{18}\text{O}_{\text{PO}_4}$ from pronghorn molar enamel and $\delta^{18}\text{O}_w$ values. All plant tissues were sampled by Fenner and Frost (2008) during the months of June and July. All $\delta^{18}\text{O}$ values from Fenner and Frost (2008) were also converted into expected phosphate values using equation 2.

5.3.4 Results and discussion

Seasonal variations in temperatures result in lower $\delta^{18}\text{O}$ values during cooler months and higher $\delta^{18}\text{O}$ values of Wyoming meteoric waters during warmer months, a common observation in North America (Koch 1998, Welker 2000, Vachon et al. 2007, Vachon 2010, Birks and Edwards 2009, Delvey et al. 2015) and in Western Europe (Rozanski et al. 1992, 1993). The interpolated $\delta^{18}\text{O}_w$ values show a sinusoidal pattern

varying from -23‰ in January to -10.6‰ in July (Bowen, 2014), which corresponds to an expected range of $\delta^{18}\text{O}_{\text{PO}_4}$ mammal body water values of 2.3‰ – 13.5‰ (a range of 11.2‰) based on equilibrium fractionation equations. Measured $\delta^{18}\text{O}_{\text{w}}$ values from Wyoming exhibit a similar sinusoidal pattern (Fig. 5.1A-B) varying in amplitude among years (Fig. 5.1A) and sites (Fig. 5.1B). Because the interpolated $\delta^{18}\text{O}$ values from waterisotopes.org are based in large part on the USNIP $\delta^{18}\text{O}$ data for 9 Wyoming sites, they fall within the range of yearly, monthly, and spatial variation of the actual measured values (note, however, that values for August tend to be low but still fall within the range of variation; Fig. 5.1A-B; black lines) and thus interpolated and actual values are highly correlated (Fig. 5.1C-D; $R^2 = 0.90$ all Wyoming, 0.82 Albany site). The interpolated data from waterisotopes.org thus represent an “average year” and smooth the effects of short-term climate variations on actual precipitation $\delta^{18}\text{O}$ values, which may be caused by climate oscillation intensities and storm track variation (e.g. El Nino, PNA-Sjostrom and Welker 2009, Welker 2012, Liu et al. 2013). In addition, Bowen and Revenaugh (2003) employ an interpolating method that reduces $\delta^{18}\text{O}_{\text{w}}$ values estimation error by 10-15% relative to older methods. The estimation error is improved in part by using an algorithm that includes latitude, longitude and altitude. Because of our interest in the general aspects of seasonality-monthly patterns of precipitation (Vachon et al. 2010) and correspondence with variation in enamel seasonality, we used the interpolated $\delta^{18}\text{O}_{\text{w}}$ (smoothed) data for the remainder of our analyses.

Serial samples (~10-14 samples per individual run in triplicate) from the third lower molars of six individual pronghorn show a sinusoidal pattern similar to seasonal variation in the $\delta^{18}\text{O}$ values of consumed water (total N = 80 run in triplicate; Fig. 5.2).

Comparison to the pattern of variation in Wyoming environmental water $\delta^{18}\text{O}$ values confirms that each sampled tooth records approximately 12-14 months of the animal's life (Fig. 5.2). Furthermore, X-ray studies of pronghorn jaws suggest that completion of third lower molar mineralization occurs between 1.5 and 2 years of age (Dow, 1962); a small amount of wear on the teeth may have truncated the $\delta^{18}\text{O}$ record in pronghorn enamel. However, the teeth of all individuals record at least a year of the animal's life.

The total range for all sampled Wyoming pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values is from 9.0 to 19.9‰ (10.9‰ range among individuals, 5-6‰ range for individuals). The highest $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel likely reflect the $\delta^{18}\text{O}$ values of water ingested (from meteoric and/or plant sources) during the summer while the lower $\delta^{18}\text{O}_{\text{PO}_4}$ values reflect water ingested during the winter. Serial samples from the third lower molars of all individual pronghorn show ^{18}O enrichment relative to expected $\delta^{18}\text{O}_{\text{PO}_4}$ values of body water that is a direct reflection of $\delta^{18}\text{O}$ values of precipitation (Fig. 5.2), suggesting that pronghorn obtain at least some of their water from evaporatively enriched sources, such as evaporated standing water bodies (ponds/lakes) that can be found throughout the Great Basin region of the Intermountain West or plant leaves. The offset between pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values and expected $\delta^{18}\text{O}_{\text{PO}_4}$ values from body water based on meteoric sources varies from 4-9‰ (Fig. 5.2). The offset between pronghorn enamel and expected $\delta^{18}\text{O}_{\text{PO}_4}$ from meteoric waters is greatest during the winter months, suggesting consumption of less evaporatively ^{18}O -enriched waters during the summer months. Pronghorn show increased reliance on pond and lake water during the dry summer months, the period of greatest evaporation in an extremely arid habitat, or

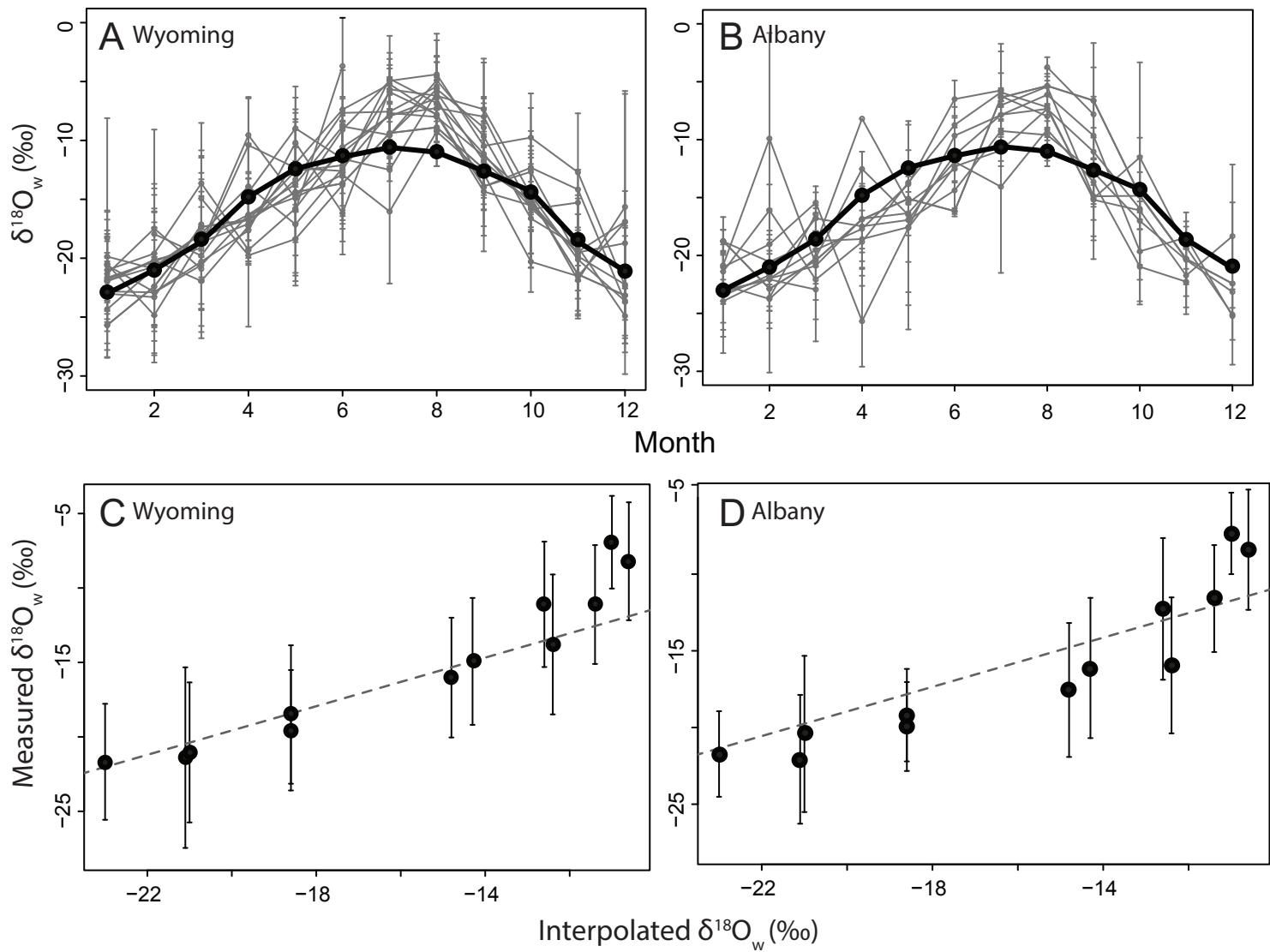


Fig. 5.1 Relationship between measured (USNIP) and interpolated (waterisotopes.org) environmental $\delta^{18}\text{O}$ values (‰ V-SMOW), (A) Monthly averages of environmental $\delta^{18}\text{O}$ values from 1989-2006 averaged across Wyoming (gray lines) and (B) within the Albany region (gray lines) for all sampled years plotted with interpolated average monthly values for Wyoming from waterisotopes.org (black lines), (C) Correlation of measured monthly environmental $\delta^{18}\text{O}$ values across Wyoming ($R^2 = 0.9$), and (D) within the Albany region ($R^2 = 0.82$) with interpolated average monthly values for Wyoming from waterisotopes.org.

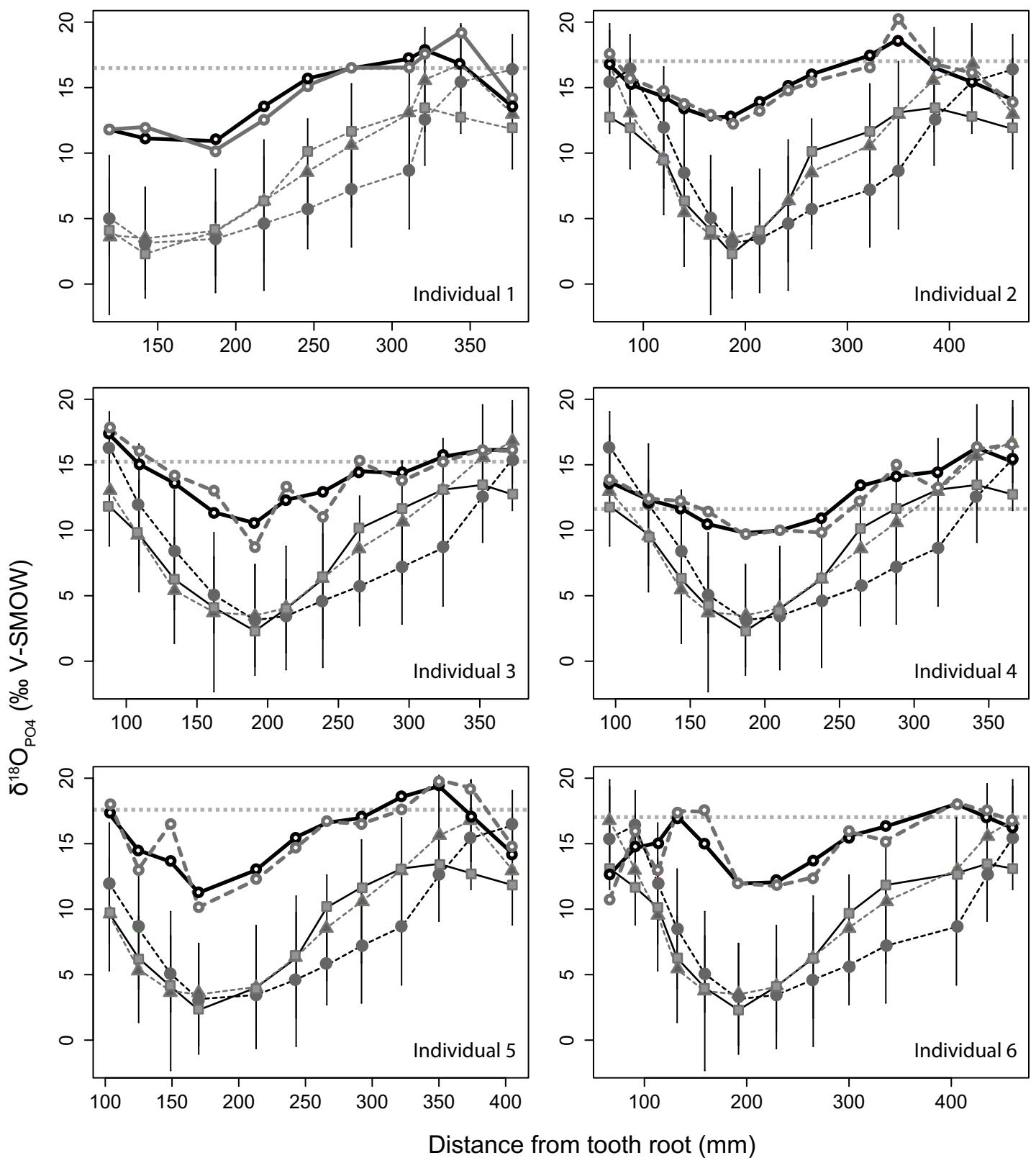


Fig. 5.2 Variation in measured (black circles) and modeled (gray circles) pronghorn enamel $\delta^{18}\text{O}$ values (‰ V-SMOW) for six specimens used in this study with variation in interpolated and measured environmental (waterisotopes.org in gray squares, all Wyoming measured gray triangles, Albany, Wyoming region in gray circles) $\delta^{18}\text{O}$ values (‰ V-SMOW). Grey dotted lines are averaged $\delta^{18}\text{O}$ (‰ V-SMOW) values from bone of the same pronghorn specimen.

increased reliance on plant water sources during the winter months (Beale and Smith, 1970, Harvey and Welker 2000).

Plant leaf water is ^{18}O -enriched relative to meteoric waters due to evapotranspiration, the rate of which is reflective of local temperatures, humidity, and root depth (Dansgaard 1964; Dongmann et al. 1974; Yakir et al. 1990; Koch 1998; Leffler and Caldwell 2005). The $\delta^{18}\text{O}$ values of Wyoming sagebrush leaves have mean of -3.1‰ (V-SMOW; +/- 2.8‰ one standard deviation) and an offset from meteoric waters of 5-8‰ during June and July (Fenner and Frost 2008). Expected $\delta^{18}\text{O}_{\text{PO}_4}$ values for body water that is a direct reflection of sagebrush leaf water have a mean of 20.2‰ (V-SMOW; +/- 2.5‰) and are ^{18}O -enriched by up to 1-5‰ relative to summer $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel (Fenner and Frost 2008). Sagebrush stems have a mean of -7.7‰ (V-SMOW; +/- 2.1) are offset from meteoric waters by ~3-4‰ during June and July (Fenner and Frost 2008). Expected $\delta^{18}\text{O}_{\text{PO}_4}$ values for body water that is a direct reflection of sagebrush stem water have a mean of 16.0‰ (V-SMOW; +/- 1.9‰) and are typically not ^{18}O -enriched relative to summer $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel (Fenner and Frost 2008). The smaller offset between sagebrush leaf and enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values suggests that pronghorn rely at least partially on evaporatively enriched plant leaves and stems. Rabbitbrush leaves show similar $\delta^{18}\text{O}$ offsets between $\delta^{18}\text{O}_w$ and $\delta^{18}\text{O}_{\text{PO}_4}$ from pronghorn enamel during the summer months (Fenner and Frost 2008).

Table 5.1 Generalized least squares regression of isotopic time series from pronghorn enamel against environmental water values and percentage of total variation in $\delta^{18}\text{O}_w$ that is reconstructed using forward modelling.

Specimen	% $\delta^{18}\text{O}_w$	R2	T-value	p-value
1	71.4	0.27	2.34	0.04
2	94.6	0.74	5.63	< 0.001
3	77.4	0.58	4.37	< 0.002
4	71.8	0.93	11.94	< 0.003
5	84.1	0.89	9.43	< 0.004
6	90.8	0.84	7.01	< 0.001

Individually, pronghorn molars record 54% to 70% of the annual environmental $\delta^{18}\text{O}$ variation before application of forward modelling (Fig. 5.2). Time averaging due to delayed enamel mineralization after amelogenesis and transgression of multiple enamel layers during sampling are the main factors driving the smoothing of isotopic time series relative to the environmental water values (Passey and Cerling 2002; Passey et al. 2005). However, the comparatively rapid rate of enamel mineralization in pronghorn means less time averaging relative to better sampled taxa such as equids (Fricke and O'Neil 1996; Hoppe et al. 2004b). $\delta^{18}\text{O}_{\text{PO}_4}$ values from Wyoming bison overlap with values from pronghorn (Fricke & O'Neil, 1996 Fig. 2B) but show a comparatively small seasonal range of only 3‰, which may be related to their larger N-S and S-N migration patterns (Larson et al. 2001, and references there in). Free-ranging bison historically grazed in the Northern Great Plains during summer (Harvey and Welker 2000) and migrated to the southern Great Plains (Fricke and O'Neil 1996). Thus, the source vegetation water that bison graze does not dramatically vary among seasons due to major forage and habitat switching. It appears that pronghorn may also capture more of the seasonal variation in $\delta^{18}\text{O}_w$ values due to their limited migration; they continuously occupy habitats that have very strong seasonality in meteoric water $\delta^{18}\text{O}$ values, a common pattern in the interior of all of North America, especially Wyoming, Colorado and Nebraska (Harvey and Welker 2000; Vachon et al. 2007; Delavau et al. 2015).

Using the inverse modelling technique of Passey et al. (2005), we reconstructed body water isotopic time series for each individual pronghorn (Fig. 5.2; gray circles). Although the pronghorn $\delta^{18}\text{O}$ values are offset due to some consumption of evaporatively enriched water, there is excellent congruence between the modeled time series from

$\delta^{18}\text{O}_{\text{PO}_4}$ values and the measured $\delta^{18}\text{O}_{\text{PO}_4}$ values as well as measured $\delta^{18}\text{O}_w$ values (Fig. 5.2). We find a significant correlation between $\delta^{18}\text{O}_{\text{PO}_4}$ and modeled $\delta^{18}\text{O}_w$ for all specimens in our study and are able to reconstruct 70-95% of the total amplitude of Wyoming $\delta^{18}\text{O}_w$ values using inverse modelling (Table 5.1). We therefore suggest that pronghorn are excellent sources of proxy data for reconstructing paleoseasonality relative to other large herbivores due to comparatively rapid enamel formation (~1.2 years compared to ~4 years for equids) and their relatively small offset from $\delta^{18}\text{O}_w$ values. We cannot presently discern whether $\delta^{18}\text{O}$ values from pronghorn enamel show a consistent offset from $\delta^{18}\text{O}_w$ values through space. Although we do not currently present a transfer function for deriving precise $\delta^{18}\text{O}_w$ values from pronghorn enamel, our data suggest that $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel can be used to estimate the amplitude of seasonal change.

Sampling 6 individuals with 80 total enamel values we have resolved nearly the full annual range of $\delta^{18}\text{O}_w$ values from Wyoming; a sample density that is similar to or larger than prior studies (MacFadden and Higgins 2004; Hoppe 2006; Martin et al. 2008; Britton et al. 2009; Pellegrini et al. 2011). Previous studies that use a serial sampling approach include similar numbers of individuals within regions or sites (i.e. 4-10) and thus it appears plausible that the full $\delta^{18}\text{O}$ amplitude of paleoseasonality may be derived from pronghorn enamel isotope values using 6-10 individuals.

$\delta^{18}\text{O}$ values from bone have archaeological applications, therefore we also sampled the jaw from all individual pronghorn in this study. The $\delta^{18}\text{O}_{\text{PO}_4}$ values from bone of the same specimens are similarly higher than $\delta^{18}\text{O}$ values for environmental waters (Fig. 5.2; dashed grey lines) and lower than $\delta^{18}\text{O}$ values of summer collected

sagebrush leaves (Fenner and Frost 2008). In all but one case, bone $\delta^{18}\text{O}_{\text{PO}_4}$ is biased toward values typical of the spring and summer, suggesting higher mineralization of bone during these months and cessation of bone re-modeling during the winter months (Fig. 5.2). Bone $\delta^{18}\text{O}$ values from pronghorn might therefore have archaeological applications such as reconstruction of summer $\delta^{18}\text{O}_w$ values. However, rapid diagenesis of bone limits its applicability in all but Quaternary paleoecology (Koch 1997).

Comparison to published $\delta^{18}\text{O}$ values from Wyoming pronghorn incisors show a similar pattern to bone. Pronghorn enamel $\delta^{18}\text{O}$ values from Fenner and Frost (2008) have a mean $\delta^{18}\text{O}_{\text{PO}_4}$ value of 16.6‰ (V-SMOW; +/- 2.8‰ one standard deviation) thus showing bias toward values typical of spring and summer; formation of incisor enamel likely occurs primarily during the warmer months. Incisor enamel might therefore have similar applications to bone such as the reconstruction of spring and summer $\delta^{18}\text{O}_w$ values. However, incisor enamel does not record as long a time series of $\delta^{18}\text{O}$ values and is thus has limited utility for reconstructing paleoseasonality.

Carbonate ($\delta^{18}\text{O}_{\text{CO}_3}$) and phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) oxygen isotope compositions are often treated as interchangeable because they are thought to derive from the same body water source and the offset between them is often considered a check for diagenesis (Kohn and Cerling 2002). If carbonate and phosphate oxygen are incorporated at the same time from the same body water, $\delta^{18}\text{O}$ values from both compartments should show a correlation with a slope of 1.0 (Pellegrini et al. 2011). Deviations from a 1:1 correlation between $\delta^{18}\text{O}_{\text{PO}_4}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ may result from: i) different sources of water for phosphate

and carbonate formation, ii) differences in the timing of phosphate and carbonate mineralization, and iii) diagenesis (Pellegrini et al. 2011).

Therefore, as a preliminary check of whether the same climatic inferences can be drawn from both the $\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values of pronghorn enamel, we also analyzed both from a select subsample of pronghorn enamel samples. The majority of our samples lie within the prediction interval reported by Lécuyer et al. (2010; Fig. 5.3). However, several of our pronghorn $\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values fall below the empirically derived $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ line. We also find that the line of best fit for pronghorn enamel $\delta^{18}\text{O}_{\text{PO}_4}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ values deviate from the predicted slope (Lécuyer et al. 2010) showing a shallower estimated slope of 0.68 (Fig. 5.3A). The variations from the predicted line appear unrelated to year of collection (Fig. 5.3A), indicating that differences likely do not relate to date of collection or potential differences in their preparation. Pellegrini et al. (2011) report similarly shallow lines of best fit for correlations between $\delta^{18}\text{O}_{\text{PO}_4}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ from *Cervus* and *Equus* (total N = 8). Given that we sampled individual pronghorn from the modern record, we can eliminate diagenesis as the source of deviation from the predicted $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ line. In addition to water source and mineralization timing difference, deviation from the predicted $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ line might indicate precipitation of carbonates out of equilibrium with body water (Lécuyer et al. 2010; Pellegrini et al. 2011). In addition, we show a linear decrease in the $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ spacing ($R^2=0.71$, slope=-0.31, $p<0.001$; Fig. 5.3B) where enamel samples corresponding to summer months show less carbonate-phosphate offset than enamel samples corresponding to winter months (Fig. 5.3B). We suggest that the apparent carbonate precipitation disequilibrium might result from temperature dependent effects

(i.e., seasonal differences in the temperature of ingesta). Our results are preliminary but with more intensive sampling, a reliable temperature proxy might be developed using variations in $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ spacing across oxygen isotopic time series from pronghorn tooth enamel.

Questions concerning the interplay between terrestrial paleoclimate and diversity are being asked more frequently (e.g., whether local and regional climate impact long-term diversity trends on land) (e.g.(Fraser et al. 2014b; Fraser et al. 2015); therefore paleoecologists require reliable sources of terrestrial paleoclimate data as we try to unravel the processes that may have accounted for the diversity of life over geologic time. We find that pronghorn enamel faithfully records the amplitude of seasonal $\delta^{18}\text{O}_w$ value changes and suggest that isotopic time series from their enamel can be confidently used as a paleoseasonality indicator when the Passey et al. (2005) model is applied. Even without the use of the modelling approach, the amplitude of seasonal changes can be reconstructed using relatively small sample sizes of pronghorn (and possibly their close relatives) and compared among regions.. The further use of our high density modern precipitation network, USNIP provides however the only site, sub-state, regional and continental basis of actual meteoric water values that are becoming increasing valuable in revealing the range of seasonality in modern precipitation (Vachon et al. 2007; Vachon et al. 2010b; Vachon et al. 2010a), the underlying mechanisms such as climate phases and storm tracks that regulate precipitation isotope temporal and spatial variation that in several cases are reflected in a suite of climate proxies (Sjostrom and Welker 2009; Liu et

al. 2010; Stevenson et al. 2010; Vachon et al. 2010b; Vachon et al. 2010a; Liu et al. 2012; Liu et al. 2013; Winnick et al. 2013; Liu et al. 2014).

Further, annual pronghorn spatial ranges are estimated to be approximately 100-200 km (Sawyer et al., 2005) meaning that reasonable interpolated reconstructions of paleoseasonality could be developed using pronghorn hard tissue isotopes; $\delta^{18}\text{O}_{\text{PO}_4}$ values from pronghorn enamel can be averaged over areas of 100-200 km thus reducing the demand on sampling intensity when developing Cenozoic terrestrial climate maps. Specific applications for which such paleoclimate data could be used include reconstructions of regional changes in seasonality through time, reconstruction of gradients in seasonality, and validation of terrestrial paleoclimate models. Further, we present the first preliminary evidence of temperature dependence in natural $\delta^{18}\text{O}_{\text{CO}_3}$: $\delta^{18}\text{O}_{\text{PO}_4}$ spacing and suggest the potential for a paleotemperature indicator.

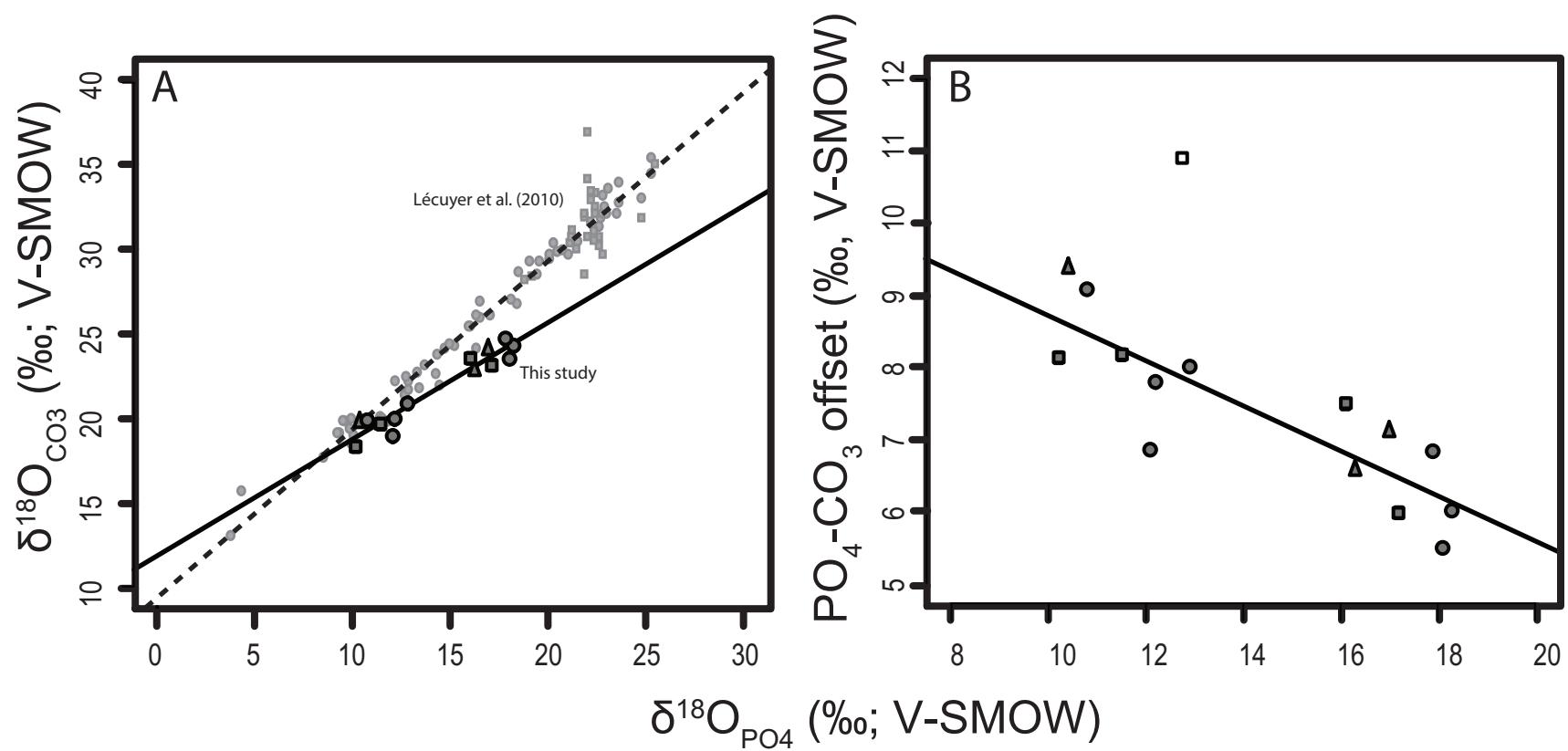


Fig. 5.3 Relationship of Wyoming pronghorn enamel (A) $\delta^{18}\text{O}_{\text{PO}_4}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ values (black best fit line) compared to the best fit line (dashed) derived from compilation of mammal and fish apatite (Bryant et al. 1996, Iacumin et al. 1996, Shahack-Gross et al. 1999, Vennemann et al. 2001, Zazzo et al. 2004, and Martin et al. 2008, Lécuyer et al. 2010), and (B) $\delta^{18}\text{O}_{\text{PO}_4}$ and carbonate-phosphate $\delta^{18}\text{O}$ offset showing a decline in spacing at higher precipitation temperatures. The linear equation is $y = -0.31x + 11.83$. Circles, triangles, and squares represent specimens collected in 2010, 1972, and 1971, respectively. The unfilled rectangle is an outlier that was excluded from the analysis.

6 Chapter: Discussion

Modern patterns of biodiversity emerge as a product of numerous contemporary and historical drivers including species sorting along modern and ancient environmental gradients, competitive interactions, dispersal, long-term climate changes, speciation and extinction events, the formation and weathering of mountain ranges, and plate tectonics (Blois and Hadly 2009). Modes of organismal response may include, but are not limited to, changes in richness as well as shifts in body size, niches, and the identity of taxa within communities (Mayhew *et al.* 2012; Secord *et al.* 2012). Neontologists, by their exclusion of historical extinction and origination, are excluding two of the most important factors in the formation of modern communities. Fortunately, the fossil record is a natural experiment that records faunal change under myriad evolutionary, climatic, and tectonic processes. Understanding climatic effects on community formation and change is becoming particularly critical in the context of ongoing anthropogenic climate change, the effects of which will reach far beyond our lifetimes. The fossil record is the best source of data on the deep-time origins of macroecological phenomena and long-term organismal response to climate change (Blois and Hadly 2009).

My dissertation focuses on changes in North American mammal community structure under conditions of long-term climate change during the Cenozoic. I have focused on metrics for community compositional change because they are more robust to time averaging in the fossil record (Kidwell 2013) and change more rapidly under climate change than other diversity metrics such as richness (Kent *et al.* 2011; Dornelas *et al.* 2014). I hypothesized that climatic influences on modern spatial diversity patterns apply equally to spatial diversity patterns through time, i.e. that the underlying ecological

processes are “ergodic.” As mentioned at the outset of this dissertation, I have not empirically tested whether rates of change in space are equal to rates of change in time but rather whether climate remains one of the primary explanatory variables of temporal diversity changes. I asked four primary questions: Are patterns of biodiversity sensitive to the processes of fossilization? When did the modern latitudinal diversity gradient emerge and were changes driven by climate? How has community composition changed as rates of extinction fluctuated under climate change? How can we best search for the proximate climatic drivers (i.e. changes in spatial climate patterns) of diversity changes?

6.1 **Mammal community compositional change**

Modern macroecological phenomena such as latitudinal diversity gradients are well characterized but interest in their deep time origins and how they might change in the context of ongoing climate change is burgeoning (Mannion et al. 2014). The answers to how and why macroecological phenomena have formed may be recorded in the fossil record but it behooves us to understand the contribution of fossil record bias. In Chapter 2, I have shown that measuring latitudinal richness gradients (likely any richness gradient) in the fossil record is highly sensitive to loss of diversity during fossilization. Quantification of latitudinal turnover gradients is much less sensitive to loss of species diversity but potentially influenced by which particular species are lost from the fossil record. Most importantly, I have proposed a unique method of re-sampling (Appendix C) that allows robust comparison of modern and fossil diversity that vastly improves our ability to interpret deep time changes in macroecological phenomena.

In Chapter 2, a very large amount of variation in estimates of latitudinal richness and latitudinal turnover gradients is explained by the fitted models that include

temperature, precipitation, and metrics for sampling bias. However, unexplained variation still remains relatively high (~30%). At present, I have little sense of which variables are missing from the fitted models or if there are in fact any variables I could include to improve their performance. Diversity does not conform as tightly to our ecological rules as we might like.

In Chapter 3 of this dissertation, I applied the methods I explored in Chapter 2 to the late Cenozoic (36 Ma – present) mammal fossil record of North America. I showed that latitudinal turnover diversity gradients of North American mammals varied considerably from the late Eocene (~ 36 Ma) through the late Pleistocene (~0.01 Ma), reaching modern magnitudes only during the late Miocene (~7 Ma) and late Pleistocene. I tie changes in the magnitude of mammal latitudinal turnover gradients to cycling in Arctic ice volumes through changes in northern hemispheric albedo and mean annual precipitation through potentially correlated changes in ecosystem productivity (see Chapter 3). I conclude that the steep modern mammal turnover gradient is a product of latest Cenozoic global cooling and aridification as well as the formation of steep latitudinal climate gradients as northern hemispheric glaciation intensified.

Intervals such as the mid Miocene (~15 Ma; +6°C relative to modern pre-industrial), during which mammalian diversity gradients are weak, are typified by global temperatures comparable to scenarios for the next 100 years under anthropogenic climate change. On the short timescales (typically < 100 years) typical of ecological studies, northward dispersal alone might produce shallower latitudinal diversity gradients and the homogenization (i.e. low β diversity) of terrestrial communities as northern ecosystems are populated by typically southern species. The effects of extinction among high latitude

species on the magnitude of the latitudinal diversity gradient will depend in part on how many taxa go extinct and whether they are replaced by low latitude species. However, I showed that latitudinal turnover gradients of modern North American mammals showed little to no change under various forecasted scenarios for ongoing climate change (Chapter 3). The limitation of the species distribution and climate space models from which predictions of organismal climate change response are derived largely exclude extinction (except where the climate space for a given species entirely disappears from the landscape) and other evolutionary processes that operate even on very short timescales (Bradshaw and Holzapfel 2006). Although the utility of climate space modeling is questioned in my dissertation, I suggest that we can develop new models that are historically, evolutionarily, and phylogenetically cognizant through the combined study of both modern and ancient patterns of biodiversity.

During the preparation of Chapter 3 for publication and this dissertation, the primary concern of reviewers and committee members has been that I have not actually tested for ergodicity or the constancy of biodiversity drivers in space and time. My critics are correct in assuming that a direct test of ergodicity requires that correlate climate on the landscape (e.g. using terrestrial climate proxies) with diversity. In Chapter 3, I have correlated the magnitude of the latitude turnover gradient with global climate, making the assumption that terrestrial climate (particularly the steepness of latitudinal climate gradients) in North America are linked to global climates through changes in northern

hemispheric glaciation and primary productivity (assumptions that I support using climate models and terrestrial climate proxies where possible).

I have also encountered methodological concerns specifically regarding the use of detrended correspondence analysis (DCA) in Chapter 3. One particular criticism has been my discussion of the magnitude or strength of the latitudinal turnover gradient rather than the slope. DCA is an ordination method, thus each fossil site with its complement of species occupies a particular position along the first and second axes (I will not discuss the particular algorithm used by DCA here). When fitting an environmental variable to the ordination, effectively testing for a relationship with the position of each site in ordination space, the result is a vector or series of vectors, which have both direction and length as well as how much of the variation among sites is explained by the environmental variable (R^2 ; herein referred to as the magnitude or strength of the gradient). Slopes are not associated with the fitted environmental vectors. In general, the word magnitude refers to the size or extent of a phenomenon and so might be equated with the term “effect size.” The term “gradient strength” mirrors my use of R^2 values, which are a measure of the strength of a correlation among variables. Both “gradient strength” and “magnitude” are therefore equivalent terms.

The study of phylogenetic community structure is one means of exploring community response to climate change that is cognizant of evolutionary history. However, the theoretical framework for the study modern animal community phylogenetics relies primarily on competitive exclusion and abiotic species sorting as explanatory mechanisms (Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Cardillo 2011; Razafindratsima et al. 2012; Qian et al. 2013). The exclusion of extinct

taxa and thus often the majority of species diversity over time, means that contemporary community phylogenetic theory cannot explain the contribution of macroevolution to the formation of modern communities. In Chapter 4, I quantified changes in phylogenetic community structure for late Cenozoic (15 Ma – 0.01 Ma) North American hoofed mammals because they experience large extinctions following the mid Miocene climatic optimum (~15 Ma) that are associated with the reduction of woodland savannah (Janis et al. 2000; Janis et al. 2004). I showed that the phylogenetic relatedness of hoofed mammals declined in North America as global climates cooled. Typically, low latitude, warm climate plant and animal communities show phylogenetic evenness (species in a community are distantly related), whereas high latitude, cool climate communities show phylogenetic clustering (species in a community are closely related) (Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Qian et al. 2013). Although, I found the opposite trend of phylogenetic evenness among cool climate hoofed mammal communities I do not suggest the uncoupling of phylogenetic community structure and climate. Rather, I showed that widespread convergence of dietary traits among North American hoofed mammals and the disproportionate extinction of dicot specialists led to phylogenetic evenness rather than clustering.

Extinction is and will continue to play a major role in shaping communities under ongoing global climate change (Parmesan and Yohe 2003; Parmesan 2006). The findings in this dissertation suggest that whether future communities show phylogenetic evenness

or clustering will depend on whether ecologically relevant traits are conserved or convergent.

In this dissertation, I suggest that climate plays a central role in shaping spatial and temporal patterns of diversity. In modern ecosystems, climate heterogeneity, through the mechanism of abiotic species sorting, is particularly important in structuring spatial diversity patterns (Rohde 1991; Fraser 1998; Mitchell 2000; Hawkins et al. 2003; Peres-Neto et al. 2012; Qian and Ricklefs 2012). For example, steep diversity gradients are typically associated with steep climate gradients. To fully test whether the coupling of climate and diversity is time invariant, paleobiologists require a terrestrial climate record with high spatial and temporal resolution.

Although numerous terrestrial paleoclimate proxies exist (*inter alia* stable oxygen and carbon isotopes from fossil hard tissues and paleosols, plant macrofossils, pollen), no one record shows high enough spatiotemporal resolution. The Cenozoic mammal hard tissue isotopic record is particularly well sampled but is phylogenetically and physiologically poorly constrained. My long-term objectives include developing a comprehensive database of mammalian hard tissue isotopic terrestrial climate proxies for the late Cenozoic of North America that incorporates phylogenetic and physiological information. In Chapter 5, I showed that pronghorn, which have a spatiotemporally rich fossil record in North America, record nearly 100% of seasonal variation in $\delta^{18}\text{O}$ (‰) of environmental waters. Pronghorn are therefore an untapped source of data on paleoseasonality. Their membership in a comprehensive paleoclimate database will

enable more direct testing of my central hypothesis that the drivers of biodiversity patterns can be generalized in both space and time.

Chapter 5 is a geographically limited study of the utility of pronghorn for reconstructing some aspect of terrestrial paleoclimate (namely seasonality). Naturally, I cannot yet conclude whether the enamel of pronghorn from different geographic regions record their external environment with the same fidelity shown here, but there are good reasons to assume that they do and that differences among regions would reflect climatic rather than physiological differences. Physiological factors that influence $\delta^{18}\text{O}$ values in tooth enamel include body temperature and rates of enamel deposition and maturation. It almost goes without saying that most mammals maintain relatively constant body temperatures (Kohn et al. 1998). Certainly, within at least eutherian species there should be no dramatic differences in body temperature or ability to maintain a constant body temperature. Similarly, rates of enamel deposition and maturation should be phylogenetically conserved. I know of no study that has tested this assumption across a wide array of species in a phylogenetic context due to the limitations of destructive sampling but many have assumed species specific rates (e.g. (Hoppe et al. 2004b)). Behavioral differences, e.g. different food and water sources, among populations might show my assumption that pronghorn are uniformly good paleoclimate indicators to be incorrect but this remains to be tested.

6.2 Future lines of inquiry

As discussed in Chapter 4, temporal changes in phylogenetic community structure are likely dependent on numerous factors, including history of clades (e.g. species composition in preceding time intervals), patterns of origination and extinction across the

phylogenetic tree (e.g. whether they are phylogenetically clumped or dispersed), climate, and tectonic processes. However, a lack of theoretical framework for studying long term trends in phylogenetic community structure means it is unclear how PCS might change throughout the history of a clade. Studying trends in phylogenetic community structure through time using both simulation and the fossil record might reveal the effects of macroevolutionary processes (Fraser et al. 2015). Some of my current and future work (as well as the subject of my upcoming postdoctoral project) is focused on answering i) how might we expect phylogenetic community structure to change under various macroevolutionary scenarios?, ii) how has the community structure of non-ungulate clades changed throughout the late Cenozoic (25 Ma – present)?, iii) what are the environmental, macroevolutionary, and ecomorphological drivers of observed community changes?, and iv) what are the deep time origins of gradients in phylogenetic community structure?

To answer how we might expect phylogenetic community structure to change I am using simulation of phylogenetic trees under different macroevolutionary scenarios and the development of a new function for simulating phylogenetic community structure change through time. The effects of speciation and extinction on phylogenetic community structure should differ and depend on their distribution across the phylogenetic tree, i.e. whether speciation and extinction are phylogenetic dispersed or phylogenetic clumped. Under a pure birth model, addition of species should lead to phylogenetic clustering (high relatedness among species in a community) as existing species give rise to new, closely related species; values of the Net Relatedness Index (standardized mean pairwise phylogenetic distances among species in a community) should increase through time.

However, when a clade is experiencing both speciation and extinction, there are two possibilities. Phylogenetically dispersed extinction and speciation should result in a trend of increasing phylogenetic evenness (low relatedness among species in a community) through time as the average phylogenetic distance among taxa increases. Conversely, if extinction and speciation are phylogenetically clumped, there should be a trend of increasing phylogenetic clustering through time as the average phylogenetic distance among taxa decreases. Further, faster rates of speciation and extinction should result in faster temporal PCS change regardless of their distribution across the phylogenetic tree.

Mammals are ecologically diverse and clade-level patterns of speciation and extinction are largely dependent on whether ecologically relevant traits (i.e. those that determine extinction risk and speciation rates) are conserved or convergent (Green et al. 2011). I therefore do not necessarily expect clades with vastly different ecologies to show the same responses to late Cenozoic climate change as the hoofed mammals. Body size is particularly important because it influences the thermal properties of individuals (e.g. surface to volume ratios), their nutritional requirements (e.g. body mass specific metabolic rates), and the spatial scales at which individuals of a species experience and are affected by climate changes (Smith et al. 2010; Secord et al. 2012). The goals for my upcoming postdoctoral project therefore involve making direct comparisons among mammalian clades with different ecologies (e.g. carnivores and herbivores) and different mean body sizes (e.g. hoofed mammals and rodents), testing whether changes in rates of speciation and extinction are associated with observed changes in phylogenetic

community structure, and identifying traits integral in structuring macroevolutionary patterns within and among clades.

As mentioned in Chapter 4, modern latitudinal diversity gradients are associated with changes in phylogenetic composition of communities (Buckley and Jetz 2008; Qian et al. 2013). In general, high latitude communities are characterized by phylogenetic clustering, which is attributed to species sorting whereby species persist into or are excluded from a region based on their abiotic tolerances. Low latitude communities often show phylogenetic evenness, which is attributed to competitive exclusion (Qian et al. 2013). Abiotic species sorting is one process to which the existence of modern latitudinal richness gradients are attributed (Gaston 2000; Currie et al. 2004; Leibold et al. 2004; Pavoine and Bonsall 2010; Peres-Neto et al. 2012). Differences in rates of speciation and extinction, namely high rates of speciation at low latitudes and high rates of extinction at high latitudes, are also implicated in the formation of latitudinal richness gradients (Jablonski 1993; Mittelbach et al. 2007; Weir and Schlüter 2007; Rolland et al. 2014; Weir 2014). Studying the deep time origins of gradients in phylogenetic community assembly might reveal the extent to which macroevolutionary patterns and rates have influenced spatial diversity gradients.

6.3 Conclusions

Diversity patterns are well characterized for extant faunas, but there is a burgeoning interest in their deep-time origins. This dissertation has addressed when modern mammal latitudinal diversity gradients evolved as well as the roles of extinction and climate change in shaping mammal community structure, and is therefore a critical step in answering “What factors have led to the emergence of communities as we know

them today?" In this dissertation I have also made direct comparisons of a-historical and historical approaches to studying biodiversity change (Chapter 3) (Fraser et al. 2014b) and suggest that understanding the contribution of macroevolution is a prerequisite to testing hypotheses on the formation of modern communities.

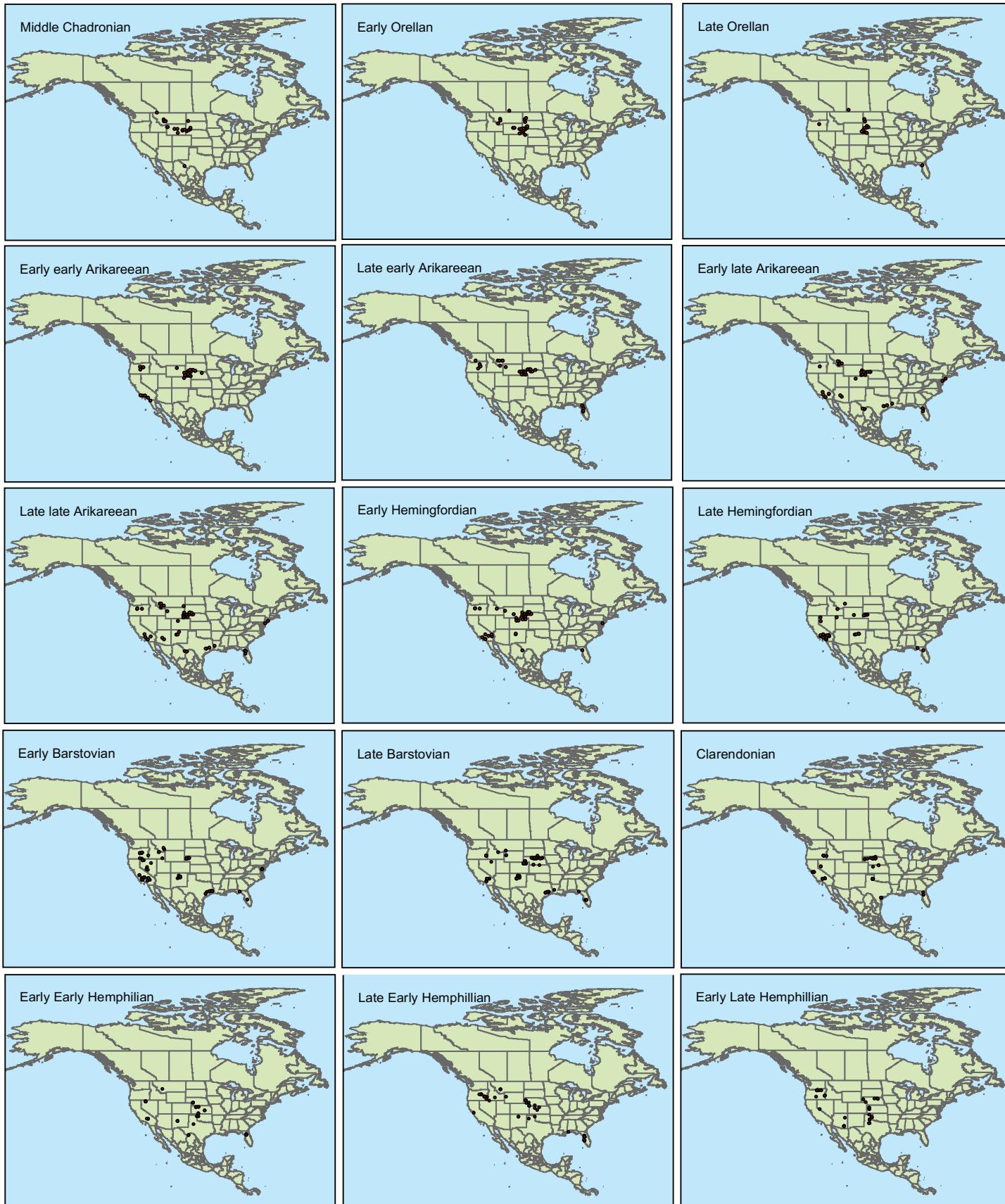
Mammalian responses to climate change vary on multiple temporal scales (Barnosky et al. 2003). On short timescales (years), mammal geographic ranges expand and contract due to local colonization and extirpation (Chen et al. 2011). On long timescales (thousands to millions of years), speciation, extinction, and adaptation dramatically alter terrestrial faunas. Modes of long-term response to climate change include, but are not limited to, shifts in body size, niches, and the identity of taxa within terrestrial communities (Mayhew et al. 2012; Secord et al. 2012). Current models for forecasting the outcomes of anthropogenic climate change use distributional information and climate data to project organismal ranges into the future under the assumption of no evolution (Lawler et al. 2006). However, rapid evolutionary changes have been observed on very short timescales (Lavergne et al. 2010); therefore current forecast models are unlikely to generate accurate predictions. Fortunately, the fossil record encompasses numerous evolutionary processes that are not yet modelled. I have shown in this dissertation that climate change has played a central role in structuring North American mammalian faunas, i.e. that the drivers of mammalian biodiversity are potentially "ergodic." Fossil faunas may therefore be used as independent tests of climate change forecasts as well as a means of generating historical data for incorporation into new forecast models (Fraser et al. 2014b).

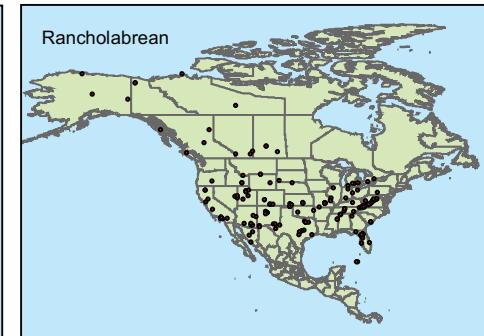
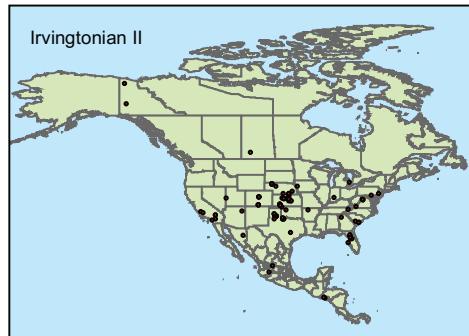
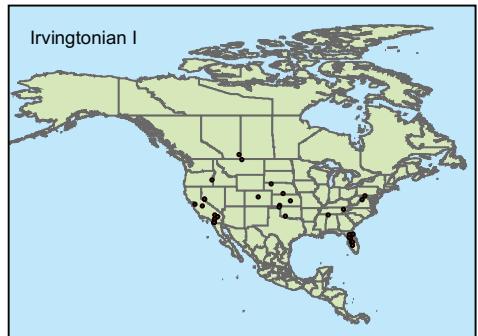
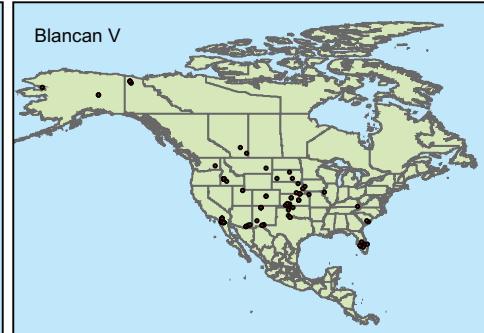
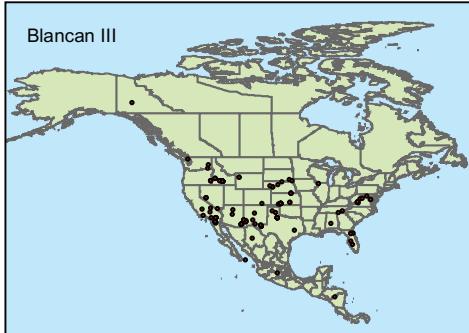
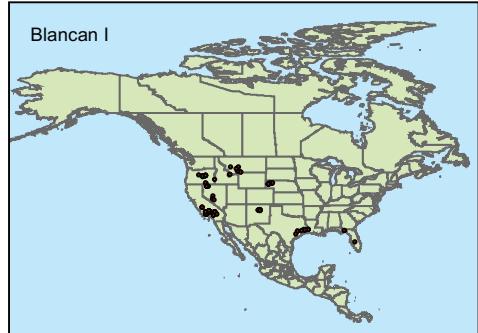
Appendices

Appendix A Maps of late Cenozoic mammalian fossil localities in North America.

For a higher resolution version of the following images please visit the following link.

http://previews.figshare.com/1667977/preview_1667977.jpg





Appendix B Modern North American mammal species included in the simulated fossilization trials.

Species	Status
<i>Abrawayaomys ruschii</i>	Not found north of equator
<i>Abrothrix andinus</i>	Not found north of equator
<i>Abrocoma bennettii</i>	Not found north of equator
<i>Abrocoma boliviensis</i>	Not found north of equator
<i>Abrocoma cinerea</i>	Not found north of equator
<i>Abrothrix hershkovitzi</i>	Not found north of equator
<i>Abrothrix illuteus</i>	Not found north of equator
<i>Abrothrix jelskii</i>	Not found north of equator
<i>Abrothrix lanosus</i>	Not found north of equator
<i>Abrothrix longipilis</i>	Not found north of equator
<i>Abrothrix markhami</i>	Not found north of equator
<i>Abrothrix olivaceus</i>	Not found north of equator
<i>Abrothrix sanborni</i>	Not found north of equator
<i>Abrocoma schistacea</i>	Not found north of equator
<i>Aconaemys fuscus</i>	Not found north of equator
<i>Aconaemys porteri</i>	Not found north of equator
<i>Aconaemys sagei</i>	Not found north of equator
<i>Aepeomys lugens</i>	INCLUDED
<i>Aepeomys reigi</i>	Less than 20 occurrences
<i>Akodon aerosus</i>	Not found north of equator
<i>Akodon affinis</i>	Less than 20 occurrences
<i>Akodon albiventer</i>	Not found north of equator
<i>Akodon aliquantulus</i>	Not found north of equator
<i>Akodon azarae</i>	Not found north of equator
<i>Akodon bogotensis</i>	INCLUDED
<i>Akodon boliviensis</i>	Not found north of equator
<i>Akodon budini</i>	Not found north of equator
<i>Akodon cursor</i>	Not found north of equator
<i>Akodon dayi</i>	Not found north of equator
<i>Akodon dolores</i>	Not found north of equator
<i>Akodon fumeus</i>	Not found north of equator
<i>Akodon iniscatus</i>	Not found north of equator
<i>Akodon juninensis</i>	Not found north of equator
<i>Akodon kofordi</i>	Not found north of equator
<i>Akodon latebricola</i>	Not found north of equator
<i>Akodon lindberghi</i>	Not found north of equator
<i>Akodon lutescens</i>	Not found north of equator

<i>Akodon mimus</i>	Not found north of equator
<i>Akodon molinae</i>	Not found north of equator
<i>Akodon mollis</i>	Not found north of equator
<i>Akodon montensis</i>	Not found north of equator
<i>Akodon mystax</i>	Not found north of equator
<i>Akodon neocenus</i>	Not found north of equator
<i>Akodon oenos</i>	Not found north of equator
<i>Akodon orophilus</i>	Not found north of equator
<i>Akodon paranaensis</i>	Not found north of equator
<i>Akodon reigi</i>	Not found north of equator
<i>Akodon sanctipaulensis</i>	Not found north of equator
<i>Akodon serrensis</i>	Not found north of equator
<i>Akodon siberiae</i>	Not found north of equator
<i>Akodon simulator</i>	Not found north of equator
<i>Akodon spegazzinii</i>	Not found north of equator
<i>Akodon subfuscus</i>	Not found north of equator
<i>Akodon surdus</i>	Not found north of equator
<i>Akodon sylvanus</i>	Not found north of equator
<i>Akodon toba</i>	Not found north of equator
<i>Akodon torques</i>	Not found north of equator
<i>Akodon varius</i>	Not found north of equator
<i>Alces americanus</i>	INCLUDED
<i>Alouatta belzebul</i>	Not found north of equator
<i>Alouatta caraya</i>	Not found north of equator
<i>Alouatta coibensis</i>	Less than 20 occurrences
<i>Alouatta guariba</i>	Not found north of equator
<i>Alouatta nigerrima</i>	Not found north of equator
<i>Alouatta palliata</i>	INCLUDED
<i>Alouatta pigra</i>	INCLUDED
<i>Alouatta sara</i>	Not found north of equator
<i>Alouatta seniculus</i>	INCLUDED
<i>Ametrida centurio</i>	INCLUDED
<i>Ammospermophilus harrisii</i>	INCLUDED
<i>Ammospermophilus insularis</i>	Less than 20 occurrences
<i>Ammospermophilus interpres</i>	INCLUDED
<i>Ammospermophilus leucurus</i>	INCLUDED
<i>Ammospermophilus nelsoni</i>	Less than 20 occurrences
<i>Amorphochilus schnablii</i>	Not found north of equator
<i>Amphinectomys savamis</i>	Not found north of equator
<i>Andalgalomys olrogi</i>	Not found north of equator
<i>Andalgalomys pearsoni</i>	Not found north of equator
<i>Andalgalomys roigi</i>	Not found north of equator
<i>Andinomys edax</i>	Not found north of equator

<i>Anatomys leander</i>	Not found north of equator
<i>Anoura caudifer</i>	INCLUDED
<i>Anoura cultrata</i>	INCLUDED
<i>Anoura geoffroyi</i>	INCLUDED
<i>Anoura latidens</i>	INCLUDED
<i>Anoura luismanueli</i>	Less than 20 occurrences
<i>Antilocapra americana</i>	INCLUDED
<i>Antrozous pallidus</i>	INCLUDED
<i>Aotus azarae</i>	Not found north of equator
<i>Aotus lemurinus</i>	INCLUDED
<i>Aotus miconax</i>	Not found north of equator
<i>Aotus nancymaae</i>	Not found north of equator
<i>Aotus nigriceps</i>	Not found north of equator
<i>Aotus trivirgatus</i>	INCLUDED
<i>Aotus vociferans</i>	INCLUDED
<i>Aplodontia rufa</i>	INCLUDED
<i>Arborimus albipes</i>	Less than 20 occurrences
<i>Arborimus longicaudus</i>	Less than 20 occurrences
<i>Arborimus pomo</i>	Less than 20 occurrences
<i>Ardops nichollsi</i>	Less than 20 occurrences
<i>Arteus flavescens</i>	Less than 20 occurrences
<i>Artibeus amplus</i>	INCLUDED
<i>Artibeus anderseni</i>	Not found north of equator
<i>Artibeus aztecus</i>	INCLUDED
<i>Artibeus cinereus</i>	INCLUDED
<i>Artibeus concolor</i>	INCLUDED
<i>Artibeus fimbriatus</i>	Not found north of equator
<i>Artibeus fraterculus</i>	Not found north of equator
<i>Artibeus glaucus</i>	INCLUDED
<i>Artibeus gnomus</i>	INCLUDED
<i>Artibeus hirsutus</i>	INCLUDED
<i>Artibeus inopinatus</i>	Less than 20 occurrences
<i>Artibeus jamaicensis</i>	INCLUDED
<i>Artibeus lituratus</i>	INCLUDED
<i>Artibeus obscurus</i>	INCLUDED
<i>Artibeus phaeotis</i>	INCLUDED
<i>Artibeus toltecus</i>	INCLUDED
<i>Artibeus triomylus</i>	INCLUDED
<i>Artibeus watsoni</i>	INCLUDED
<i>Ateles belzebuth</i>	INCLUDED
<i>Ateles chamek</i>	Not found north of equator
<i>Ateles fusciceps</i>	INCLUDED
<i>Ateles geoffroyi</i>	INCLUDED

<i>Ateles hybridus</i>	INCLUDED
<i>Ateles marginatus</i>	Not found north of equator
<i>Atelocynus microtis</i>	INCLUDED
<i>Ateles paniscus</i>	INCLUDED
<i>Auliscomys boliviensis</i>	Not found north of equator
<i>Auliscomys pictus</i>	Not found north of equator
<i>Auliscomys sublimis</i>	Not found north of equator
<i>Baiomys musculus</i>	INCLUDED
<i>Baiomys taylori</i>	INCLUDED
<i>Balantiopteryx infusca</i>	Less than 20 occurrences
<i>Balantiopteryx io</i>	INCLUDED
<i>Balantiopteryx plicata</i>	INCLUDED
<i>Bassaricyon alleni</i>	Not found north of equator
<i>Bassariscus astutus</i>	INCLUDED
<i>Bassaricyon beddardi</i>	INCLUDED
<i>Bassaricyon gabbii</i>	INCLUDED
<i>Bassaricyon lasius</i>	Less than 20 occurrences
<i>Bassaricyon pauli</i>	Less than 20 occurrences
<i>Bassariscus sumichrasti</i>	INCLUDED
<i>Bauerus dubiaquercus</i>	INCLUDED
<i>Bibimys chacoensis</i>	Not found north of equator
<i>Bibimys labiosus</i>	Not found north of equator
<i>Bibimys torresi</i>	Not found north of equator
<i>Blarinomys breviceps</i>	Not found north of equator
<i>Blarina carolinensis</i>	INCLUDED
<i>Blarina hylophaga</i>	INCLUDED
<i>Blastocerus dichotomus</i>	Not found north of equator
<i>Bos bison</i>	INCLUDED
<i>Brachyteles arachnoides</i>	Not found north of equator
<i>Brachyphylla cavernarum</i>	Less than 20 occurrences
<i>Brachyteles hypoxanthus</i>	Not found north of equator
<i>Brachylagus idahoensis</i>	INCLUDED
<i>Brachyphylla nana</i>	INCLUDED
<i>Bradypus torquatus</i>	Not found north of equator
<i>Bradypus tridactylus</i>	INCLUDED
<i>Bradypus variegatus</i>	INCLUDED
<i>Brucepattersonius albinasus</i>	Not found north of equator
<i>Brucepattersonius griserufescens</i>	Not found north of equator
<i>Brucepattersonius guarani</i>	Not found north of equator
<i>Brucepattersonius igniventris</i>	Not found north of equator
<i>Brucepattersonius iheringi</i>	Not found north of equator
<i>Brucepattersonius misionensis</i>	Not found north of equator

<i>Brucepattersonius paradisus</i>	Not found north of equator
<i>Brucepattersonius soricinus</i>	Not found north of equator
<i>Cabassous centralis</i>	INCLUDED
<i>Cabassous chacoensis</i>	Not found north of equator
<i>Cabassous tatouay</i>	Not found north of equator
<i>Cabassous unicinctus</i>	INCLUDED
<i>Cacajao calvus</i>	Not found north of equator
<i>Cacajao melanocephalus</i>	Less than 20 occurrences
<i>Caenolestes caniventer</i>	Not found north of equator
<i>Caenolestes convelatus</i>	Less than 20 occurrences
<i>Caenolestes fuliginosus</i>	INCLUDED
<i>Callithrix acariensis</i>	Not found north of equator
<i>Callithrix argentata</i>	Not found north of equator
<i>Callicebus aureipalatii</i>	Not found north of equator
<i>Callithrix aurita</i>	Not found north of equator
<i>Callicebus baptista</i>	Not found north of equator
<i>Callicebus barbarabrownae</i>	Not found north of equator
<i>Callicebus bernhardi</i>	Not found north of equator
<i>Callicebus brunneus</i>	Not found north of equator
<i>Callicebus caligatus</i>	Not found north of equator
<i>Callithrix chrysoleuca</i>	Not found north of equator
<i>Callicebus cinerascens</i>	Not found north of equator
<i>Callicebus coimbrai</i>	Not found north of equator
<i>Callicebus cupreus</i>	Not found north of equator
<i>Callicebus discolor</i>	Not found north of equator
<i>Callicebus donacophilus</i>	Not found north of equator
<i>Callicebus dubius</i>	Not found north of equator
<i>Callithrix emiliae</i>	Not found north of equator
<i>Callithrix flaviceps</i>	Not found north of equator
<i>Callithrix geoffroyi</i>	Not found north of equator
<i>Callimico goeldii</i>	Not found north of equator
<i>Callicebus hoffmannsi</i>	Not found north of equator
<i>Callithrix humeralifera</i>	Not found north of equator
<i>Callibella humilis</i>	Not found north of equator
<i>Callithrix intermedia</i>	Not found north of equator
<i>Callithrix jacchus</i>	Not found north of equator
<i>Callithrix kuhlii</i>	Not found north of equator
<i>Callithrix leucippe</i>	Not found north of equator
<i>Callicebus lucifer</i>	Not found north of equator
<i>Callicebus lugens</i>	INCLUDED
<i>Callithrix manicorensis</i>	Not found north of equator
<i>Callithrix marcai</i>	Not found north of equator
<i>Callithrix mauesi</i>	Not found north of equator

<i>Callicebus medemi</i>	Not found north of equator
<i>Callithrix melanura</i>	Not found north of equator
<i>Callicebus modestus</i>	Not found north of equator
<i>Callicebus moloch</i>	Not found north of equator
<i>Callithrix nigriceps</i>	Not found north of equator
<i>Callicebus oenanthe</i>	Not found north of equator
<i>Callicebus olallae</i>	Not found north of equator
<i>Callicebus ornatus</i>	Less than 20 occurrences
<i>Callicebus pallescens</i>	Not found north of equator
<i>Callithrix penicillata</i>	Not found north of equator
<i>Callicebus personatus</i>	Not found north of equator
<i>Callistomys pictus</i>	Not found north of equator
<i>Callicebus purinus</i>	Not found north of equator
<i>Callithrix pygmaea</i>	Not found north of equator
<i>Callicebus regulus</i>	Not found north of equator
<i>Callithrix saterei</i>	Not found north of equator
<i>Callicebus stephennashi</i>	Not found north of equator
<i>Callicebus torquatus</i>	Not found north of equator
<i>Calomys boliviae</i>	Not found north of equator
<i>Calomys callidus</i>	Not found north of equator
<i>Calomys callosus</i>	Not found north of equator
<i>Calomys hummelincki</i>	INCLUDED
<i>Calomys laucha</i>	Less than 20 occurrences
<i>Calomys lepidus</i>	Not found north of equator
<i>Calomys musculinus</i>	Not found north of equator
<i>Calomys sorellus</i>	Not found north of equator
<i>Calomys tener</i>	Not found north of equator
<i>Calomys tocantinsi</i>	Not found north of equator
<i>Caluromys derbianus</i>	INCLUDED
<i>Caluromysiops irrupta</i>	Not found north of equator
<i>Caluromys lanatus</i>	INCLUDED
<i>Caluromys philander</i>	INCLUDED
<i>Calyptophractus retusus</i>	Not found north of equator
<i>Canis latrans</i>	INCLUDED
<i>Canis lupus</i>	INCLUDED
<i>Canis rufus</i>	INCLUDED
<i>Capromys pilorides</i>	Less than 20 occurrences
<i>Carollia brevicauda</i>	INCLUDED
<i>Carollia castanea</i>	INCLUDED
<i>Carollia manu</i>	Not found north of equator
<i>Carollia perspicillata</i>	INCLUDED
<i>Carollia sowelli</i>	INCLUDED
<i>Carollia subrufa</i>	INCLUDED

<i>Carterodon sulcidens</i>	Not found north of equator
<i>Castor canadensis</i>	INCLUDED
<i>Catagonus wagneri</i>	Not found north of equator
<i>Cavia aperea</i>	INCLUDED
<i>Cavia fulgida</i>	Not found north of equator
<i>Cavia magna</i>	Not found north of equator
<i>Cavia porcellus</i>	INCLUDED
<i>Cavia tschudii</i>	Not found north of equator
<i>Cebus albifrons</i>	INCLUDED
<i>Cebus apella</i>	INCLUDED
<i>Cebus capucinus</i>	INCLUDED
<i>Cebus kaapori</i>	Not found north of equator
<i>Cebus libidinosus</i>	Not found north of equator
<i>Cebus nigritus</i>	Not found north of equator
<i>Cebus olivaceus</i>	INCLUDED
<i>Cebus xanthosternos</i>	Not found north of equator
<i>Centronycteris centralis</i>	INCLUDED
<i>Centronycteris maximiliani</i>	INCLUDED
<i>Centurio senex</i>	INCLUDED
<i>Cerdocyon thous</i>	INCLUDED
<i>Cervus canadensis</i>	INCLUDED
<i>Chaetodipus arenarius</i>	INCLUDED
<i>Chaetodipus artus</i>	Less than 20 occurrences
<i>Chaetodipus baileyi</i>	INCLUDED
<i>Chaetodipus californicus</i>	INCLUDED
<i>Chaetodipus eremicus</i>	INCLUDED
<i>Chaetodipus fallax</i>	Less than 20 occurrences
<i>Chaetodipus formosus</i>	INCLUDED
<i>Chaetodipus goldmani</i>	Less than 20 occurrences
<i>Chaetodipus hispidus</i>	INCLUDED
<i>Chaetodipus intermedius</i>	INCLUDED
<i>Chaetodipus lineatus</i>	Less than 20 occurrences
<i>Chaetophractus nationi</i>	Not found north of equator
<i>Chaetodipus nelsoni</i>	INCLUDED
<i>Chaetodipus penicillatus</i>	INCLUDED
<i>Chaetodipus pernix</i>	INCLUDED
<i>Chaetodipus rufinoris</i>	INCLUDED
<i>Chaetodipus spinatus</i>	INCLUDED
<i>Chaetomys subspinosus</i>	Not found north of equator
<i>Chaetophractus vellerosus</i>	Not found north of equator
<i>Chaetophractus villosus</i>	Not found north of equator
<i>Chelemys delfini</i>	Not found north of equator
<i>Chelemys macronyx</i>	Not found north of equator

<i>Chelemys megalonyx</i>	Not found north of equator
<i>Chibchanomys orcesi</i>	Not found north of equator
<i>Chibchanomys trichotis</i>	INCLUDED
<i>Chiromys instans</i>	INCLUDED
<i>Chilonatalus micropus</i>	INCLUDED
<i>Chilonatalus tumidifrons</i>	INCLUDED
<i>Chinchilla chinchilla</i>	Not found north of equator
<i>Chinchilla lanigera</i>	Not found north of equator
<i>Chinchillula sahamae</i>	Not found north of equator
<i>Chiropotes albinasus</i>	Not found north of equator
<i>Chiropotes chiropotes</i>	INCLUDED
<i>Chiroderma doriae</i>	Not found north of equator
<i>Chiroderma improvisum</i>	Less than 20 occurrences
<i>Chironectes minimus</i>	INCLUDED
<i>Chiroderma salvini</i>	INCLUDED
<i>Chiropotes satanas</i>	Not found north of equator
<i>Chiroderma trinitatum</i>	INCLUDED
<i>Chiropotes utahickae</i>	Not found north of equator
<i>Chiroderma villosum</i>	INCLUDED
<i>Chlamyphorus truncatus</i>	Not found north of equator
<i>Choeroniscus godmani</i>	INCLUDED
<i>Choeronycteris mexicana</i>	INCLUDED
<i>Choeroniscus minor</i>	INCLUDED
<i>Choeroniscus periosus</i>	Less than 20 occurrences
<i>Choloepus didactylus</i>	INCLUDED
<i>Choloepus hoffmanni</i>	INCLUDED
<i>Chrotopterus auritus</i>	INCLUDED
<i>Chrysocyon brachyurus</i>	Not found north of equator
<i>Clyomys bishopi</i>	Not found north of equator
<i>Clyomys laticeps</i>	Not found north of equator
<i>Coendou bicolor</i>	Less than 20 occurrences
<i>Coendou nycthemera</i>	Not found north of equator
<i>Coendou prehensilis</i>	INCLUDED
<i>Coendou rothschildi</i>	Less than 20 occurrences
<i>Condylura cristata</i>	INCLUDED
<i>Conepatus chinga</i>	Not found north of equator
<i>Conepatus humboldtii</i>	Not found north of equator
<i>Conepatus leuconotus</i>	INCLUDED
<i>Conepatus semistriatus</i>	INCLUDED
<i>Cormura brevirostris</i>	INCLUDED
<i>Corynorhinus mexicanus</i>	INCLUDED
<i>Corynorhinus rafinesquii</i>	INCLUDED
<i>Corynorhinus townsendii</i>	INCLUDED

<i>Cratogeomys castanops</i>	INCLUDED
<i>Cratogeomys fumosus</i>	Less than 20 occurrences
<i>Cratogeomys gymnurus</i>	Less than 20 occurrences
<i>Cratogeomys merriami</i>	Less than 20 occurrences
<i>Cratogeomys neglectus</i>	Less than 20 occurrences
<i>Cratogeomys tylorhinus</i>	Less than 20 occurrences
<i>Cratogeomys zinseri</i>	Less than 20 occurrences
<i>Cryptotis alticola</i>	Less than 20 occurrences
<i>Cryptotis colombiana</i>	Less than 20 occurrences
<i>Cryptotis endersi</i>	Less than 20 occurrences
<i>Cryptotis equatoris</i>	Not found north of equator
<i>Cryptotis goldmani</i>	Less than 20 occurrences
<i>Cryptotis goodwini</i>	Less than 20 occurrences
<i>Cryptotis gracilis</i>	Less than 20 occurrences
<i>Cryptotis griseoventris</i>	Less than 20 occurrences
<i>Cryptotis hondurensis</i>	Less than 20 occurrences
<i>Cryptotis magna</i>	Less than 20 occurrences
<i>Cryptotis mayensis</i>	INCLUDED
<i>Cryptotis medellinia</i>	Less than 20 occurrences
<i>Cryptotis mera</i>	Less than 20 occurrences
<i>Cryptotis meridensis</i>	Less than 20 occurrences
<i>Cryptotis merriami</i>	INCLUDED
<i>Cryptotis mexicana</i>	Less than 20 occurrences
<i>Cryptotis montivaga</i>	Not found north of equator
<i>Cryptotis nelsoni</i>	Less than 20 occurrences
<i>Cryptotis nigrescens</i>	INCLUDED
<i>Cryptotis obscura</i>	Less than 20 occurrences
<i>Cryptotis parva</i>	INCLUDED
<i>Cryptotis peregrina</i>	Less than 20 occurrences
<i>Cryptotis phillipsii</i>	Less than 20 occurrences
<i>Cryptotis squamipes</i>	Less than 20 occurrences
<i>Cryptotis tamensis</i>	Less than 20 occurrences
<i>Cryptotis thomasi</i>	Less than 20 occurrences
<i>Ctenomys argentinus</i>	Not found north of equator
<i>Ctenomys australis</i>	Not found north of equator
<i>Ctenomys azarae</i>	Not found north of equator
<i>Ctenomys bergi</i>	Not found north of equator
<i>Ctenomys boliviensis</i>	Not found north of equator
<i>Ctenomys bonettoi</i>	Not found north of equator
<i>Ctenomys brasiliensis</i>	Not found north of equator
<i>Ctenomys colburni</i>	Not found north of equator
<i>Ctenomys conoveri</i>	Not found north of equator
<i>Ctenomys dorbignyi</i>	Not found north of equator

<i>Ctenomys dorsalis</i>	Not found north of equator
<i>Ctenomys emilianus</i>	Not found north of equator
<i>Ctenomys flamarioni</i>	Not found north of equator
<i>Ctenomys frater</i>	Not found north of equator
<i>Ctenomys fulvus</i>	Not found north of equator
<i>Ctenomys goodfellowi</i>	Not found north of equator
<i>Ctenomys haigi</i>	Not found north of equator
<i>Ctenomys knighti</i>	Not found north of equator
<i>Ctenomys latro</i>	Not found north of equator
<i>Ctenomys leucodon</i>	Not found north of equator
<i>Ctenomys lewisi</i>	Not found north of equator
<i>Ctenomys magellanicus</i>	Not found north of equator
<i>Ctenomys maulinus</i>	Not found north of equator
<i>Ctenomys mendocinus</i>	Not found north of equator
<i>Ctenomys minutus</i>	Not found north of equator
<i>Ctenomys occultus</i>	Not found north of equator
<i>Ctenomys opimus</i>	Not found north of equator
<i>Ctenomys osvaldoreigi</i>	Not found north of equator
<i>Ctenomys pearsoni</i>	Not found north of equator
<i>Ctenomys perrensi</i>	Not found north of equator
<i>Ctenomys peruanus</i>	Not found north of equator
<i>Ctenomys pontifex</i>	Not found north of equator
<i>Ctenomys porteousi</i>	Not found north of equator
<i>Ctenomys rionegrensis</i>	Not found north of equator
<i>Ctenomys saltarius</i>	Not found north of equator
<i>Ctenomys sericeus</i>	Not found north of equator
<i>Ctenomys sociabilis</i>	Not found north of equator
<i>Ctenomys steinbachi</i>	Not found north of equator
<i>Ctenomys talarum</i>	Not found north of equator
<i>Ctenomys torquatus</i>	Not found north of equator
<i>Ctenomys tuconax</i>	Not found north of equator
<i>Ctenomys tucumanus</i>	Not found north of equator
<i>Ctenomys validus</i>	Not found north of equator
<i>Cuniculus paca</i>	INCLUDED
<i>Cuniculus taczanowskii</i>	INCLUDED
<i>Cuscomys ashaninka</i>	Not found north of equator
<i>Cyclopes didactylus</i>	INCLUDED
<i>Cynomops abrasus</i>	INCLUDED
<i>Cynomys gunnisoni</i>	INCLUDED
<i>Cynomys leucurus</i>	INCLUDED
<i>Cynomys ludovicianus</i>	INCLUDED
<i>Cynomops mexicanus</i>	Less than 20 occurrences
<i>Cynomops paranus</i>	INCLUDED

<i>Cynomys parvidens</i>	Less than 20 occurrences
<i>Cynomops planirostris</i>	INCLUDED
<i>Cyttarops alecto</i>	INCLUDED
<i>Dactylomys boliviensis</i>	Not found north of equator
<i>Dactylomys dactylinus</i>	Less than 20 occurrences
<i>Dactylomys peruanus</i>	Not found north of equator
<i>Dasyprocta azarae</i>	Not found north of equator
<i>Dasyprocta coibae</i>	Less than 20 occurrences
<i>Dasyprocta fuliginosa</i>	INCLUDED
<i>Dasyprocta guamara</i>	Less than 20 occurrences
<i>Dasyproctus hybridus</i>	Not found north of equator
<i>Dasyprocta kalinowskii</i>	Not found north of equator
<i>Dasyproctus kappleri</i>	INCLUDED
<i>Dasyprocta leporina</i>	INCLUDED
<i>Dasyprocta mexicana</i>	INCLUDED
<i>Dasyproctus novemcinctus</i>	INCLUDED
<i>Dasyproctus pilosus</i>	Not found north of equator
<i>Dasyprocta prymnolopha</i>	Not found north of equator
<i>Dasyprocta punctata</i>	INCLUDED
<i>Dasyprocta ruatanica</i>	Not found north of equator
<i>Dasyproctus sabanicola</i>	INCLUDED
<i>Dasyproctus septemcinctus</i>	Not found north of equator
<i>Delomys dorsalis</i>	Not found north of equator
<i>Delomys sublineatus</i>	Not found north of equator
<i>Deltamys kempfi</i>	Not found north of equator
<i>Desmodus rotundus</i>	INCLUDED
<i>Diaeetus youngi</i>	INCLUDED
<i>Diclidurus albus</i>	INCLUDED
<i>Diclidurus ingens</i>	INCLUDED
<i>Diclidurus isabellus</i>	INCLUDED
<i>Diclidurus scutatus</i>	INCLUDED
<i>Dicrostonyx groenlandicus</i>	INCLUDED
<i>Dicrostonyx hudsonius</i>	INCLUDED
<i>Dicrostonyx nelsoni</i>	INCLUDED
<i>Dicrostonyx nunatakensis</i>	INCLUDED
<i>Dicrostonyx richardsoni</i>	INCLUDED
<i>Dicrostonyx unalascensis</i>	Less than 20 occurrences
<i>Didelphis albiventris</i>	INCLUDED
<i>Didelphis aurita</i>	Not found north of equator
<i>Didelphis imperfecta</i>	INCLUDED
<i>Didelphis marsupialis</i>	INCLUDED
<i>Didelphis pernigra</i>	INCLUDED
<i>Didelphis virginiana</i>	INCLUDED

<i>Dynomys branickii</i>	INCLUDED
<i>Diphylla ecaudata</i>	INCLUDED
<i>Diplomys caniceps</i>	Less than 20 occurrences
<i>Diplomys labilis</i>	Less than 20 occurrences
<i>Diplomys rufodorsalis</i>	Less than 20 occurrences
<i>Dipodomys agilis</i>	Less than 20 occurrences
<i>Dipodomys californicus</i>	INCLUDED
<i>Dipodomys compactus</i>	Less than 20 occurrences
<i>Dipodomys deserti</i>	INCLUDED
<i>Dipodomys elator</i>	Less than 20 occurrences
<i>Dipodomys gravipes</i>	Less than 20 occurrences
<i>Dipodomys heermanni</i>	Less than 20 occurrences
<i>Dipodomys ingens</i>	Less than 20 occurrences
<i>Dipodomys merriami</i>	INCLUDED
<i>Dipodomys microps</i>	INCLUDED
<i>Dipodomys nelsoni</i>	INCLUDED
<i>Dipodomys nitratoides</i>	Less than 20 occurrences
<i>Dipodomys ordii</i>	INCLUDED
<i>Dipodomys panamintinus</i>	Less than 20 occurrences
<i>Dipodomys phillipsii</i>	INCLUDED
<i>Dipodomys simulans</i>	INCLUDED
<i>Dipodomys spectabilis</i>	INCLUDED
<i>Dipodomys stephensi</i>	Less than 20 occurrences
<i>Dipodomys venustus</i>	Less than 20 occurrences
<i>Dolichotis patagonum</i>	Not found north of equator
<i>Dolichotis salinicola</i>	Not found north of equator
<i>Dromiciops gliroides</i>	Not found north of equator
<i>Echimys chrysurus</i>	INCLUDED
<i>Echinoprocta rufescens</i>	Less than 20 occurrences
<i>Echimys saturnus</i>	Not found north of equator
<i>Echimys semivillosus</i>	INCLUDED
<i>Ectophylla alba</i>	INCLUDED
<i>Eira barbara</i>	INCLUDED
<i>Eligmodontia moreni</i>	Not found north of equator
<i>Eligmodontia morgani</i>	Not found north of equator
<i>Eligmodontia puerulus</i>	Not found north of equator
<i>Eligmodontia typus</i>	Not found north of equator
<i>Enchisthenes hartii</i>	INCLUDED
<i>Eptesicus andinus</i>	INCLUDED
<i>Eptesicus brasiliensis</i>	INCLUDED
<i>Eptesicus chiriquinus</i>	INCLUDED
<i>Eptesicus diminutus</i>	Not found north of equator
<i>Eptesicus furinalis</i>	INCLUDED

<i>Eptesicus fuscus</i>	INCLUDED
<i>Eptesicus guadeloupensis</i>	Less than 20 occurrences
<i>Eptesicus innoxius</i>	Not found north of equator
<i>Erethizon dorsatum</i>	INCLUDED
<i>Erophylla bombifrons</i>	Less than 20 occurrences
<i>Erophylla sezekorni</i>	Less than 20 occurrences
<i>Euderma maculatum</i>	INCLUDED
<i>Eumops auripendulus</i>	INCLUDED
<i>Eumops bonariensis</i>	INCLUDED
<i>Eumops dabbenei</i>	INCLUDED
<i>Eumops glaucinus</i>	INCLUDED
<i>Eumops hansae</i>	INCLUDED
<i>Eumops maurus</i>	INCLUDED
<i>Eumops perotis</i>	INCLUDED
<i>Eumops trumbulli</i>	INCLUDED
<i>Eumops underwoodi</i>	INCLUDED
<i>Euneomys chinchilloides</i>	Not found north of equator
<i>Euneomys fossor</i>	Not found north of equator
<i>Euneomys mordax</i>	Not found north of equator
<i>Euneomys petersoni</i>	Not found north of equator
<i>Euphractus sexcinctus</i>	Less than 20 occurrences
<i>Euryzygomatomys spinosus</i>	Not found north of equator
<i>Furipterus horrens</i>	INCLUDED
<i>Galea flavidens</i>	Not found north of equator
<i>Galenomys garleppi</i>	Not found north of equator
<i>Galea musteloides</i>	Not found north of equator
<i>Galea spixii</i>	Not found north of equator
<i>Galictis cuja</i>	Not found north of equator
<i>Galictis vittata</i>	INCLUDED
<i>Geocapromys brownii</i>	Less than 20 occurrences
<i>Geocapromys ingrahami</i>	Less than 20 occurrences
<i>Geomys arenarius</i>	INCLUDED
<i>Geomys attwateri</i>	Less than 20 occurrences
<i>Geomys breviceps</i>	INCLUDED
<i>Geomys bursarius</i>	INCLUDED
<i>Geomys knoxjonesi</i>	Less than 20 occurrences
<i>Geomys personatus</i>	INCLUDED
<i>Geomys pinetis</i>	INCLUDED
<i>Geomys streckeri</i>	Less than 20 occurrences
<i>Geomys texensis</i>	Less than 20 occurrences
<i>Geoxus valdivianus</i>	Not found north of equator
<i>Glaucomys sabrinus</i>	INCLUDED
<i>Glaucomys volans</i>	INCLUDED

<i>Glironia venusta</i>	Not found north of equator
<i>Glossophaga commissarisi</i>	INCLUDED
<i>Glossophaga leachii</i>	INCLUDED
<i>Glossophaga longirostris</i>	INCLUDED
<i>Glossophaga morenoi</i>	INCLUDED
<i>Glossophaga soricina</i>	INCLUDED
<i>Glyphonycteris behnii</i>	Not found north of equator
<i>Glyphonycteris daviesi</i>	INCLUDED
<i>Glyphonycteris sylvestris</i>	INCLUDED
<i>Gracilinanus aceramarcae</i>	Not found north of equator
<i>Gracilinanus agilis</i>	Less than 20 occurrences
<i>Gracilinanus dryas</i>	Less than 20 occurrences
<i>Gracilinanus emiliae</i>	Less than 20 occurrences
<i>Gracilinanus marica</i>	INCLUDED
<i>Gracilinanus microtarsus</i>	Not found north of equator
<i>Graomys domorum</i>	Not found north of equator
<i>Graomys edithae</i>	Not found north of equator
<i>Graomys griseoflavus</i>	Not found north of equator
<i>Gulo gulo</i>	INCLUDED
<i>Habromys chinanteco</i>	Less than 20 occurrences
<i>Habromys lepturus</i>	Less than 20 occurrences
<i>Habromys lophurus</i>	Less than 20 occurrences
<i>Habromys simulatus</i>	Less than 20 occurrences
<i>Handleymys fuscatus</i>	Less than 20 occurrences
<i>Handleymys intectus</i>	Less than 20 occurrences
<i>Herpestes javanicus</i>	INCLUDED
<i>Heteromys anomalus</i>	INCLUDED
<i>Heteromys australis</i>	INCLUDED
<i>Heteromys desmarestianus</i>	INCLUDED
<i>Heteromys gaumeri</i>	INCLUDED
<i>Heteromys nelsoni</i>	Less than 20 occurrences
<i>Heteromys oasicus</i>	Less than 20 occurrences
<i>Heteromys oresterus</i>	Less than 20 occurrences
<i>Heteromys teleus</i>	Not found north of equator
<i>Hippocamelus antisensis</i>	Not found north of equator
<i>Hippocamelus bisulcus</i>	Not found north of equator
<i>Histiotus alienus</i>	Not found north of equator
<i>Histiotus humboldti</i>	INCLUDED
<i>Histiotus macrotus</i>	Not found north of equator
<i>Histiotus montanus</i>	INCLUDED
<i>Histiotus velatus</i>	Not found north of equator
<i>Hodomys allenii</i>	INCLUDED
<i>Holochilus brasiliensis</i>	Not found north of equator

<i>Holochilus chacarius</i>	Not found north of equator
<i>Holochilus sciureus</i>	INCLUDED
<i>Hoplomys gymnurus</i>	Less than 20 occurrences
<i>Hydrochoerus hydrochaeris</i>	INCLUDED
<i>Hyladelphys kalinowskii</i>	Less than 20 occurrences
<i>Hylonycteris underwoodi</i>	INCLUDED
<i>Ichthyomys hydrobates</i>	INCLUDED
<i>Ichthyomys pittieri</i>	Less than 20 occurrences
<i>Ichthyomys stolzmanni</i>	Not found north of equator
<i>Ichthyomys tweedii</i>	Less than 20 occurrences
<i>Idionycteris phyllotis</i>	INCLUDED
<i>Irenomys tarsalis</i>	Not found north of equator
<i>Isolobodon montanus</i>	Less than 20 occurrences
<i>Isolobodon portoricensis</i>	Less than 20 occurrences
<i>Isothrix bistriata</i>	Less than 20 occurrences
<i>Isothrix negrensis</i>	Not found north of equator
<i>Isothrix pagurus</i>	Not found north of equator
<i>Isothrix sinnamariensis</i>	Less than 20 occurrences
<i>Isthmomys flavidus</i>	Less than 20 occurrences
<i>Isthmomys pirrensis</i>	Less than 20 occurrences
<i>Juliomys pictipes</i>	Not found north of equator
<i>Juliomys rimofrons</i>	Not found north of equator
<i>Juscelinomys guaporensis</i>	Not found north of equator
<i>Juscelinomys huanchacae</i>	Not found north of equator
<i>Kannabateomys amblyonyx</i>	Not found north of equator
<i>Kerodon acrobata</i>	Not found north of equator
<i>Kerodon rupestris</i>	Not found north of equator
<i>Kunsia fronto</i>	Not found north of equator
<i>Kunsia tomentosus</i>	Not found north of equator
<i>Lagidium peruanum</i>	Not found north of equator
<i>Lagidium viscacia</i>	Not found north of equator
<i>Lagidium wolffsohni</i>	Not found north of equator
<i>Lagothrix cana</i>	Not found north of equator
<i>Lagothrix lagothricha</i>	Less than 20 occurrences
<i>Lagothrix lugens</i>	INCLUDED
<i>Lagostomus maximus</i>	Not found north of equator
<i>Lagothrix poeppigii</i>	Not found north of equator
<i>Lama lama</i>	Not found north of equator
<i>Lampronycteris brachyotis</i>	INCLUDED
<i>Lasiurus blossevillii</i>	INCLUDED
<i>Lasiurus borealis</i>	INCLUDED
<i>Lasiurus castaneus</i>	INCLUDED
<i>Lasiurus cinereus</i>	INCLUDED

<i>Lasiurus degelidus</i>	Less than 20 occurrences
<i>Lasiurus ebenus</i>	Not found north of equator
<i>Lasiurus egregius</i>	INCLUDED
<i>Lasiurus insularis</i>	Less than 20 occurrences
<i>Lasiurus intermedius</i>	INCLUDED
<i>Lasiurus minor</i>	Less than 20 occurrences
<i>Lasionycteris noctivagans</i>	INCLUDED
<i>Lasiurus pfeifferi</i>	Less than 20 occurrences
<i>Lasiurus seminolus</i>	INCLUDED
<i>Lasiurus varius</i>	Not found north of equator
<i>Lasiurus xanthinus</i>	INCLUDED
<i>Lemmiscus curtatus</i>	INCLUDED
<i>Lemmus trimucronatus</i>	INCLUDED
<i>Lenoxus apicalis</i>	Not found north of equator
<i>Leontopithecus caissara</i>	Not found north of equator
<i>Leontopithecus chrysomelas</i>	Not found north of equator
<i>Leontopithecus chrysopygus</i>	Not found north of equator
<i>Leontopithecus rosalia</i>	Not found north of equator
<i>Leopardus braccatus</i>	Not found north of equator
<i>Leopardus colocolo</i>	Not found north of equator
<i>Leopardus geoffroyi</i>	Not found north of equator
<i>Leopardus guigna</i>	Not found north of equator
<i>Leopardus jacobitus</i>	Not found north of equator
<i>Leopardus pajeros</i>	Not found north of equator
<i>Leopardus pardalis</i>	INCLUDED
<i>Leopardus tigrinus</i>	INCLUDED
<i>Leopardus wiedii</i>	INCLUDED
<i>Leptonycteris curasoae</i>	INCLUDED
<i>Leptonycteris nivalis</i>	INCLUDED
<i>Leptonycteris yerbabuenae</i>	INCLUDED
<i>Lepus alleni</i>	INCLUDED
<i>Lepus americanus</i>	INCLUDED
<i>Lepus arcticus</i>	INCLUDED
<i>Lepus californicus</i>	INCLUDED
<i>Lepus callotis</i>	INCLUDED
<i>Lepus flavigularis</i>	Less than 20 occurrences
<i>Lepus insularis</i>	Less than 20 occurrences
<i>Lepus othus</i>	INCLUDED
<i>Lepus townsendii</i>	INCLUDED
<i>Lestodelphys halli</i>	Not found north of equator
<i>Lestoros inca</i>	Not found north of equator
<i>Lichonycteris obscura</i>	INCLUDED
<i>Liomys adspersus</i>	Less than 20 occurrences

<i>Liomys irroratus</i>	INCLUDED
<i>Liomys pictus</i>	INCLUDED
<i>Liomys salvini</i>	INCLUDED
<i>Liomys spectabilis</i>	Less than 20 occurrences
<i>Lionycteris spurrelli</i>	INCLUDED
<i>Lonchorhina aurita</i>	INCLUDED
<i>Lonchophylla bokermanni</i>	Not found north of equator
<i>Lonchophylla chocoana</i>	Not found north of equator
<i>Lonchophylla dekeyseri</i>	Not found north of equator
<i>Lonchothrix emiliae</i>	Not found north of equator
<i>Lonchorhina fernandezi</i>	Less than 20 occurrences
<i>Lonchophylla handleyi</i>	INCLUDED
<i>Lonchophylla hesperia</i>	Not found north of equator
<i>Lonchorhina inusitata</i>	INCLUDED
<i>Lonchorhina marinkellei</i>	Not found north of equator
<i>Lonchophylla mordax</i>	INCLUDED
<i>Lonchorhina orinocensis</i>	INCLUDED
<i>Lonchophylla robusta</i>	INCLUDED
<i>Lonchophylla thomasi</i>	INCLUDED
<i>Lontra canadensis</i>	INCLUDED
<i>Lontra felina</i>	Not found north of equator
<i>Lontra longicaudis</i>	INCLUDED
<i>Lontra provocax</i>	Not found north of equator
<i>Lophostoma brasiliense</i>	INCLUDED
<i>Lophostoma carrikeri</i>	INCLUDED
<i>Lophostoma evotis</i>	INCLUDED
<i>Lophostoma schulzi</i>	Less than 20 occurrences
<i>Lophostoma silvicolum</i>	INCLUDED
<i>Loxodontomys micropus</i>	Not found north of equator
<i>Loxodontomys pikumche</i>	Not found north of equator
<i>Lundomys molitor</i>	Not found north of equator
<i>Lutreolina crassicaudata</i>	INCLUDED
<i>Lycalopex culpaeus</i>	Less than 20 occurrences
<i>Lycalopex fulvipes</i>	Not found north of equator
<i>Lycalopex griseus</i>	Not found north of equator
<i>Lycalopex gymnocercus</i>	Not found north of equator
<i>Lycalopex sechurae</i>	Not found north of equator
<i>Lycalopex vetulus</i>	Not found north of equator
<i>Lyncodon patagonicus</i>	Not found north of equator
<i>Lynx canadensis</i>	INCLUDED
<i>Lynx rufus</i>	INCLUDED
<i>Macrotus californicus</i>	INCLUDED
<i>Macrophyllum macrophyllum</i>	INCLUDED

<i>Macrotus waterhousii</i>	INCLUDED
<i>Makalata didelphoides</i>	INCLUDED
<i>Makalata grandis</i>	Not found north of equator
<i>Makalata macrura</i>	Not found north of equator
<i>Makalata occasius</i>	Not found north of equator
<i>Makalata rhipidura</i>	Not found north of equator
<i>Marmosa andersoni</i>	Not found north of equator
<i>Marmosops bishopi</i>	Not found north of equator
<i>Marmota breweri</i>	INCLUDED
<i>Marmota caligata</i>	INCLUDED
<i>Marmosops cracens</i>	Less than 20 occurrences
<i>Marmosops creightoni</i>	Not found north of equator
<i>Marmota flaviventris</i>	INCLUDED
<i>Marmosops fuscatus</i>	INCLUDED
<i>Marmosops impavidus</i>	Less than 20 occurrences
<i>Marmosops incanus</i>	Not found north of equator
<i>Marmosops invictus</i>	Less than 20 occurrences
<i>Marmosops juninensis</i>	Not found north of equator
<i>Marmosa lepida</i>	INCLUDED
<i>Marmosa mexicana</i>	INCLUDED
<i>Marmota monax</i>	INCLUDED
<i>Marmosa murina</i>	INCLUDED
<i>Marmosops neblina</i>	Not found north of equator
<i>Marmosops noctivagus</i>	Not found north of equator
<i>Marmosops ocellatus</i>	Not found north of equator
<i>Marmota olympus</i>	Less than 20 occurrences
<i>Marmosops parvidens</i>	INCLUDED
<i>Marmosops paulensis</i>	Not found north of equator
<i>Marmosops pinheiroi</i>	INCLUDED
<i>Marmosa robinsoni</i>	INCLUDED
<i>Marmosa rubra</i>	Not found north of equator
<i>Marmosa tyleriana</i>	Less than 20 occurrences
<i>Marmota vancouverensis</i>	Less than 20 occurrences
<i>Marmosa xerophila</i>	Less than 20 occurrences
<i>Martes americana</i>	INCLUDED
<i>Martes pennanti</i>	INCLUDED
<i>Mazama americana</i>	INCLUDED
<i>Mazama bricenii</i>	Less than 20 occurrences
<i>Mazama chunyi</i>	Not found north of equator
<i>Mazama gouazoubira</i>	INCLUDED
<i>Mazama nana</i>	Not found north of equator
<i>Mazama pandora</i>	Less than 20 occurrences
<i>Mazama rufina</i>	Not found north of equator

<i>Megadontomys cryophilus</i>	Less than 20 occurrences
<i>Megasorex gigas</i>	INCLUDED
<i>Megadontomys nelsoni</i>	Less than 20 occurrences
<i>Megadontomys thomasi</i>	Less than 20 occurrences
<i>Melanomys caliginosus</i>	INCLUDED
<i>Melanomys robustulus</i>	Not found north of equator
<i>Melanomys zunigae</i>	Not found north of equator
<i>Mephitis macroura</i>	INCLUDED
<i>Mephitis mephitis</i>	INCLUDED
<i>Mesocapromys auritus</i>	Less than 20 occurrences
<i>Mesomys hispidus</i>	INCLUDED
<i>Mesomys leniceps</i>	Not found north of equator
<i>Mesophylla macconnelli</i>	INCLUDED
<i>Mesocapromys melanurus</i>	Less than 20 occurrences
<i>Mesocapromys nanus</i>	Less than 20 occurrences
<i>Mesomys stimulax</i>	Less than 20 occurrences
<i>Metachirus nudicaudatus</i>	INCLUDED
<i>Micoureus alstoni</i>	INCLUDED
<i>Micoureus constantiae</i>	Not found north of equator
<i>Micoureus demerarae</i>	INCLUDED
<i>Micoureus paraguayanus</i>	Not found north of equator
<i>Micoureus regina</i>	Less than 20 occurrences
<i>Microsciurus alfari</i>	INCLUDED
<i>Microryzomys altissimus</i>	Less than 20 occurrences
<i>Microcavia australis</i>	Not found north of equator
<i>Micronycteris brosseti</i>	Not found north of equator
<i>Microtus californicus</i>	INCLUDED
<i>Microtus canicaudus</i>	Less than 20 occurrences
<i>Microtus chrotorrhinus</i>	INCLUDED
<i>Microsciurus flaviventer</i>	INCLUDED
<i>Microtus guatemalensis</i>	Less than 20 occurrences
<i>Micronycteris hirsuta</i>	INCLUDED
<i>Micronycteris homezi</i>	Less than 20 occurrences
<i>Microtus longicaudus</i>	INCLUDED
<i>Microdipodops megacephalus</i>	INCLUDED
<i>Microtus mexicanus</i>	INCLUDED
<i>Micronycteris microtis</i>	INCLUDED
<i>Microsciurus mimulus</i>	INCLUDED
<i>Microryzomys minutus</i>	INCLUDED
<i>Microtus miurus</i>	INCLUDED
<i>Microtus mogollonensis</i>	INCLUDED
<i>Microtus montanus</i>	INCLUDED
<i>Microcavia niata</i>	Not found north of equator

<i>Microtus oaxacensis</i>	Less than 20 occurrences
<i>Microtus ochrogaster</i>	INCLUDED
<i>Microtus oeconomus</i>	INCLUDED
<i>Microtus oregoni</i>	INCLUDED
<i>Microdipodops pallidus</i>	Less than 20 occurrences
<i>Microtus pennsylvanicus</i>	INCLUDED
<i>Microtus pinetorum</i>	INCLUDED
<i>Microtus quasiater</i>	Less than 20 occurrences
<i>Microtus richardsoni</i>	INCLUDED
<i>Micronycteris sanborni</i>	Not found north of equator
<i>Microsciurus santanderensis</i>	INCLUDED
<i>Micronycteris schmidtorum</i>	INCLUDED
<i>Microcavia shiptoni</i>	Not found north of equator
<i>Microtus townsendii</i>	INCLUDED
<i>Microakodontomys transitorius</i>	Not found north of equator
<i>Microtus umbrosus</i>	Less than 20 occurrences
<i>Microtus xanthognathus</i>	INCLUDED
<i>Mimon bennettii</i>	INCLUDED
<i>Mimon cozumelae</i>	INCLUDED
<i>Mimon crenulatum</i>	INCLUDED
<i>Mimon koepckeae</i>	Not found north of equator
<i>Molossops aequatorianus</i>	Not found north of equator
<i>Molossus barnesi</i>	Less than 20 occurrences
<i>Molossus coibensis</i>	INCLUDED
<i>Molossus currentium</i>	INCLUDED
<i>Molossops mattogrossensis</i>	INCLUDED
<i>Molossus molossus</i>	INCLUDED
<i>Molossus pretiosus</i>	INCLUDED
<i>Molossus rufus</i>	INCLUDED
<i>Molossus sinaloae</i>	INCLUDED
<i>Molossops temminckii</i>	INCLUDED
<i>Monodelphis adusta</i>	Less than 20 occurrences
<i>Monodelphis americana</i>	Not found north of equator
<i>Monodelphis brevicaudata</i>	INCLUDED
<i>Monodelphis dimidiata</i>	Not found north of equator
<i>Monodelphis domestica</i>	Not found north of equator
<i>Monodelphis emiliae</i>	Not found north of equator
<i>Monodelphis iheringi</i>	Not found north of equator
<i>Monodelphis kunsi</i>	Not found north of equator
<i>Monodelphis maraxina</i>	Not found north of equator
<i>Monodelphis osgoodi</i>	Not found north of equator
<i>Monophyllus plethodon</i>	Less than 20 occurrences
<i>Monophyllus redmani</i>	INCLUDED

<i>Monodelphis rubida</i>	Not found north of equator
<i>Monodelphis scalops</i>	Not found north of equator
<i>Monodelphis sorex</i>	Not found north of equator
<i>Monodelphis theresa</i>	Not found north of equator
<i>Monodelphis unistriata</i>	Not found north of equator
<i>Mormoops blainvillii</i>	INCLUDED
<i>Mormopterus kalinowskii</i>	Not found north of equator
<i>Mormoops megalophylla</i>	INCLUDED
<i>Mormopterus minutus</i>	Less than 20 occurrences
<i>Mormopterus phrudus</i>	Not found north of equator
<i>Musonycteris harrisoni</i>	Less than 20 occurrences
<i>Mustela africana</i>	Less than 20 occurrences
<i>Mustela erminea</i>	INCLUDED
<i>Mustela felipei</i>	Less than 20 occurrences
<i>Mustela frenata</i>	INCLUDED
<i>Mustela nigripes</i>	INCLUDED
<i>Mustela nivalis</i>	INCLUDED
<i>Myocastor coypus</i>	INCLUDED
<i>Myodes californicus</i>	INCLUDED
<i>Myodes gapperi</i>	INCLUDED
<i>Myodes rutilus</i>	INCLUDED
<i>Myoprocta acouchy</i>	INCLUDED
<i>Myoprocta pratti</i>	Less than 20 occurrences
<i>Myotis aelleni</i>	Not found north of equator
<i>Myotis albescens</i>	INCLUDED
<i>Myotis atacamensis</i>	Not found north of equator
<i>Myotis auriculus</i>	INCLUDED
<i>Myotis austroriparius</i>	INCLUDED
<i>Myotis californicus</i>	INCLUDED
<i>Myotis chiloensis</i>	Not found north of equator
<i>Myotis ciliolabrum</i>	INCLUDED
<i>Myotis dominicensis</i>	Not found north of equator
<i>Myotis elegans</i>	INCLUDED
<i>Myotis evotis</i>	INCLUDED
<i>Myotis findleyi</i>	Not found north of equator
<i>Myotis fortidens</i>	INCLUDED
<i>Myotis grisescens</i>	INCLUDED
<i>Myotis keaysi</i>	INCLUDED
<i>Myotis keenii</i>	INCLUDED
<i>Myotis leibii</i>	INCLUDED
<i>Myotis levis</i>	Not found north of equator
<i>Myotis lucifugus</i>	INCLUDED
<i>Myotis martiniquensis</i>	Not found north of equator

<i>Myotis nesopolus</i>	Less than 20 occurrences
<i>Myotis nigricans</i>	INCLUDED
<i>Myotis occultus</i>	INCLUDED
<i>Myotis oxyotus</i>	INCLUDED
<i>Myotis peninsularis</i>	Less than 20 occurrences
<i>Myotis planiceps</i>	Less than 20 occurrences
<i>Myotis riparius</i>	INCLUDED
<i>Myotis ruber</i>	Not found north of equator
<i>Myotis septentrionalis</i>	INCLUDED
<i>Myotis simus</i>	Less than 20 occurrences
<i>Myotis sodalis</i>	INCLUDED
<i>Myotis thysanodes</i>	INCLUDED
<i>Myotis velifer</i>	INCLUDED
<i>Myotis vivesi</i>	INCLUDED
<i>Myotis volans</i>	INCLUDED
<i>Myotis yumanensis</i>	INCLUDED
<i>Myrmecophaga tridactyla</i>	INCLUDED
<i>Mysateles meridionalis</i>	Not found north of equator
<i>Mysateles prehensilis</i>	Less than 20 occurrences
<i>Napaeozapus insignis</i>	INCLUDED
<i>Nasua narica</i>	INCLUDED
<i>Nasua nasua</i>	INCLUDED
<i>Nasuella olivacea</i>	INCLUDED
<i>Natalus jamaicensis</i>	Less than 20 occurrences
<i>Natalus major</i>	Less than 20 occurrences
<i>Natalus primus</i>	Less than 20 occurrences
<i>Natalus stramineus</i>	INCLUDED
<i>Neacomys dubosti</i>	Less than 20 occurrences
<i>Neacomys guianae</i>	INCLUDED
<i>Neacomys minutus</i>	Not found north of equator
<i>Neacomys musseri</i>	Not found north of equator
<i>Neacomys paracou</i>	INCLUDED
<i>Neacomys pictus</i>	Less than 20 occurrences
<i>Neacomys spinosus</i>	Less than 20 occurrences
<i>Neacomys tenuipes</i>	INCLUDED
<i>Necromys amoenus</i>	Not found north of equator
<i>Necromys lactens</i>	Not found north of equator
<i>Necromys lasiurus</i>	Not found north of equator
<i>Necromys lenguarum</i>	Not found north of equator
<i>Necromys obscurus</i>	Not found north of equator
<i>Necromys punctulatus</i>	Not found north of equator
<i>Necromys temchuki</i>	Not found north of equator
<i>Necromys urichi</i>	INCLUDED

<i>Nectomys apicalis</i>	Not found north of equator
<i>Nectomys magdalena</i> ne	Less than 20 occurrences
<i>Nectomys palmipes</i>	INCLUDED
<i>Nectomys ratus</i>	INCLUDED
<i>Nectomys squamipes</i>	Not found north of equator
<i>Nelsonia goldmani</i>	Less than 20 occurrences
<i>Nelsonia neotomodon</i>	Less than 20 occurrences
<i>Neofiber alleni</i>	Less than 20 occurrences
<i>Neonycteris pusilla</i>	Not found north of equator
<i>Neotoma albicula</i>	INCLUDED
<i>Neotamias alpinus</i>	Less than 20 occurrences
<i>Neotomodon alstoni</i>	Less than 20 occurrences
<i>Neotamias amoenus</i>	INCLUDED
<i>Neotoma angustapalata</i>	Less than 20 occurrences
<i>Neotoma bryanti</i>	Not found north of equator
<i>Neotamias bulleri</i>	Less than 20 occurrences
<i>Neotamias canipes</i>	Less than 20 occurrences
<i>Neotoma chrysomelas</i>	Less than 20 occurrences
<i>Neotoma cinerea</i>	INCLUDED
<i>Neotoma devia</i>	Less than 20 occurrences
<i>Neotamias dorsalis</i>	INCLUDED
<i>Neotamias durangae</i>	Less than 20 occurrences
<i>Neotomys ebriosus</i>	Not found north of equator
<i>Neotoma floridana</i>	INCLUDED
<i>Neotoma fuscipes</i>	INCLUDED
<i>Neotoma goldmani</i>	INCLUDED
<i>Neotoma lepida</i>	INCLUDED
<i>Neotoma leucodon</i>	INCLUDED
<i>Neotoma macrotis</i>	INCLUDED
<i>Neotoma magister</i>	INCLUDED
<i>Neotamias merriami</i>	INCLUDED
<i>Neotoma mexicana</i>	INCLUDED
<i>Neotoma micropus</i>	INCLUDED
<i>Neotamias minimus</i>	INCLUDED
<i>Neotoma nelsoni</i>	Less than 20 occurrences
<i>Neotamias obscurus</i>	Less than 20 occurrences
<i>Neotamias ochrogenys</i>	Less than 20 occurrences
<i>Neotoma palatina</i>	Less than 20 occurrences
<i>Neotamias palmeri</i>	Less than 20 occurrences
<i>Neotamias panamintinus</i>	Less than 20 occurrences
<i>Neotoma phenax</i>	Less than 20 occurrences
<i>Neotamias quadrimaculatus</i>	Less than 20 occurrences
<i>Neotamias quadrivittatus</i>	INCLUDED

<i>Neotamias ruficaudus</i>	INCLUDED
<i>Neotamias rufus</i>	INCLUDED
<i>Neotamias senex</i>	INCLUDED
<i>Neotamias siskiyou</i>	Less than 20 occurrences
<i>Neotamias sonomae</i>	Less than 20 occurrences
<i>Neotamias speciosus</i>	INCLUDED
<i>Neotoma stephensi</i>	INCLUDED
<i>Neotamias townsendii</i>	INCLUDED
<i>Neotamias umbrinus</i>	INCLUDED
<i>Neovison vison</i>	INCLUDED
<i>Nesoryzomys darwini</i>	Not found north of equator
<i>Nesoryzomys fernandinae</i>	Not found north of equator
<i>Nesoryzomys indefessus</i>	Not found north of equator
<i>Nesoryzomys swarthi</i>	Not found north of equator
<i>Neurotrichus gibbsii</i>	INCLUDED
<i>Neusticomys monticolus</i>	Less than 20 occurrences
<i>Neusticomys mussoi</i>	Less than 20 occurrences
<i>Neusticomys oyapocki</i>	Less than 20 occurrences
<i>Neusticomys peruviensis</i>	Not found north of equator
<i>Neusticomys venezuelae</i>	INCLUDED
<i>Noctilio albiventris</i>	INCLUDED
<i>Noctilio leporinus</i>	INCLUDED
<i>Notiosorex crawfordi</i>	INCLUDED
<i>Notiomys edwardsii</i>	Not found north of equator
<i>Notiosorex evotis</i>	INCLUDED
<i>Notiosorex villai</i>	Less than 20 occurrences
<i>Nyctinomops aurispinosus</i>	INCLUDED
<i>Nyctinomops femorosaccus</i>	INCLUDED
<i>Nycticeius humeralis</i>	INCLUDED
<i>Nyctinomops laticaudatus</i>	INCLUDED
<i>Nyctiellus lepidus</i>	Less than 20 occurrences
<i>Nyctinomops macrotis</i>	INCLUDED
<i>Nyctomys sumichrasti</i>	INCLUDED
<i>Ochotona collaris</i>	INCLUDED
<i>Ochotona princeps</i>	INCLUDED
<i>Ochrotomys nuttalli</i>	INCLUDED
<i>Octodon bridgesi</i>	Not found north of equator
<i>Octodon degus</i>	Not found north of equator
<i>Octodontomys gliroides</i>	Not found north of equator
<i>Octodon lunatus</i>	Not found north of equator
<i>Octomys mimax</i>	Not found north of equator
<i>Odocoileus hemionus</i>	INCLUDED
<i>Odocoileus virginianus</i>	INCLUDED

<i>Oecomys auyantepui</i>	INCLUDED
<i>Oecomys bicolor</i>	INCLUDED
<i>Oecomys cleberi</i>	Not found north of equator
<i>Oecomys concolor</i>	INCLUDED
<i>Oecomys flavigans</i>	INCLUDED
<i>Oecomys mamorae</i>	Not found north of equator
<i>Oecomys paricola</i>	Not found north of equator
<i>Oecomys phaeotis</i>	Not found north of equator
<i>Oecomys rex</i>	INCLUDED
<i>Oecomys roberti</i>	INCLUDED
<i>Oecomys rutilus</i>	INCLUDED
<i>Oecomys speciosus</i>	INCLUDED
<i>Oecomys superans</i>	Less than 20 occurrences
<i>Oecomys trinitatis</i>	INCLUDED
<i>Olallamys albicauda</i>	Less than 20 occurrences
<i>Olallamys edax</i>	Less than 20 occurrences
<i>Oligoryzomys andinus</i>	Not found north of equator
<i>Oligoryzomys arenalis</i>	Not found north of equator
<i>Oligoryzomys chacoensis</i>	Not found north of equator
<i>Oligoryzomys delticola</i>	Not found north of equator
<i>Oligoryzomys destructor</i>	Less than 20 occurrences
<i>Oligoryzomys eliurus</i>	Not found north of equator
<i>Oligoryzomys flavescens</i>	Not found north of equator
<i>Oligoryzomys fulvescens</i>	INCLUDED
<i>Oligoryzomys griseolus</i>	Less than 20 occurrences
<i>Oligoryzomys longicaudatus</i>	Not found north of equator
<i>Oligoryzomys magellanicus</i>	Not found north of equator
<i>Oligoryzomys microtis</i>	Not found north of equator
<i>Oligoryzomys nigripes</i>	Not found north of equator
<i>Oligoryzomys stramineus</i>	Not found north of equator
<i>Oligoryzomys vegetus</i>	Less than 20 occurrences
<i>Oligoryzomys victus</i>	Not found north of equator
<i>Ondatra zibethicus</i>	INCLUDED
<i>Onychomys arenicola</i>	INCLUDED
<i>Onychomys leucogaster</i>	INCLUDED
<i>Onychomys torridus</i>	INCLUDED
<i>Oreamnos americanus</i>	INCLUDED
<i>Oreonax flavicauda</i>	Not found north of equator
<i>Orthogeomys cavator</i>	Less than 20 occurrences
<i>Orthogeomys cherriei</i>	Less than 20 occurrences
<i>Orthogeomys cuniculus</i>	Less than 20 occurrences
<i>Orthogeomys dariensis</i>	Less than 20 occurrences
<i>Orthogeomys grandis</i>	INCLUDED

<i>Orthogeomys heterodus</i>	Less than 20 occurrences
<i>Orthogeomys hispidus</i>	INCLUDED
<i>Orthogeomys lanius</i>	Less than 20 occurrences
<i>Orthogeomys matagalpae</i>	Less than 20 occurrences
<i>Orthogeomys thaeleri</i>	Less than 20 occurrences
<i>Orthogeomys underwoodi</i>	Less than 20 occurrences
<i>Oryzomys albicularis</i>	INCLUDED
<i>Oryzomys alfaroi</i>	INCLUDED
<i>Oryzomys angouya</i>	Not found north of equator
<i>Oryzomys auriventer</i>	Not found north of equator
<i>Oryzomys balneator</i>	Not found north of equator
<i>Oryzomys bolivaris</i>	INCLUDED
<i>Oryzomys chapmani</i>	INCLUDED
<i>Oryzomys couesi</i>	INCLUDED
<i>Oryzomys devius</i>	Less than 20 occurrences
<i>Oryzomys dimidiatus</i>	Less than 20 occurrences
<i>Oryzomys emmonsae</i>	Not found north of equator
<i>Oryzomys galapagoensis</i>	Not found north of equator
<i>Oryzomys gorgasi</i>	Less than 20 occurrences
<i>Oryzomys hammondi</i>	Not found north of equator
<i>Oryzomys keaysi</i>	Not found north of equator
<i>Oryzomys laticeps</i>	Not found north of equator
<i>Oryzomys levipes</i>	Not found north of equator
<i>Oryzomys macconnelli</i>	INCLUDED
<i>Oryzomys megacephalus</i>	Less than 20 occurrences
<i>Oryzomys melanotis</i>	INCLUDED
<i>Oryzomys nelsoni</i>	Not found north of equator
<i>Oryzomys nitidus</i>	Not found north of equator
<i>Oryzomys palustris</i>	INCLUDED
<i>Oryzomys perenensis</i>	Not found north of equator
<i>Oryzomys polius</i>	Not found north of equator
<i>Oryzomys rhabdops</i>	Less than 20 occurrences
<i>Oryzomys rostratus</i>	INCLUDED
<i>Oryzomys russatus</i>	Not found north of equator
<i>Oryzomys saturatior</i>	INCLUDED
<i>Oryzomys seuanezi</i>	Not found north of equator
<i>Oryzomys subflavus</i>	Not found north of equator
<i>Oryzomys talamancae</i>	INCLUDED
<i>Oryzomys tatei</i>	Not found north of equator
<i>Oryzomys xanthaeolus</i>	Not found north of equator
<i>Oryzomys yunganus</i>	INCLUDED
<i>Osgoodomys banderanus</i>	INCLUDED
<i>Otonyctomys hatti</i>	Less than 20 occurrences

<i>Ototylomys phyllotis</i>	INCLUDED
<i>Ovibos moschatus</i>	INCLUDED
<i>Ovis canadensis</i>	INCLUDED
<i>Ovis dalli</i>	INCLUDED
<i>Oxymycterus akodontius</i>	Not found north of equator
<i>Oxymycterus amazonicus</i>	Not found north of equator
<i>Oxymycterus angularis</i>	Not found north of equator
<i>Oxymycterus caparaeae</i>	Not found north of equator
<i>Oxymycterus hiska</i>	Not found north of equator
<i>Oxymycterus hispidus</i>	Not found north of equator
<i>Oxymycterus hucucha</i>	Not found north of equator
<i>Oxymycterus inca</i>	Not found north of equator
<i>Oxymycterus josei</i>	Not found north of equator
<i>Oxymycterus nasutus</i>	Not found north of equator
<i>Oxymycterus paramensis</i>	Not found north of equator
<i>Oxymycterus roberti</i>	Not found north of equator
<i>Oxymycterus rufus</i>	Not found north of equator
<i>Ozotoceros bezoarticus</i>	Not found north of equator
<i>Panthera onca</i>	INCLUDED
<i>Pappogeomys alcicornis</i>	Less than 20 occurrences
<i>Pappogeomys bulleri</i>	Less than 20 occurrences
<i>Parascalops breweri</i>	INCLUDED
<i>Paralomys gerbillus</i>	Not found north of equator
<i>Pearsonomys annectens</i>	Not found north of equator
<i>Pecari tajacu</i>	INCLUDED
<i>Perimyotis subflavus</i>	INCLUDED
<i>Perognathus alticolus</i>	Less than 20 occurrences
<i>Perognathus amplus</i>	INCLUDED
<i>Peromyscus attwateri</i>	INCLUDED
<i>Peromyscus aztecus</i>	Less than 20 occurrences
<i>Peromyscus beatae</i>	INCLUDED
<i>Peromyscus boylii</i>	INCLUDED
<i>Peromyscus bullatus</i>	Less than 20 occurrences
<i>Peromyscus californicus</i>	INCLUDED
<i>Peromyscus crinitus</i>	INCLUDED
<i>Peromyscus difficilis</i>	INCLUDED
<i>Peromyscus eremicus</i>	INCLUDED
<i>Peromyscus eva</i>	Less than 20 occurrences
<i>Perognathus fasciatus</i>	INCLUDED
<i>Perognathus flavescens</i>	INCLUDED
<i>Perognathus flavus</i>	INCLUDED
<i>Peromyscus fraterculus</i>	INCLUDED
<i>Peromyscus furvus</i>	Less than 20 occurrences

<i>Peromyscus gossypinus</i>	INCLUDED
<i>Peromyscus grandis</i>	Less than 20 occurrences
<i>Peromyscus gratus</i>	INCLUDED
<i>Peromyscus guardia</i>	Less than 20 occurrences
<i>Peromyscus guatemalensis</i>	Less than 20 occurrences
<i>Peromyscus gymnotis</i>	Less than 20 occurrences
<i>Peromyscus hooperi</i>	Less than 20 occurrences
<i>Perognathus inornatus</i>	Less than 20 occurrences
<i>Peropteryx kappleri</i>	INCLUDED
<i>Peromyscus keeni</i>	INCLUDED
<i>Peromyscus leucopus</i>	INCLUDED
<i>Peromyscus levipes</i>	INCLUDED
<i>Perognathus longimembris</i>	INCLUDED
<i>Peropteryx macrotis</i>	INCLUDED
<i>Peromyscus madrensis</i>	Not found north of equator
<i>Peromyscus maniculatus</i>	INCLUDED
<i>Peromyscus mayensis</i>	Less than 20 occurrences
<i>Peromyscus megalops</i>	Less than 20 occurrences
<i>Peromyscus mekisturus</i>	Less than 20 occurrences
<i>Peromyscus melanocarpus</i>	Less than 20 occurrences
<i>Peromyscus melanophrys</i>	INCLUDED
<i>Peromyscus melanotis</i>	INCLUDED
<i>Peromyscus melanurus</i>	Less than 20 occurrences
<i>Peromyscus merriami</i>	INCLUDED
<i>Peromyscus mexicanus</i>	INCLUDED
<i>Peromyscus nasutus</i>	INCLUDED
<i>Peromyscus ochraventer</i>	Less than 20 occurrences
<i>Perognathus parvus</i>	INCLUDED
<i>Peromyscus pectoralis</i>	INCLUDED
<i>Peromyscus perfulvus</i>	Less than 20 occurrences
<i>Peromyscus polionotus</i>	INCLUDED
<i>Peromyscus polius</i>	Less than 20 occurrences
<i>Peromyscus sagax</i>	Less than 20 occurrences
<i>Peromyscus schmidlyi</i>	Less than 20 occurrences
<i>Peromyscus simulus</i>	Less than 20 occurrences
<i>Peromyscus spicilegus</i>	INCLUDED
<i>Peromyscus stirtoni</i>	Less than 20 occurrences
<i>Peromyscus truei</i>	INCLUDED
<i>Peromyscus winkelmanni</i>	Less than 20 occurrences
<i>Peromyscus yucatanicus</i>	Less than 20 occurrences
<i>Peromyscus zarhynchus</i>	Less than 20 occurrences
<i>Phaenomys ferrugineus</i>	Not found north of equator
<i>Phenacomys intermedius</i>	INCLUDED

<i>Phenacomys ungava</i>	INCLUDED
<i>Philander andersoni</i>	Less than 20 occurrences
<i>Philander frenatus</i>	Not found north of equator
<i>Philander mcilhennyi</i>	Not found north of equator
<i>Philander opossum</i>	INCLUDED
<i>Phyllotis amicus</i>	Not found north of equator
<i>Phyllotis andium</i>	Not found north of equator
<i>Phyllonycteris aphylla</i>	Less than 20 occurrences
<i>Phyllostomus blainvillii</i>	Not found north of equator
<i>Phyllostomus bonariensis</i>	Not found north of equator
<i>Phyllostomus brasiliensis</i>	Not found north of equator
<i>Phyllostomus caprinus</i>	Not found north of equator
<i>Phyllostomus darwini</i>	Not found north of equator
<i>Phyllostomus dasythrix</i>	Not found north of equator
<i>Phyllostomus definitus</i>	Not found north of equator
<i>Phyllostomus discolor</i>	INCLUDED
<i>Phyllostomus elongatus</i>	INCLUDED
<i>Phyllops falcatus</i>	INCLUDED
<i>Phyllotis haggardi</i>	Not found north of equator
<i>Phyllostomus hastatus</i>	INCLUDED
<i>Phyllostomus kerri</i>	Not found north of equator
<i>Phyllostomus lamarum</i>	Not found north of equator
<i>Phyllostomus latifolius</i>	INCLUDED
<i>Phyllotis limatus</i>	Not found north of equator
<i>Phyllostomus lundi</i>	Not found north of equator
<i>Phyllotis magister</i>	Not found north of equator
<i>Phyllostomus medius</i>	Not found north of equator
<i>Phyllostomus nigrispinus</i>	Not found north of equator
<i>Phyllotis osgoodi</i>	Not found north of equator
<i>Phyllotis osilae</i>	Not found north of equator
<i>Phyllostomus pattoni</i>	Not found north of equator
<i>Phyllonycteris poeyi</i>	INCLUDED
<i>Phylloderma stenops</i>	INCLUDED
<i>Phyllostomus thomasi</i>	Not found north of equator
<i>Phyllotis wolffsohni</i>	Not found north of equator
<i>Phyllotis xanthopygus</i>	Not found north of equator
<i>Pipistrellus hesperus</i>	INCLUDED
<i>Pithecia aequatorialis</i>	Not found north of equator
<i>Pithecia albicans</i>	Not found north of equator
<i>Pithecia irrorata</i>	Not found north of equator
<i>Pithecia monachus</i>	Less than 20 occurrences
<i>Pithecia pithecia</i>	INCLUDED
<i>Plagiodontia aedium</i>	Less than 20 occurrences

<i>Plagiodontia araeum</i>	Less than 20 occurrences
<i>Plagiodontia ipnaeum</i>	Less than 20 occurrences
<i>Platyrrhinus aurarius</i>	INCLUDED
<i>Platyrrhinus brachycephalus</i>	INCLUDED
<i>Platyrrhinus chocoensis</i>	Less than 20 occurrences
<i>Platyrrhinus dorsalis</i>	INCLUDED
<i>Platalina genovensium</i>	Not found north of equator
<i>Platyrrhinus helleri</i>	INCLUDED
<i>Platyrrhinus infuscus</i>	INCLUDED
<i>Platyrrhinus lineatus</i>	INCLUDED
<i>Platyrrhinus recifinus</i>	INCLUDED
<i>Platyrrhinus umbratus</i>	Less than 20 occurrences
<i>Platyrrhinus vittatus</i>	INCLUDED
<i>Podomys floridanus</i>	Less than 20 occurrences
<i>Podoxymys roraimae</i>	Less than 20 occurrences
<i>Potos flavus</i>	INCLUDED
<i>Priodontes maximus</i>	INCLUDED
<i>Procyon cancrivorus</i>	INCLUDED
<i>Procyon lotor</i>	INCLUDED
<i>Procyon pygmaeus</i>	Less than 20 occurrences
<i>Proechimys brevicauda</i>	Less than 20 occurrences
<i>Proechimys canicollis</i>	Less than 20 occurrences
<i>Proechimys chrysaeolus</i>	Less than 20 occurrences
<i>Proechimys cuvieri</i>	INCLUDED
<i>Proechimys decumanus</i>	Not found north of equator
<i>Proechimys echinothrix</i>	Not found north of equator
<i>Proechimys gardneri</i>	Not found north of equator
<i>Proechimys goeldii</i>	Not found north of equator
<i>Proechimys guairae</i>	INCLUDED
<i>Proechimys guyannensis</i>	INCLUDED
<i>Proechimys hoplomyoides</i>	INCLUDED
<i>Proechimys kulinae</i>	Not found north of equator
<i>Proechimys longicaudatus</i>	Not found north of equator
<i>Proechimys magdalena</i>	INCLUDED
<i>Proechimys mincae</i>	Less than 20 occurrences
<i>Proechimys oconnelli</i>	Less than 20 occurrences
<i>Proechimys pattoni</i>	Not found north of equator
<i>Proechimys poliopus</i>	Less than 20 occurrences
<i>Proechimys quadruplicatus</i>	Less than 20 occurrences
<i>Proechimys roberti</i>	Not found north of equator
<i>Proechimys semispinosus</i>	Less than 20 occurrences
<i>Proechimys simonsi</i>	Less than 20 occurrences
<i>Proechimys steerei</i>	Not found north of equator

<i>Proechimys trinitatis</i>	Less than 20 occurrences
<i>Proechimys urichi</i>	Less than 20 occurrences
<i>Promops centralis</i>	INCLUDED
<i>Promops nasutus</i>	INCLUDED
<i>Pseudoryzomys simplex</i>	Not found north of equator
<i>Pteronura brasiliensis</i>	INCLUDED
<i>Pteronotus davyi</i>	INCLUDED
<i>Pteronotus gymnonotus</i>	INCLUDED
<i>Pteronotus macleayii</i>	Less than 20 occurrences
<i>Pteronotus parnellii</i>	INCLUDED
<i>Pteronotus personatus</i>	INCLUDED
<i>Pteronotus quadridens</i>	INCLUDED
<i>Pudu mephistophiles</i>	Less than 20 occurrences
<i>Pudu puda</i>	Not found north of equator
<i>Puma concolor</i>	INCLUDED
<i>Puma yagouaroundi</i>	INCLUDED
<i>Punomys kofordi</i>	Not found north of equator
<i>Punomys lemminus</i>	Not found north of equator
<i>Pygoderma bilabiatum</i>	Less than 20 occurrences
<i>Rangifer tarandus</i>	INCLUDED
<i>Reithrodon auritus</i>	Not found north of equator
<i>Reithrodontomys bakeri</i>	Less than 20 occurrences
<i>Reithrodontomys brevirostris</i>	Less than 20 occurrences
<i>Reithrodontomys burti</i>	Less than 20 occurrences
<i>Reithrodontomys chrysopsis</i>	Less than 20 occurrences
<i>Reithrodontomys creper</i>	Less than 20 occurrences
<i>Reithrodontomys darienensis</i>	Less than 20 occurrences
<i>Reithrodontomys fulvescens</i>	INCLUDED
<i>Reithrodontomys gracilis</i>	INCLUDED
<i>Reithrodontomys hirsutus</i>	Less than 20 occurrences
<i>Reithrodontomys humulis</i>	INCLUDED
<i>Reithrodontomys megalotis</i>	INCLUDED
<i>Reithrodontomys mexicanus</i>	INCLUDED
<i>Reithrodontomys microdon</i>	INCLUDED
<i>Reithrodontomys montanus</i>	INCLUDED
<i>Reithrodontomys paradoxus</i>	Less than 20 occurrences
<i>Reithrodontomys raviventris</i>	Less than 20 occurrences
<i>Reithrodontomys rodriguezi</i>	Less than 20 occurrences
<i>Reithrodontomys spectabilis</i>	Less than 20 occurrences
<i>Reithrodontomys sumichrasti</i>	INCLUDED
<i>Reithrodontomys tenuirostris</i>	Less than 20 occurrences
<i>Reithrodontomys zacatecae</i>	INCLUDED
<i>Rhagomys longilingua</i>	Not found north of equator

<i>Rheomys mexicanus</i>	Less than 20 occurrences
<i>Rheomys raptor</i>	Less than 20 occurrences
<i>Rheomys thomasi</i>	Less than 20 occurrences
<i>Rheomys underwoodi</i>	Less than 20 occurrences
<i>Rhinophylla alethina</i>	Less than 20 occurrences
<i>Rhinophylla fischerae</i>	Less than 20 occurrences
<i>Rhinophylla pumilio</i>	INCLUDED
<i>Rhipidomys austrinus</i>	Not found north of equator
<i>Rhipidomys caucensis</i>	Less than 20 occurrences
<i>Rhipidomys couesi</i>	INCLUDED
<i>Rhipidomys fulviventer</i>	Less than 20 occurrences
<i>Rhipidomys gardneri</i>	Not found north of equator
<i>Rhipidomys latimanus</i>	INCLUDED
<i>Rhipidomys leucodactylus</i>	INCLUDED
<i>Rhipidomys macconnelli</i>	INCLUDED
<i>Rhipidomys mastacalis</i>	Not found north of equator
<i>Rhipidomys nitela</i>	INCLUDED
<i>Rhipidomys ochrogaster</i>	Not found north of equator
<i>Rhipidomys venezuelae</i>	INCLUDED
<i>Rhipidomys venustus</i>	INCLUDED
<i>Rhipidomys wetzeli</i>	INCLUDED
<i>Rhogeessa aeneus</i>	Less than 20 occurrences
<i>Rhogeessa allenii</i>	INCLUDED
<i>Rhogeessa genowaysi</i>	Less than 20 occurrences
<i>Rhogeessa gracilis</i>	INCLUDED
<i>Rhogeessa minutilla</i>	INCLUDED
<i>Rhogeessa mira</i>	Less than 20 occurrences
<i>Rhogeessa parvula</i>	INCLUDED
<i>Rhogeessa tumida</i>	INCLUDED
<i>Rhynchoycteris naso</i>	INCLUDED
<i>Rhyncholestes raphanurus</i>	Not found north of equator
<i>Romerolagus diazi</i>	Less than 20 occurrences
<i>Saccopteryx bilineata</i>	INCLUDED
<i>Saccopteryx canescens</i>	INCLUDED
<i>Saccopteryx gymnura</i>	Less than 20 occurrences
<i>Saccopteryx leptura</i>	INCLUDED
<i>Saguinus bicolor</i>	Not found north of equator
<i>Saguinus fuscicollis</i>	Not found north of equator
<i>Saguinus geoffroyi</i>	Less than 20 occurrences
<i>Saguinus graellsi</i>	Not found north of equator
<i>Saguinus imperator</i>	Not found north of equator
<i>Saguinus inustus</i>	Less than 20 occurrences
<i>Saguinus labiatus</i>	Not found north of equator

<i>Saguinus leucopus</i>	Less than 20 occurrences
<i>Saguinus martinsi</i>	Not found north of equator
<i>Saguinus midas</i>	INCLUDED
<i>Saguinus mystax</i>	Not found north of equator
<i>Saguinus niger</i>	Not found north of equator
<i>Saguinus nigricollis</i>	Less than 20 occurrences
<i>Saguinus oedipus</i>	Less than 20 occurrences
<i>Saguinus tripartitus</i>	Not found north of equator
<i>Saimiri boliviensis</i>	Not found north of equator
<i>Saimiri oerstedii</i>	Less than 20 occurrences
<i>Saimiri sciureus</i>	INCLUDED
<i>Saimiri ustus</i>	Not found north of equator
<i>Saimiri vanzolinii</i>	Not found north of equator
<i>Salinomys delicatus</i>	Not found north of equator
<i>Salinoctomys loschalcalerosorum</i>	Not found north of equator
<i>Scalopus aquaticus</i>	INCLUDED
<i>Scapteromys aquaticus</i>	Not found north of equator
<i>Scapanus latimanus</i>	INCLUDED
<i>Scapanus orarius</i>	INCLUDED
<i>Scapanus townsendii</i>	INCLUDED
<i>Scapteromys tumidus</i>	Not found north of equator
<i>Sciurus aberti</i>	INCLUDED
<i>Sciurus aestuans</i>	INCLUDED
<i>Sciurus alleni</i>	Less than 20 occurrences
<i>Sciurus arizonensis</i>	Less than 20 occurrences
<i>Sciurus aureogaster</i>	INCLUDED
<i>Sciurus carolinensis</i>	INCLUDED
<i>Sciurus colliae</i>	INCLUDED
<i>Sciurus deppei</i>	INCLUDED
<i>Sciurus flamnifer</i>	INCLUDED
<i>Sciurus gilvigularis</i>	Less than 20 occurrences
<i>Sciurus granatensis</i>	INCLUDED
<i>Sciurus griseus</i>	INCLUDED
<i>Sciurus ignitus</i>	Not found north of equator
<i>Sciurus igniventris</i>	INCLUDED
<i>Sciurus nayaritensis</i>	INCLUDED
<i>Sciurus niger</i>	INCLUDED
<i>Sciurus oculatus</i>	INCLUDED
<i>Sciurus pucheranii</i>	INCLUDED
<i>Sciurillus pusillus</i>	INCLUDED
<i>Sciurus pyrrhinus</i>	Not found north of equator
<i>Sciurus richmondi</i>	Less than 20 occurrences

<i>Sciurus sanborni</i>	Not found north of equator
<i>Sciurus spadiceus</i>	Less than 20 occurrences
<i>Sciurus stramineus</i>	Not found north of equator
<i>Sciurus variegatoides</i>	INCLUDED
<i>Sciurus yucatanensis</i>	INCLUDED
<i>Scleronycteris ega</i>	Less than 20 occurrences
<i>Scolomys melanops</i>	Not found north of equator
<i>Scolomys ucayalensis</i>	Not found north of equator
<i>Scotinomys teguina</i>	INCLUDED
<i>Scotinomys xerampelinus</i>	Less than 20 occurrences
<i>Sigmodontomys alfari</i>	INCLUDED
<i>Sigmodon alleni</i>	INCLUDED
<i>Sigmodon alstoni</i>	INCLUDED
<i>Sigmodontomys aphrastus</i>	Less than 20 occurrences
<i>Sigmodon arizonae</i>	INCLUDED
<i>Sigmodon fulviventer</i>	INCLUDED
<i>Sigmodon hispidus</i>	INCLUDED
<i>Sigmodon inopinatus</i>	Not found north of equator
<i>Sigmodon leucotis</i>	INCLUDED
<i>Sigmodon mascotensis</i>	INCLUDED
<i>Sigmodon ochrognathus</i>	INCLUDED
<i>Sigmodon peruanus</i>	Not found north of equator
<i>Solenodon cubanus</i>	Less than 20 occurrences
<i>Solenodon paradoxus</i>	Less than 20 occurrences
<i>Sorex alaskanus</i>	Less than 20 occurrences
<i>Sorex arcticus</i>	INCLUDED
<i>Sorex arizonae</i>	Less than 20 occurrences
<i>Sorex bairdi</i>	Less than 20 occurrences
<i>Sorex bendirii</i>	INCLUDED
<i>Sorex cinereus</i>	INCLUDED
<i>Sorex dispar</i>	INCLUDED
<i>Sorex emarginatus</i>	Less than 20 occurrences
<i>Sorex fontinalis</i>	Less than 20 occurrences
<i>Sorex fumeus</i>	INCLUDED
<i>Sorex gaspensis</i>	Less than 20 occurrences
<i>Sorex haydeni</i>	INCLUDED
<i>Sorex hoyi</i>	INCLUDED
<i>Sorex longirostris</i>	INCLUDED
<i>Sorex lyelli</i>	Less than 20 occurrences
<i>Sorex macrodon</i>	Less than 20 occurrences
<i>Sorex merriami</i>	INCLUDED
<i>Sorex milleri</i>	Less than 20 occurrences
<i>Sorex monticolus</i>	INCLUDED

<i>Sorex nanus</i>	INCLUDED
<i>Sorex neomexicanus</i>	Less than 20 occurrences
<i>Sorex oreopolus</i>	Less than 20 occurrences
<i>Sorex ornatus</i>	INCLUDED
<i>Sorex pacificus</i>	INCLUDED
<i>Sorex palustris</i>	INCLUDED
<i>Sorex preblei</i>	INCLUDED
<i>Sorex rohweri</i>	Less than 20 occurrences
<i>Sorex saussurei</i>	INCLUDED
<i>Sorex sclateri</i>	Less than 20 occurrences
<i>Sorex sonomae</i>	INCLUDED
<i>Sorex stizodon</i>	Less than 20 occurrences
<i>Sorex tenellus</i>	Less than 20 occurrences
<i>Sorex trowbridgii</i>	INCLUDED
<i>Sorex tundrensis</i>	INCLUDED
<i>Sorex ugyunak</i>	INCLUDED
<i>Sorex vagrans</i>	INCLUDED
<i>Sorex ventralis</i>	INCLUDED
<i>Sorex veraepacis</i>	Less than 20 occurrences
<i>Spalacopus cygnus</i>	Not found north of equator
<i>Speothos venaticus</i>	INCLUDED
<i>Spermophilus adocetus</i>	Less than 20 occurrences
<i>Spermophilus annulatus</i>	Less than 20 occurrences
<i>Spermophilus armatus</i>	INCLUDED
<i>Spermophilus atricapillus</i>	Less than 20 occurrences
<i>Spermophilus beecheyi</i>	INCLUDED
<i>Spermophilus beldingi</i>	INCLUDED
<i>Spermophilus brunneus</i>	Less than 20 occurrences
<i>Spermophilus canus</i>	INCLUDED
<i>Spermophilus columbianus</i>	INCLUDED
<i>Spermophilus elegans</i>	INCLUDED
<i>Spermophilus franklinii</i>	INCLUDED
<i>Spermophilus lateralis</i>	INCLUDED
<i>Spermophilus madrensis</i>	Less than 20 occurrences
<i>Spermophilus mexicanus</i>	INCLUDED
<i>Spermophilus mohavensis</i>	Less than 20 occurrences
<i>Spermophilus mollis</i>	INCLUDED
<i>Spermophilus parryii</i>	INCLUDED
<i>Spermophilus perotensis</i>	Less than 20 occurrences
<i>Spermophilus richardsonii</i>	INCLUDED
<i>Spermophilus saturatus</i>	INCLUDED
<i>Spermophilus spilosoma</i>	INCLUDED
<i>Spermophilus tereticaudus</i>	INCLUDED

<i>Spermophilus townsendii</i>	Less than 20 occurrences
<i>Spermophilus tridecemlineatus</i>	INCLUDED
<i>Spermophilus variegatus</i>	INCLUDED
<i>Spermophilus washingtoni</i>	Less than 20 occurrences
<i>Sphaeronycteris toxophyllum</i>	INCLUDED
<i>Sphiggurus ichillus</i>	Not found north of equator
<i>Sphiggurus insidiosus</i>	Not found north of equator
<i>Sphiggurus melanurus</i>	INCLUDED
<i>Sphiggurus mexicanus</i>	INCLUDED
<i>Sphiggurus pruinosus</i>	INCLUDED
<i>Sphiggurus roosmalenorum</i>	Not found north of equator
<i>Sphiggurus spinosus</i>	Not found north of equator
<i>Sphiggurus vestitus</i>	Less than 20 occurrences
<i>Sphiggurus villosus</i>	Not found north of equator
<i>Spilogale gracilis</i>	INCLUDED
<i>Spilogale putorius</i>	INCLUDED
<i>Spilogale pygmaea</i>	INCLUDED
<i>Stenoderma rufum</i>	Less than 20 occurrences
<i>Sturnira aratathomasi</i>	Less than 20 occurrences
<i>Sturnira bidens</i>	INCLUDED
<i>Sturnira bogotensis</i>	INCLUDED
<i>Sturnira erythromos</i>	INCLUDED
<i>Sturnira koopmanhilli</i>	Less than 20 occurrences
<i>Sturnira lilium</i>	INCLUDED
<i>Sturnira ludovici</i>	INCLUDED
<i>Sturnira luisi</i>	INCLUDED
<i>Sturnira magna</i>	Less than 20 occurrences
<i>Sturnira mordax</i>	Less than 20 occurrences
<i>Sturnira nana</i>	Not found north of equator
<i>Sturnira oporaphilum</i>	Not found north of equator
<i>Sturnira thomasi</i>	Less than 20 occurrences
<i>Sturnira tildae</i>	INCLUDED
<i>Sylvilagus aquaticus</i>	INCLUDED
<i>Sylvilagus audubonii</i>	INCLUDED
<i>Sylvilagus bachmani</i>	INCLUDED
<i>Sylvilagus brasiliensis</i>	INCLUDED
<i>Sylvilagus cognatus</i>	Less than 20 occurrences
<i>Sylvilagus cunicularius</i>	INCLUDED
<i>Sylvilagus dicei</i>	Less than 20 occurrences
<i>Sylvilagus floridanus</i>	INCLUDED
<i>Sylvilagus graysoni</i>	Not found north of equator
<i>Sylvilagus insonus</i>	Less than 20 occurrences
<i>Sylvilagus mansuetus</i>	Less than 20 occurrences

<i>Sylvilagus nuttallii</i>	INCLUDED
<i>Sylvilagus obscurus</i>	INCLUDED
<i>Sylvilagus palustris</i>	INCLUDED
<i>Sylvilagus robustus</i>	Less than 20 occurrences
<i>Sylvilagus transitionalis</i>	INCLUDED
<i>Synaptomys borealis</i>	INCLUDED
<i>Synaptomys cooperi</i>	INCLUDED
<i>Syntheosciurus brochus</i>	Less than 20 occurrences
<i>Tadarida brasiliensis</i>	INCLUDED
<i>Tamandua mexicana</i>	INCLUDED
<i>Tamandua tetradactyla</i>	INCLUDED
<i>Tamiasciurus douglasii</i>	INCLUDED
<i>Tamiasciurus hudsonicus</i>	INCLUDED
<i>Tamiasciurus mearnsi</i>	Less than 20 occurrences
<i>Tamias striatus</i>	INCLUDED
<i>Tapecomys primus</i>	Not found north of equator
<i>Tapirus bairdii</i>	INCLUDED
<i>Tapirus pinchaque</i>	INCLUDED
<i>Tapirus terrestris</i>	INCLUDED
<i>Taxidea taxus</i>	INCLUDED
<i>Tayassu pecari</i>	INCLUDED
<i>Thalpomys cerradensis</i>	Not found north of equator
<i>Thalpomys lasiotis</i>	Not found north of equator
<i>Thaptomys nigrita</i>	Not found north of equator
<i>Thomasomys apeco</i>	Not found north of equator
<i>Thomasomys aureus</i>	INCLUDED
<i>Thomasomys baeops</i>	Not found north of equator
<i>Thomasomys bombycinus</i>	Less than 20 occurrences
<i>Thomomys bottae</i>	INCLUDED
<i>Thomomys bulbivorus</i>	Less than 20 occurrences
<i>Thomasomys cinereiventer</i>	INCLUDED
<i>Thomasomys cinereus</i>	Not found north of equator
<i>Thomomys clusius</i>	Less than 20 occurrences
<i>Thomasomys daphne</i>	Not found north of equator
<i>Thomasomys eleusis</i>	Not found north of equator
<i>Thomasomys erro</i>	Not found north of equator
<i>Thomasomys gracilis</i>	Not found north of equator
<i>Thomasomys hylophilus</i>	INCLUDED
<i>Thomomys idahoensis</i>	INCLUDED
<i>Thomasomys incanus</i>	Not found north of equator
<i>Thomasomys ischyurus</i>	Not found north of equator
<i>Thomasomys kalinowskii</i>	Not found north of equator
<i>Thomasomys ladewi</i>	Not found north of equator

<i>Thomasomys laniger</i>	INCLUDED
<i>Thomasomys macrotis</i>	Not found north of equator
<i>Thomomys mazama</i>	INCLUDED
<i>Thomasomys monochromos</i>	Less than 20 occurrences
<i>Thomomys monticola</i>	Less than 20 occurrences
<i>Thomasomys niveipes</i>	Less than 20 occurrences
<i>Thomasomys notatus</i>	Not found north of equator
<i>Thomasomys onkiro</i>	Not found north of equator
<i>Thomasomys oreas</i>	Not found north of equator
<i>Thomasomys paramorum</i>	Not found north of equator
<i>Thomasomys pyrrhonotus</i>	Not found north of equator
<i>Thomasomys rhoadsi</i>	Not found north of equator
<i>Thomasomys rosalinda</i>	Not found north of equator
<i>Thomasomys silvestris</i>	Not found north of equator
<i>Thomasomys taczanowskii</i>	Not found north of equator
<i>Thomomys talpoides</i>	INCLUDED
<i>Thomomys townsendii</i>	INCLUDED
<i>Thomasomys ucucha</i>	Not found north of equator
<i>Thomomys umbrinus</i>	INCLUDED
<i>Thomasomys vestitus</i>	Less than 20 occurrences
<i>Thrichomys apereoides</i>	Not found north of equator
<i>Thylamys cinderella</i>	Not found north of equator
<i>Thylamys elegans</i>	Not found north of equator
<i>Thylamys macrurus</i>	Not found north of equator
<i>Thylamys pallidior</i>	Not found north of equator
<i>Thylamys pusillus</i>	Not found north of equator
<i>Thylamys tatei</i>	Not found north of equator
<i>Thylamys velutinus</i>	Not found north of equator
<i>Thylamys venustus</i>	Not found north of equator
<i>Thyroptera discifera</i>	INCLUDED
<i>Thyroptera lavalii</i>	Not found north of equator
<i>Thyroptera tricolor</i>	INCLUDED
<i>Tlacuatzin canescens</i>	INCLUDED
<i>Tolypeutes matacus</i>	Not found north of equator
<i>Tolypeutes tricinctus</i>	Not found north of equator
<i>Tomopeas ravus</i>	Not found north of equator
<i>Tonatia bidens</i>	INCLUDED
<i>Tonatia saurophila</i>	INCLUDED
<i>Trachops cirrhosus</i>	INCLUDED
<i>Tremarctos ornatus</i>	INCLUDED
<i>Trinomys albispinus</i>	Not found north of equator
<i>Trinomys dimidiatus</i>	Not found north of equator
<i>Trinomys gratiosus</i>	Not found north of equator

<i>Trinomys iheringi</i>	Not found north of equator
<i>Trinomys myosuros</i>	Not found north of equator
<i>Trinycteris nicefori</i>	INCLUDED
<i>Trinomys paratus</i>	Not found north of equator
<i>Trinomys setosus</i>	Not found north of equator
<i>Tylomys bullaris</i>	Less than 20 occurrences
<i>Tylomys fulviventer</i>	Less than 20 occurrences
<i>Tylomys mirae</i>	INCLUDED
<i>Tylomys nudicaudus</i>	INCLUDED
<i>Tylomys panamensis</i>	Less than 20 occurrences
<i>Tylomys tumbalensis</i>	Less than 20 occurrences
<i>Tylomys watsoni</i>	Less than 20 occurrences
<i>Tympanoctomys barrerae</i>	Not found north of equator
<i>Urocyon cinereoargenteus</i>	INCLUDED
<i>Urocyon littoralis</i>	Less than 20 occurrences
<i>Uroderma bilobatum</i>	INCLUDED
<i>Uroderma magnirostrum</i>	INCLUDED
<i>Ursus americanus</i>	INCLUDED
<i>Ursus arctos</i>	INCLUDED
<i>Vampyriscus bidens</i>	INCLUDED
<i>Vampyriscus brocki</i>	Less than 20 occurrences
<i>Vampyrodes caraccioli</i>	INCLUDED
<i>Vampyressa melissa</i>	INCLUDED
<i>Vampyressa nymphaea</i>	INCLUDED
<i>Vampyressa pusilla</i>	Not found north of equator
<i>Vampyrum spectrum</i>	INCLUDED
<i>Vampyressa thyone</i>	INCLUDED
<i>Vicugna vicugna</i>	Not found north of equator
<i>Vulpes lagopus</i>	INCLUDED
<i>Vulpes macrotis</i>	INCLUDED
<i>Vulpes velox</i>	INCLUDED
<i>Vulpes vulpes</i>	INCLUDED
<i>Wiedomys pyrrhorhinos</i>	Not found north of equator
<i>Wilfredomys oenax</i>	Not found north of equator
<i>Xenomys nelsoni</i>	Less than 20 occurrences
<i>Zaedyus pichiy</i>	Not found north of equator
<i>Zapus hudsonius</i>	INCLUDED
<i>Zapus princeps</i>	INCLUDED
<i>Zapus trinotatus</i>	INCLUDED
<i>Zygodontomys brevicauda</i>	INCLUDED
<i>Zygodontomys brunneus</i>	Less than 20 occurrences
<i>Zygogeomys trichopus</i>	Less than 20 occurrences

Appendix C R code for simulated fossilization of modern North American mammals.

```
# Re-sampling simulated fossilization code without bias
library(MASS)
library(maptools)
library(sp)
require(adehabitatHR)
require(vegan)
require(fossil)

# Reading in the species matrix grid

Speciesmatrix<-read.table("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3
Biogeography\\Biogeography Ordination\\Projected
matrices\\observed.PA_matrix.txt",header=TRUE)
attach(Speciesmatrix)

# Reading in a map of North America
NA_map<-readShapePoly("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3
Biogeography\\Biogeography Ordination\\Extant mammal data\\New
stuff\\Dani_NA_map.shp")
NA_map_sp<-as(NA_map, "SpatialPolygons")

# Fitting the frequency distribution

setwd("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3 Biogeography\\Biogeography
Ordination\\CSV files\\")
plio<- read.csv("Early_late_hemphillian_species_latlong.csv",header=T,row.names=1)
attach(plio)
xt <- plio$Lat/( max(plio$Lat) + .0001 )
hemplat<-fitdistr(xt,"beta",start=list(shape1=3.0871523,shape2=0.3944608))
hemplat2<-fitdistr(abs(plio$Long),"normal")

# Creating empty matrices to fill with data
# LocalitY based
slopes_lat<-matrix(nrow=10000,ncol=1)
T_lat<-matrix(nrow=10000,ncol=1)
p_lat<-matrix(nrow=10000,ncol=1)

# Latitudinal bands
slopes_lat3<-matrix(nrow=10000,ncol=1)
T_lat3<-matrix(nrow=10000,ncol=1)
p_lat3<-matrix(nrow=10000,ncol=1)
```

```

# Beta diversity
rlat<-matrix(nrow=10000,ncol=1)
rlong<-matrix(nrow=10000,ncol=1)
plat<-matrix(nrow=10000,ncol=1)
plong<-matrix(nrow=10000,ncol=1)

# The function
for (ab in 1:10000){

  sample_x<-NA
  sample_y<-NA

  print(paste("Big run number",ab))
  flush.console()

  for (x in 1:1000){

    gammadist <- rbeta(1,hemplat$estimate[[1]],hemplat$estimate[[2]])#
    create random latitudinal points
    gammadist <- gammadist*(max(plio$Lat) + .0001)
    gammadist2 <- rnorm(1,hemplat2$estimate[[1]],hemplat2$estimate[[2]])#
    create random longitudinal points
    gammadist2<--(gammadist2)
    x_coord<-gammadist
    y_coord<-gammadist2

    print(x)# Probably not needed right here?
    flush.console()

    # This code creates a SpatialPointsDataFrame object from the x,y
    coordinate created above:
    test_point<-data.frame(cbind(y_coord,x_coord))
    colnames(test_point)<-c("longitude","latitude")
    coordinates(test_point)<-c("longitude","latitude")

    # This uses the "over" function to assign the attributes of a polygon to the
    point. If there are no attributes (i.e. the point falls outside the polygon), then "NA" is
    returned. If NA is not returned, the coordinates are added to the vectors from above.
    if(!is.na(over(test_point,NA_map_sp))) {sample_x<-
      c(sample_x,x_coord);sample_y<-c(sample_y,y_coord)} else {next} # tell it to be in US,
    index out US polygon
    # When we reach 100 coordinates (including the dummmmy NA at the start)
    the dummy NA is dropped and the loop breaks.
  }
}

```

```

if(length(sample_x)==47) {sample_x<-sample_x[-1];sample_y<-sample_y[-1];break}
}
# Turn the sampling points into a SpatialPointsDataFrame object
sample_locations<-data.frame(cbind(sample_y,sample_x))
colnames(sample_locations)<-c("longitude","latitude")
coordinates(sample_locations)<-c("longitude","latitude")

# Assign closest points to points
(http://www.nceas.ucsb.edu/scicomp/usecases/AssignClosestPointsToPoints)
closestSiteVec <- vector(mode = "numeric",length =
length(sample_locations))
minDistVec <- vector(mode = "numeric",length =
length(sample_locations))

# For each of the sample locations, find the nearest data point from
another data.frame
for (i in 1 : length(sample_locations))
{
  distVec <- spDistsN1(as.matrix(Speciesmatrix[,c(1,2)]),sample_locations[i],longlat =
TRUE)
  minDistVec[i] <- min(distVec)
  closestSiteVec[i] <- which.min(distVec)
}

PointAssignTemps <- Speciesmatrix[closestSiteVec,3:ncol(Speciesmatrix)]
FinalTable = data.frame(coordinates(sample_locations),PointAssignTemps)
names(FinalTable) <-
c("Long","Lat",names(Speciesmatrix[,3:ncol(Speciesmatrix)]))

FinalTable2<-
FinalTable[rowSums(FinalTable[,3:ncol(FinalTable)])>1,3:ncol(FinalTable)]

time_code<-as.vector(Sys.time())
write.table(FinalTable,paste("C:\\\\Users\\\\Dani\\\\Documents\\\\PhD\\\\Chapter 7 constraining
biogeo error\\\\2014\\\\Location change\\\\Coordinates\\\\No bias\\\\Coordinates with
bats",time_code,".txt",sep=""))

d <- FinalTable2

e<-FinalTable[,1:2]
e<-e[rownames(d),]

rich<-data.frame(rowSums(d))
latrich<-cbind(rich,e)

```

```

# locality based

b<-glm(latrich$rowSums.d.~latrich$Long+latrich$Lat)
slopes_lat[ab,]<-b$coefficients[3]
T_lat[ab,]<-summary(b)$coefficients[3,3]
p_lat[ab,]<-summary(b)$coefficients[3,4]

# Latitudinal bands

maxi<-60# Max latitude
mini<-25# Min latitude
range<-round(((maxi-mini)/2),digits=0)

richness<-matrix(ncol=5,nrow=nrow(d))

for(k in 1:range){
  maxm<-mini+2
  grp1locs<-subset(latrich,latrich$Lat<maxm&latrich$Lat>=mini)

  if(nrow(grp1locs)>1){

    # Unrarefied richness in latitudinal bands
    d1<-d[rownames(grp1locs),]
    cols<-colSums(d1)

    for(j in 1:length(cols)){
      if(cols[j]>1){
        cols[j]<-1
      }else{
        cols[j]<-cols[j]
      }
    }

    richness[k,1]<-median(grp1locs$Lat)# median lat
    richness[k,2]<-sum(cols)

    l<-jack1(d1,taxa.row=FALSE,abund=FALSE)
    richness[k,5]<-l[1]

    e1<-e[rownames(d1),]

  }else{

    richness[k,2]<-NA
    richness[k,3]<-NA
  }
}

```

```

richness[k,4]<-NA
richness[k,5]<-NA
}

mini<-maxm #updating mini

}

b<-glm(richness[,2]~richness[,1])
slopes_lat3[ab,]<-b$coefficients[2]
T_lat3[ab,]<-summary(b)$coefficients[2,3]
p_lat3[ab,]<-summary(b)$coefficients[2,4]

# Beta diversity

cca <- decorana(d[,colSums(d)>0])
latfit<- envfit(cca,e)
r<-latfit$vectors
r2<-r[2]
r3<-r2$r
longituder<-r3[1]
latituder<-r3[2]

p<-r[4]
p2<-p$pvals
longitudep<-p2[1]
latitudep<-p2[2]

rlat[ab,]<-latituder
rlong[ab,]<-longituder
plat[ab,]<-longitudep
plong[ab,]<-longitudep

}

time_code<-as.vector(Sys.time())
Dani_results<-
cbind(slopes_lat,T_lat,p_lat,slopes_lat3,T_lat3,p_lat3,rlat,rlong,plat,plong)
colnames(Dani_results)<-c("Latslope","T value lat","P value lat",
"Bands slope","T value bands","P value bands",
"rlat","rlong","plat","plong")
write.table(Dani_results,paste("C:\\\\Users\\\\Dani\\\\Documents\\\\PhD\\\\Chapter 7
constraining bioge error\\\\2014\\\\Location change\\\\No bias\\\\EL Hemphillian RICHNESS
GRADIENT no bias with bats",time_code,".txt",sep=""))

```

```

# Re-sampling simulated fossilization code with bias

# Read in the species grid matrix
Speciesmatrix<-read.table("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3
Biogeography\\Biogeography Ordination\\Projected
matrices\\observed.PA_matrix.txt",header=TRUE)
attach(Speciesmatrix)

# Removing bats from the sample if required
files <- list.files(path="C:\\Users\\Dani\\Documents\\PhD\\Chapter 7 constraining bioge
error\\2014\\Mammals_3.0\\Bats under 15 kg\\",pattern=".shp",recursive=TRUE)
require(stringr)
bats<-word(files[1:length(files)],2,sep = fixed("/"))
bats<-word(bats,sep = fixed(".shp"))

speciesnames<-colnames(Speciesmatrix)

for(i in 1:length(speciesnames)){
  for(j in 1:length(bats)){
    if(speciesnames[i]==bats[j]){
      Speciesmatrix<-Speciesmatrix[,-i]
    }
  }
}

# Calculate total number of grid cells
tots<-colSums(Speciesmatrix[,3:ncol(Speciesmatrix)])
one_hundred<-nrow(Speciesmatrix)

probs<-tots/one_hundred # Weights based on range size

# Weighted probability based on mass

files <- list.files(path="C:\\Users\\Dani\\Documents\\PhD\\Chapter 7 constraining bioge
error\\2014\\Mammals_3.0\\Bigger than 15 kg\\",pattern=".shp",recursive=TRUE)
require(stringr)
bigger<-word(files[1:length(files)],2,sep = fixed("/"))
bigger<-word(bigger,sep = fixed(".shp"))

```

```

probs[bigger]<-probs[bigger]*0.95
probs<-na.omit(probs)

files <- list.files(path="C:\\Users\\Dani\\Documents\\PhD\\Chapter 7 constraining bioge
error\\2014\\Mammals_3.0\\Veg smaller than 15 kg\\",pattern=".shp",recursive=TRUE)
require(stringr)
smaller<-word(files[1:length(files)],2,sep = fixed("/"))
smaller<-word(smaller,sep = fixed(".shp"))

probs[smaller]<-probs[smaller]*0.6
probs<-na.omit(probs)

files <- list.files(path="C:\\Users\\Dani\\Documents\\PhD\\Chapter 7 constraining bioge
error\\2014\\Mammals_3.0\\Carnivores under 15 kg\\",pattern=".shp",recursive=TRUE)
require(stringr)
carn<-word(files[1:length(files)],2,sep = fixed("/"))
carn<-word(carn,sep = fixed(".shp"))

probs[carn]<-probs[carn]*0.21
probs<-na.omit(probs)

# Read in map of North America
NA_map<-readShapePoly("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3
Biogeography\\Biogeography Ordination\\Extant mammal data\\New
stuff\\Dani_NA_map.shp")
NA_map_sp<-as(NA_map, "SpatialPolygons")

# Fit frequency distribution
setwd("C:\\Users\\Dani\\Documents\\PhD\\Chapter 3 Biogeography\\Biogeography
Ordination\\CSV files\\")
plio<- read.csv("Early_late_hemphillian_species_latlong.csv",header=T,row.names=1)
attach(plio)
xt <- plio$Lat/( max(plio$Lat) + .0001 )
hemplat<-fitdistr(xt,"beta",start=list(shape1=3.0871523,shape2=0.3944608))
hemplat2<-fitdistr(abs(plio$Long),"normal")

# The function

for (ab in 1:100){ # pick a bigger number when doing for realz

# LocalitY based
slopes_lat<-matrix(nrow=100,ncol=1)
T_lat<-matrix(nrow=100,ncol=1)
p_lat<-matrix(nrow=100,ncol=1)

```

```

slopes_lat2<-matrix(nrow=100,ncol=1)
T_lat2<-matrix(nrow=100,ncol=1)
p_lat2<-matrix(nrow=100,ncol=1)

# Latitudinal bands
slopes_lat3<-matrix(nrow=100,ncol=1)
T_lat3<-matrix(nrow=100,ncol=1)
p_lat3<-matrix(nrow=100,ncol=1)

slopes_lat4<-matrix(nrow=100,ncol=1)
T_lat4<-matrix(nrow=100,ncol=1)
p_lat4<-matrix(nrow=100,ncol=1)

# Beta diversity

rlat<-matrix(nrow=100,ncol=1)
rlong<-matrix(nrow=100,ncol=1)
plat<-matrix(nrow=100,ncol=1)
plong<-matrix(nrow=100,ncol=1)

# These two vectors will contain the sampling points built up iteratively in the loop
sample_x<-NA # Do we need this????? YES!!!
sample_y<-NA

print(paste("Big run number",ab))
flush.console()

for (x in 1:1000){

  gammadist <- rbeta(1,hemplat$estimate[[1]],hemplat$estimate[[2]])#
  create random latitudinal points
    gammadist <- gammadist*(max(plio$Lat) + .0001)
    gammadist2 <- rnorm(1,hemplat2$estimate[[1]],hemplat2$estimate[[2]])#
  create random longitudinal points
    gammadist2<--(gammadist2)
    x_coord<-gammadist
    y_coord<-gammadist2

  print(x)# Probably not needed right here?
  flush.console()

  # This code creates a SpatialPointsDataFrame object from the x,y
  coordinate created above:
  test_point<-data.frame(cbind(y_coord,x_coord))
}

```

```

colnames(test_point)<-c("longitude","latitude")
coordinates(test_point)<-c("longitude","latitude")

# This uses the "over" function to assign the attributes of a polygon to the
point. If there are no attributes (i.e. the point falls outside the polygon), then "NA" is
returned. If NA is not returned, the coordinates are added to the vectors from above.
if(!is.na(over(test_point,NA_map_sp))) {sample_x<-
c(sample_x,x_coord);sample_y<-c(sample_y,y_coord)} else {next} # tell it to be in US,
index out US polygon
# When we reach 100 coordinates (including the dummmmy NA at the start)
the dummy NA is dropped and the loop breaks.
if(length(sample_x)==47) {sample_x<-sample_x[-1];sample_y<-
sample_y[-1];break}
#
# Turn the sampling points into a SpatialPointsDataFrame object
sample_locations<-data.frame(cbind(sample_y,sample_x))
colnames(sample_locations)<-c("longitude","latitude")
coordinates(sample_locations)<-c("longitude","latitude")

# Assign closest points to points
(http://www.nceas.ucsb.edu/scicomp/usecases/AssignClosestPointsToPoints)
closestSiteVec <- vector(mode = "numeric",length =
length(sample_locations))
minDistVec <- vector(mode = "numeric",length =
length(sample_locations))

# For each of the sample locations, find the nearest data point from
another data.frame
for (i in 1 : length(sample_locations))
{
  distVec <- spDistsN1(as.matrix(Speciesmatrix[,c(1,2)]),sample_locations[i,],longlat =
TRUE)
  minDistVec[i] <- min(distVec)
  closestSiteVec[i] <- which.min(distVec)
}

PointAssignTemps <- Speciesmatrix[closestSiteVec,3:ncol(Speciesmatrix)]
FinalTable = data.frame(coordinates(sample_locations),PointAssignTemps)
names(FinalTable) <-
c("Long","Lat",names(Speciesmatrix[,3:ncol(Speciesmatrix)]))

FinalTable2<-
FinalTable[rowSums(FinalTable[,3:ncol(FinalTable)])>1,3:ncol(FinalTable)]

time_code<-as.vector(Sys.time())

```

```

write.table(FinalTable,paste("C:\\Users\\Dani\\Documents\\PhD\\Chapter 7 constraining
biogeo error\\2014\\Location change\\Coordinates\\Coordinates with
bats",time_code,".txt",sep=""))

# Somehow incorporate the probabilities of sampling, combined probability for BM and
GR?
# Combine the weights....just reduce the weights of the small mammals?

for(g in 1:100){

  num<-sample(colnames(FinalTable2),size=0.25*ncol(FinalTable2),
replace = FALSE, prob = probs)
  d <- FinalTable2[,num]

  e<-FinalTable[,1:2]
  e<-e[rownames(d),]

  rich<-data.frame(rowSums(d))
  latrich<-cbind(rich,e)

  # locality based

  b<-glm(latrich$rowSums.d.~latrich$Long+latrich$Lat)
  slopes_lat[g,<-b$coefficients[3]
  T_lat[g,<-summary(b)$coefficients[3,3]
  p_lat[g,<-summary(b)$coefficients[3,4]

  richness<-matrix(ncol=2,nrow=nrow(d))

  for(k in 1:nrow(d)){ # Jackknife probably makes most sense
    l<-jack1(d[k,],taxa.row=FALSE,abund=FALSE)
    richness[k,2]<-l[1]
  }

  b<-glm(richness[,2]~latrich$Lat)
  slopes_lat2[g,<-b$coefficients[2]
  T_lat2[g,<-summary(b)$coefficients[2,3]
  p_lat2[g,<-summary(b)$coefficients[2,4]

  # Latitudinal bands

  maxi<-60# Max latitude
  mini<-25# Min latitude
  range<-round(((maxi-mini)/2),digits=0)

  richness<-matrix(ncol=5,nrow=nrow(d))
}

```

```

for(k in 1:range){
  maxm<-mini+2
  grp1locs<-subset(latrich,latrich$Lat<maxm&latrich$Lat>=mini)

  if(nrow(grp1locs)>1){

    # Unrarefied richness in latitudinal bands
    d1<-d[rownames(grp1locs),]
    cols<-colSums(d1)

    for(j in 1:length(cols)){
      if(cols[j]>1){
        cols[j]<-1
      }else{
        cols[j]<-cols[j]
      }
    }

    richness[k,1]<-median(grp1locs$Lat)# median lat

    richness[k,2]<-sum(cols)

    l<-jack1(d1, taxa.row=FALSE, abund=FALSE)
    richness[k,5]<-l[1]

    e1<-e[rownames(d1),]

  }else{

    richness[k,2]<-NA
    richness[k,3]<-NA
    richness[k,4]<-NA
    richness[k,5]<-NA
  }
}

mini<-maxm #updating mini

}

b<-glm(richness[,2]~richness[,1])
slopes_lat3[g,]<-b$coefficients[2]
T_lat3[g,]<-summary(b)$coefficients[2,3]
p_lat3[g,]<-summary(b)$coefficients[2,4]

```

```

b<-glm(richness[,5]~richness[,1])
slopes_lat4[g,]<-b$coefficients[2]
T_lat4[g,]<-summary(b)$coefficients[2,3]
p_lat4[g,]<-summary(b)$coefficients[2,4]

# Beta diversity

cca <- decorana(d[,colSums(d)>0])
latfit<- envfit(cca,e)
r<-latfit$vectors
r2<-r[2]
r3<-r2$r
longituder<-r3[1]
latituder<-r3[2]

p<-r[4]
p2<-p$pvals
longitudep<-p2[1]
latitudep<-p2[2]

rlat[g,]<-latituder
rlong[g,]<-longituder
plat[g,]<-latitudep
plong[g,]<-longitudep

print(g)

}

time_code<-as.vector(Sys.time())
Dani_results<-
cbind(slopes_lat,T_lat,p_lat,slopes_lat2,T_lat,p_lat2,slopes_lat3,T_lat3,p_lat3,slopes_lat4,T_lat4,p_lat4,rlat,rlong,plat,plong)
colnames(Dani_results)<-c("Latslope","T value lat","P value lat","Latslope JACK","T value lat JACK","P value lat JACK",
"Bands slope","T value bands","P value bands","Bands slope JACK","T value bands JACK","P value bands JACK",
"rlat","rlong","plat","plong")
write.table(Dani_results,paste("C:\\\\Users\\\\Dani\\\\Documents\\\\PhD\\\\Chapter 7 constraining biogeo error\\\\2014\\\\Location change\\\\EL Hemphillian RICHNESS GRADIENT ALL 75 taxa removed with bats",time_code,".txt",sep=""))
}

```

Appendix D Sources for the majority of mammal occurrence data downloaded from the Fossilworks database

- X. Wang, R. H. Tedford, and B. E. Taylor. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* **243**:1-392 [206 collections, 668 occurrences]
- A. F. Pajak, III, E. Scott, and C. J. Bell. 1996. *PaleoBios* **17(2-4)**:28-49 [118 collections, 315 occurrences]
- L. M. Abraczinskas. 1993. Pleistocene proboscidean sites in Michigan: New records and an update on published sites. *Michigan Academician* **25(4)**:443-490 [186 collections, 189 occurrences]
- J. R. Macdonald. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. *Bulletin of the Los Angeles County Museum of Natural History, Science* **8**:165-82 [113 collections, 195 occurrences]
- M. L. Cassiliano. 1999. Biostratigraphy of Blancan and Irvingtonian mammals in the Fish Creek-Vallecito Creek section, southern California, and a review of the Blancan-Irvingtonian boundary. *Journal of Vertebrate Paleontology* **19(1)**:169-186 [48 collections, 420 occurrences]
- C. B. Schultz and C. H. Falkenbach. 1968. *Bulletin of the American Museum of Natural History* **139** [135 collections, 137 occurrences]
- X. Wang. 1994. Phylogenetic systematics of the Hesperocyoninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* **221**:1-207 [76 collections, 196 occurrences]
- M. R. Voorhies. 1990. In T. C. Gustavson (ed.), *Bureau of Economic Geology Guidebook* [18 collections, 683 occurrences]
- G. T. James. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley badlands, California; Part 1, Geology, faunal interpretations, and systematic descriptions

of Chiroptera, Insectivora, and Rodentia. *University of California Publications in Geological Sciences* **45**:1-154 [60 collections, 109 occurrences]

G. T. Jefferson. 1991. A catalogue of late Quaternary vertebrates from California. Part two, mammals. *Natural History Museum of Los Angeles County Technical Report* **7**:1-129 [37 collections, 165 occurrences]

M. F. Skinner, S. M. Skinner, and R. J. Gooris. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western Nebraska. *Bulletin of the American Museum of Natural History* **158(5)**:263-370 [44 collections, 105 occurrences]

R. Eshelman and F. Grady. 1986. Quaternary vertebrate localities of Virginia and their avian and mammalian fauna. *Virginia Division of Mineral Resources, Publication* **75**:43-70 [28 collections, 163 occurrences]

E. H. Lindsay. 1972. Small mammal fossils from the Barstow Formation, California. *University of California Publications in Geological Sciences* **93**:1-104 [35 collections, 128 occurrences]

P. R. Bjork. 1970. *Transactions of the American Philosophical Society* **60(7)** [56 collections, 79 occurrences]

S. D. Webb. 1974. Chronology of Florida Pleistocene mammals. In S. D. Webb (ed.), *Pleistocene Mammals of Florida* 5-31 [17 collections, 254 occurrences]

J. A. Holman, D. C. Fisher, and R. O. Kapp. 1986. Recent discoveries of fossil vertebrates in the lower peninsula of Michigan. *Michigan Academician* **18(3)**:431-463 [56 collections, 60 occurrences]

B. E. Bailey. 2004. Biostratigraphy and biochronology of early Arikareean through late Hemingfordian small mammal faunas from the Nebraska Panhandle and adjacent areas. *Paludicola* **4(3)**:81-113 [11 collections, 250 occurrences]

S. D. Webb. 1969. *University of California Publications in Geological Sciences* **78** [22 collections, 110 occurrences]

E. H. Lindsay and N. T. Tessman. 1974. *Journal of the Arizona Academy of Sciences* **9** [24 collections, 96 occurrences]

G. S. Morgan and R. C. Hulbert, Jr. 1995. *Bulletin of the Florida Museum of Natural History* **37(1)** [12 collections, 187 occurrences]

Appendix E $\delta^{18}\text{O}$ (‰) values from serial samples of Wyoming pronghorn tooth enamel.

Sample	Specimen	Year	Sample	$\delta^{18}\text{O}_{\text{PO}_4}$ (‰ V-SMOW)	Distance	$\delta^{18}\text{O}_{\text{CO}_3}$ (‰ VPDB)
1	47873	2010	47873-1	11.8	8.5	
1	47873	2010	47873-2	10.8	10.7	-10.7
1	47873	2010	47873-2	11.1	10.7	
1	47873	2010	47873-2	11.3	10.7	
1	47873	2010	47873-3	11	15.26	
1	47873	2010	47873-3	10.7	15.26	
1	47873	2010	47873-3	11	15.26	
1	47873	2010	47873-4	13.4	18.4	
1	47873	2010	47873-4	13.8	18.4	
1	47873	2010	47873-5	15.6	21.2	
1	47873	2010	47873-5	15.5	21.2	
1	47873	2010	47873-5	15.9	21.2	
1	47873	2010	47873-6	16.4	24.1	
1	47873	2010	47873-6	16.7	24.1	
1	47873	2010	47873-6	16.5	24.1	
1	47873	2010	47873-8	17.3	27.8	
1	47873	2010	47873-8	17.6	27.8	
1	47873	2010	47873-8	16.8	27.8	
1	47873	2010	47873-9	18.1	28.75	-7.1
1	47873	2010	47873-9	17.4	28.75	
1	47873	2010	47873-9	17.8	28.75	
1	47873	2010	47873-10	16.7	31.1	
1	47873	2010	47873-10	16.9	31.1	
1	47873	2010	47873-11	13.8	34.3	
1	47873	2010	47873-11	13.4	34.3	
1	47873	2010	Jaw	17.0	-	
1	47873	2010	Jaw	16.8	-	
1	47873	2010	Jaw	16.3	-	
2	47868	2010	47868-1	17	3.7	
2	47868	2010	47868-1	16.3	3.7	
2	47868	2010	47868-1	17.1	3.7	
2	47868	2010	47868-2	15.2	5.6	
2	47868	2010	47868-2	15.4	5.6	
2	47868	2010	47868-2	14.9	5.6	
2	47868	2010	47868-3	14.4	8.8	
2	47868	2010	47868-3	14.3	8.8	
2	47868	2010	47868-3	14.3	8.8	
2	47868	2010	47868-4	12.8	10.9	
2	47868	2010	47868-4	13.6	10.9	

2	47868	2010	47868-4	13.7	10.9	
2	47868	2010	47868-5	12.9	13.6	-9.7
2	47868	2010	47868-5	13	13.6	
2	47868	2010	47868-5	12.2	13.6	
2	47868	2010	47868-6	12.1	15.6	
2	47868	2010	47868-6	13.3	15.6	
2	47868	2010	47868-6	12.9	15.6	
2	47868	2010	47868-7	13.9	18.2	
2	47868	2010	47868-7	13.9	18.2	
2	47868	2010	47868-7	14	18.2	
2	47868	2010	47868-8	15.4	21	
2	47868	2010	47868-8	14.7	21	
2	47868	2010	47868-9	16.3	23.4	
2	47868	2010	47868-9	16.3	23.4	
2	47868	2010	47868-9	15.3	23.4	
2	47868	2010	47868-10	17.6	29.1	
2	47868	2010	47868-10	17.3	29.1	
2	47868	2010	47868-10	17.4	29.1	
2	47868	2010	47868-11	18.3	31.9	-6.4
2	47868	2010	47868-11	19.9	31.9	
2	47868	2010	47868-11	18	31.9	
2	47868	2010	47868-12	16.6	35.3	
2	47868	2010	47868-12	16.5	35.3	
2	47868	2010	47868-12	16.6	35.3	
2	47868	2010	47868-13	15.9	39.1	
2	47868	2010	47868-13	15.4	39.1	
2	47868	2010	47868-13	15	39.1	
2	47868	2010	47868-14	13.9	43	
2	47868	2010	47868-14	14.5	43	
2	47868	2010	47868-14	14	43	
2	47868	2010	Jaw	16.7	-	
2	47868	2010	Jaw	17.4	-	
2	47868	2010	Jaw	17.1	-	
3	9244b	1972	9244b-2	17	6	-6.6
3	9244b	1972	9244b-2	17.3	6	
3	9244b	1972	9244b-2	17.7	6	
3	9244b	1972	9244b-3	15.3	8.1	
3	9244b	1972	9244b-3	15.4	8.1	
3	9244b	1972	9244b-3	14.7	8.1	
3	9244b	1972	9244b-4	13.7	10.6	
3	9244b	1972	9244b-4	13.5	10.6	
3	9244b	1972	9244b-4	13.7	10.6	
3	9244b	1972	9244b-5	11	13.5	
3	9244b	1972	9244b-5	11.4	13.5	
3	9244b	1972	9244b-5	11.6	13.5	

3	9244b	1972	9244b-6	10.4	16.3	-10.8
3	9244b	1972	9244b-6	10.6	16.3	
3	9244b	1972	9244b-6	10.9	16.3	
3	9244b	1972	9244b-7	12.1	18.4	
3	9244b	1972	9244b-7	12.4	18.4	
3	9244b	1972	9244b-7	12.5	18.4	
3	9244b	1972	9244b-8	13.3	21	
3	9244b	1972	9244b-8	12.7	21	
3	9244b	1972	9244b-8	12.6	21	
3	9244b	1972	9244b-9	14.6	23.5	
3	9244b	1972	9244b-9	14.3	23.5	
3	9244b	1972	9244b-9	14.5	23.5	
3	9244b	1972	9244b-10	15.5	26.5	
3	9244b	1972	9244b-10	15.7	26.5	
3	9244b	1972	9244b-10	15.1	26.5	
3	9244b	1972	9244b-11	15.9	29.4	
3	9244b	1972	9244b-11	15.3	29.4	
3	9244b	1972	9244b-11	15.7	29.4	
3	9244b	1972	9244b-12	16.4	32.1	
3	9244b	1972	9244b-12	16.1	32.1	
3	9244b	1972	9244b-12	15.8	32.1	
3	9244b	1972	9244b-13	16.3	34.2	-7.8
3	9244b	1972	9244b-13	15.9	34.2	
3	9244b	1972	9244b-13	16.1	34.2	
3	9244b	1972	9244b-14	16.1	36.8	
3	9244b	1972	9244b-14	15.7	36.8	
3	9244b	1972	9244b-14	15.6	36.8	
3	9244b	1972	Jaw	15.2	-	
3	9244b	1972	Jaw	15.6	-	
3	9244b	1972	Jaw	15.4	-	
4	9216b	1971	9216b-1	14.1	6.8	
4	9216b	1971	9216b-1	13	6.8	
4	9216b	1971	9216b-1	13.9	6.8	
4	9216b	1971	9216b-2	12.7	9.4	-7.1
4	9216b	1971	9216b-2	11.6	9.4	
4	9216b	1971	9216b-2	12.5	9.4	
4	9216b	1971	9216b-3	11.4	11.7	
4	9216b	1971	9216b-3	11.6	11.7	
4	9216b	1971	9216b-3	11.7	11.7	
4	9216b	1971	9216b-4	10.7	13.5	
4	9216b	1971	9216b-4	10.5	13.5	
4	9216b	1971	9216b-4	10.4	13.5	
4	9216b	1971	9216b-5	10.2	16.1	
4	9216b	1971	9216b-5	10.2	16.1	
4	9216b	1971	9216b-5	9	16.1	

4	9216b	1971	9216b-6	10.2	18.4	-12.2
4	9216b	1971	9216b-6	9.7	18.4	
4	9216b	1971	9216b-6	10.2	18.4	
4	9216b	1971	9216b-7	11.5	21.1	
4	9216b	1971	9216b-7	10.6	21.1	
4	9216b	1971	9216b-8	13.5	23.7	
4	9216b	1971	9216b-8	13.2	23.7	
4	9216b	1971	9216b-8	13.2	23.7	
4	9216b	1971	9216b-9	14	26.2	
4	9216b	1971	9216b-9	14.1	26.2	
4	9216b	1971	9216b-9	14.2	26.2	
4	9216b	1971	9216b-10	14.3	28.9	
4	9216b	1971	9216b-10	14.5	28.9	
4	9216b	1971	9216b-10	14.8	28.9	
4	9216b	1971	9216b-11	16.1	31.4	-7.1
4	9216b	1971	9216b-11	16.3	31.4	
4	9216b	1971	9216b-11	16.3	31.4	
4	9216b	1971	9216b-12	14.7	34	
4	9216b	1971	9216b-12	15.7	34	
4	9216b	1971	Jaw	12.0	-	
4	9216b	1971	Jaw	11.9	-	
4	9216b	1971	Jaw	11.9	-	
5	9215b	1971	9215b-1	17.7	7.2	
5	9215b	1971	9215b-1	17.2	7.2	
5	9215b	1971	9215b-1	17.1	7.2	
5	9215b	1971	9215b-2	14.3	9.5	
5	9215b	1971	9215b-2	14.6	9.5	
5	9215b	1971	9215b-2	14.7	9.5	
5	9215b	1971	9215b-3	13.6	12	
5	9215b	1971	9215b-3	13.8	12	
5	9215b	1971	9215b-4	11.5	14.1	-10.9
5	9215b	1971	9215b-4	11.2	14.1	
5	9215b	1971	9215b-4	11.3	14.1	
5	9215b	1971	9215b-5	12.9	18.4	
5	9215b	1971	9215b-5	12.9	18.4	
5	9215b	1971	9215b-5	13.2	18.4	
5	9215b	1971	9215B-6	15.9	21.2	
5	9215b	1971	9215B-6	15	21.2	
5	9215b	1971	9215B-6	15.5	21.2	
5	9215b	1971	9215b-7	16.8	23.3	
5	9215b	1971	9215b-7	16.2	23.3	
5	9215b	1971	9215b-7	16.7	23.3	
5	9215b	1971	9215b-8	17	26.1	
5	9215b	1971	9215b-8	17	26.1	
5	9215b	1971	9215b-8	17.1	26.1	

5	9215b	1971	9215b-9	18.6	29.1	
5	9215b	1971	9215b-9	18.8	29.1	
5	9215b	1971	9215b-9	18.2	29.1	
5	9215b	1971	9215b-10	19.3	32	
5	9215b	1971	9215b-10	19.3	32	
5	9215b	1971	9215b-10	18.8	32	
5	9215b	1971	9215b-11	17.2	34.5	-7.5
5	9215b	1971	9215b-11	17.6	34.5	
5	9215b	1971	9215b-11	16.7	34.5	
5	9215b	1971	9215b-12	14.4	37.6	
5	9215b	1971	9215b-12	14.5	37.6	
5	9215b	1971	9215b-12	13.9	37.6	
5	9215b	1971	Jaw	18.1	-	
5	9215b	1971	Jaw	17.2	-	
5	9215b	1971	Jaw	17.8	-	
6	47875	2010	47875-1	12.2	3.2	-10.6
6	47875	2010	47875-1	13.2	3.2	
6	47875	2010	47875-2	14.6	5.6	
6	47875	2010	47875-2	14.9	5.6	
6	47875	2010	47875-2	14.7	5.6	
6	47875	2010	47875-3	15.1	7.9	
6	47875	2010	47875-3	15.3	7.9	
6	47875	2010	47875-3	15.1	7.9	
6	47875	2010	47875-4	17.3	9.8	
6	47875	2010	47875-4	16.8	9.8	
6	47875	2010	47875-4	17.1	9.8	
6	47875	2010	47875-5	15.2	12.4	
6	47875	2010	47875-5	14.7	12.4	
6	47875	2010	47875-5	15	12.4	
6	47875	2010	47875-6	12.1	15.7	-11.6
6	47875	2010	47875-6	11.7	15.7	
6	47875	2010	47875-6	12.1	15.7	
6	47875	2010	47875-7	11.7	19.4	
6	47875	2010	47875-7	12.1	19.4	
6	47875	2010	47875-7	12.2	19.4	
6	47875	2010	47875-8	13.4	22.9	
6	47875	2010	47875-8	13.5	22.9	
6	47875	2010	47875-8	14.3	22.9	
6	47875	2010	47875-9	15.8	26.3	
6	47875	2010	47875-9	15.4	26.3	
6	47875	2010	47875-9	15.7	26.3	
6	47875	2010	47875-10	16.7	29.8	
6	47875	2010	47875-10	16.4	29.8	
6	47875	2010	47875-10	15.8	29.8	
6	47875	2010	47875-11	17.9	36.7	-6

6	47875	2010	47875-11	18.2	36.7
6	47875	2010	47875-11	18	36.7
6	47875	2010	47875-12	17.4	39.6
6	47875	2010	47875-12	16.7	39.6
6	47875	2010	47875-12	17.1	39.6
6	47875	2010	47875-13	16.7	42.1
6	47875	2010	47875-13	16.2	42.1
6	47875	2010	47875-13	15.6	42.1
6	47875	2010	Jaw	17.7	-
6	47875	2010	Jaw	17.2	-

Appendix F Summary of USNIP sites in Wyoming

USNIP Site ID	Site Name	County	Latitude	Longitude	Elevation	Start Date
WY00	Snowy Range	Albany	41.38	-106.26	3269	4/22/1986
WY02	Sinks Canyon	Fremont	42.73	-108.85	2164	8/21/1984
WY06	Pinedale	Sublette	42.93	-109.79	2388	1/26/1982
WY08	Yellowstone National Park-Tower Falls	Park	44.92	-110.42	1912	6/5/1980
WY94	Grand Tetons National Park	Teton	43.83	-110.70		9/27/2011
WY95	Brooklyn Lake	Albany	41.36	-106.24	3181	9/22/1992
WY97	South Pass City	Fremont	42.49	-108.83	2524	4/30/1985
WY98	Gypsum Creek	Sublette	43.22	-109.99	2428	12/26/1984
WY99	Newcastle	Weston	43.87	-104.19	1466	8/11/1981

Appendix G Final published copies of Chapters 3 and 4.



Mean Annual Precipitation Explains Spatiotemporal Patterns of Cenozoic Mammal Beta Diversity and Latitudinal Diversity Gradients in North America

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Abstract

Spatial diversity patterns are thought to be driven by climate-mediated processes. However, temporal patterns of community composition remain poorly studied. We provide two complementary analyses of North American mammal diversity, using (i) a paleontological dataset (2077 localities with 2493 taxon occurrences) spanning 21 discrete subdivisions of the Cenozoic based on North American Land Mammal Ages (36 Ma – present), and (ii) climate space model predictions for 744 extant mammals under eight scenarios of future climate change. Spatial variation in fossil mammal community structure (β diversity) is highest at intermediate values of continental mean annual precipitation (MAP) estimated from paleosols (~450 mm/year) and declines under both wetter and drier conditions, reflecting diversity patterns of modern mammals. Latitudinal gradients in community change (latitudinal turnover gradients, aka LTGs) increase in strength through the Cenozoic, but also show a cyclical pattern that is significantly explained by MAP. In general, LTGs are weakest when continental MAP is highest, similar to modern tropical ecosystems in which latitudinal diversity gradients are weak or undetectable. Projections under modeled climate change show no substantial change in β diversity or LTG strength for North American mammals. Our results suggest that similar climate-mediated mechanisms might drive spatial and temporal patterns of community composition in both fossil and extant mammals. We also provide empirical evidence that the ecological processes on which climate space models are based are insufficient for accurately forecasting long-term mammalian response to anthropogenic climate change and inclusion of historical parameters may be essential.

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Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All the data are available on the Paleobiology Database (fossilworks.org) and MIOMAP (<http://www.ucmp.berkeley.edu/miomap/>).

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Introduction

Terrestrial species from all major taxonomic groups show dramatic changes in richness and diversity across the landscape [1]. One of the fundamental goals in ecology is therefore to ascertain why there are more species in some places than in others. A satisfactory answer would identify and disentangle the drivers of biodiversity at all spatial scales, from the microhabitat to the globe, as well as explain changes through time. Attempts to provide such an answer have produced many studies of species richness patterns and community composition in extant organisms [1–8]. Prime examples are the numerous studies of latitudinal richness gradients (LRGs), which have been observed in many terrestrial groups including angiosperms, birds, mammals, insects and other invertebrates. The best supported hypotheses show that richness declines toward the poles in correlation with reductions in precipitation, temperature, and net primary productivity [9]. Correlation of global climate with animal richness over the past

65 Ma, specifically a decline in richness as climates cooled, similarly supports a link between diversity and climate [10–12]. However, of the spatial and temporal dimensions of diversity, spatial patterns of community differences (“ β diversity”) are infrequently studied despite considerable variation on both local and regional scales [2,13,14] and their influential role in the structuring of continental-scale richness patterns including LRGs [3,4].

β diversity has been defined most broadly as the differentiation in community composition (i.e. the species that make up the community) among regions or along environmental gradients [15]. Similar to LRGs, β diversity generally declines from the tropics to the poles in correlation with climate [2]. However, temporal changes in β diversity remain poorly studied despite their potential power for illuminating the drivers of past and present richness patterns and importance in modern conservation [16–18]. This study therefore tests the hypothesis that climatic influences on

mammalian β diversity apply equally to temporal patterns, i.e. that the underlying ecological processes are “ergodic” (dynamic processes that are the same in both time and space).

The mid to late Cenozoic (36 Ma to present) has been a time of dramatic mammalian diversity change, shaped in part by the transition from the productive ice-free ecosystems of the early to mid Cenozoic to the more temperate glaciated ecosystems of the late Cenozoic. Under these changing climatic conditions, mammalian communities show dramatic reductions in richness, changes in community composition, and morphology [10,19–24]. The most dramatic changes occurred at high latitudes, where ecosystems transitioned from *Metasequoia* forests during the early to mid Cenozoic [25,26] to boreal-type forests during the later Cenozoic and to modern tundra [27]. Associated with Cenozoic climate change, were changes in latitudinal climate gradients; overall, the intensity of latitudinal climate gradients increased toward the present, reflecting disproportionate polar cooling due to the formation of permanent Arctic glaciation [28,29]. We therefore predict that latitudinal diversity gradients increased in strength under cooler, less productive environmental conditions just as modern LRGs are steeper in temperate than in tropical regions. Further, we predict that β diversity declined under cooler, less productive environmental conditions just as modern β diversity declines toward the poles [2,7].

Quaternary (2.6 Ma to present) climates have been cool relative to the majority of the late Cenozoic. Recently, however, high latitudes have experienced disproportionate increases in annual temperature (up to 2°C to date), increases in plant primary productivity, and loss of large areas of perennial ice under anthropogenic global warming [30]. Flora and fauna have responded through shifts in phenology [31], *in situ* evolution [32], and, in some cases, extinction [33]. However, perhaps the most often recorded response is the climatically-correlated pattern of extirpations and colonization that manifest as shifts in the location of a species’ geographic range. Distributional studies over ecological timescales (<100 yrs) have recorded dramatic poleward range shifts and expansions for a wide range of terrestrial taxa in response to northern warming [34,35]. Projections (i.e. Special Report on Emissions Scenarios) for the next 100 years predict levels of global warming similar to the middle Miocene (+6°C) – a time of reduced or absent perennial Arctic glaciation [36,37] – or warmer (+11°C for the most extreme case; Table S1). We therefore expect continued range expansion, extinction, evolution, and community level changes among North American animals and plants.

A common approach to predicting the long-term outcomes of climate change for terrestrial organisms is climate space modeling (CSM). CSMs use distributional information and climate data to project species ranges into the future, usually under the assumption of no evolution and without adjustment for dispersal differences among species [38–40]. Rapid evolutionary changes on very short timescales and high degrees of variation in dispersal ability under climate change have been observed across a wide range of organisms [34,39,41], therefore CSMs are unlikely to generate accurate forecasts of climate change response. The fossil record, which encompasses many disparate environments and climates, might serve as record of a natural experiment by which ecological hypotheses can be tested in the temporal dimension. Fossil collections are a rich historical record of response to various climatic events that can be incorporated into predictive models, and mammals, in particular, are an excellent group for testing the generality of ecological hypotheses because they have an extensive Cenozoic fossil record. However, studies of extinct organisms have focused largely on richness [12,22,23,42,43] or morphology [44],

with limited focus on community composition [20,22]. Because changes in biological communities are not always associated with changes in richness, spatiotemporal patterns of community composition may be better indicators of climate change response [13,18].

We propose that integrating the study of fossil, modern, and projected spatiotemporal patterns of community composition i) allows for the testing of ecological principles in the temporal dimension, ii) provides the most complete picture of diversity responses to climate change, and iii) enables evaluation of the performance of commonly employed CSMs. Our approach of combining the study of fossil, modern, and projected diversity patterns provides novel insights into the ecological and evolutionary processes that drive continental patterns of biodiversity in space and time.

Methods

Data collection and preparation

We downloaded occurrences for modern North American mammals from NatureServe Canada. The extant mammal dataset included 744 species after the exclusion of a small number of unreadable or corrupted files [45]. We restricted our study of fossil mammals to the late Eocene through Pleistocene, thus avoiding the confounding effects of the early Paleogene mammal radiation. We partitioned the fossil mammal occurrence data by North American Land Mammal Age (NALMA) subdivisions because they delineate relatively temporally stable community assemblages and allowed us to obtain a nearly continuous sequence of mammal community change without large intervening gaps. Using NALMA subdivisions leads to time averaging of mammal communities and to differences in sampling (i.e. intensity, geographic coverage etc.) among time periods. However, we use a statistical approach to reduce these biases, described below. We based the dates for all NALMA subdivisions on Woodburne (2004). Further, we combined data for the entire Clarendonian and excluded for the Whitneyan, late Late Hemphillian, and early Chadronian due to poor sampling (Table 1).

We downloaded fossil mammal occurrence data for the Eocene, Oligocene, Pliocene, and Pleistocene from the the Paleobiology Database using the Fossilworks Gateway (fossilworks.org) in July and August, 2012, using the group name ‘mammalia’ and the following parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial (primary contributor: John Alroy; literature sources summarized in Appendix S1). We downloaded Miocene mammal occurrence data from the Miocene Mammal Mapping Project in March 2011 [46] using the NALMA subdivision as our search criterion. For all analyses, with the exception of the Miocene, we used paleolatitudes and paleolongitudes. We chose to use MIOMAP for the Miocene data because it is the most complete Miocene dataset. However, MIOMAP does not provide paleo-coordinates. Fortunately, there are only small differences between modern and Miocene latitudes for the downloaded localities. We removed all taxa with equivocal species identifications (e.g. *Equus* sp.) unless they were the only occurrence for a genus. We assumed all occurrences of open nomenclature (e.g. *Equus cf. simplicidens*) were correct identifications.

We did not use latitudinal grids for fossil or extant mammals as in previous studies of latitudinal richness gradients [1,47] because our study is focused on community composition. We therefore do not need to clump localities by spatial proximity to employ rarefaction methods. In addition, the uneven spatial distribution of fossil localities makes the use of a grid method impractical. Instead,

Table 1. Summary of sampled North American Land Mammal Age (NALMA) subdivisions.

Epoch	NALMA subdivision	Age Range (Ma)	Midpoint Age (M)	Number of species	Number of fossil localities	Area (km ²)
Pleistocene	Rancholabrean	0.25–0.011	0.1305	222	180	176615.9
Pliocene	Irvingtonian II	0.85–0.25	0.55	189	94	144745.5
Pliocene	Irvingtonian I	1.72–0.85	1.285	102	37	60361.4
Pliocene	Blancan V	2.5–1.72	2.11	165	130	125042.6
Pliocene	Blancan III	4.1–2.5	3.3	183	163	122839.5
Pliocene	Blancan I	4.9–4.1	4.5	85	66	140433.4
Miocene	Early late Hemphillian	6.7–5.9	6.3	68	46	20108.2
Miocene	Late early Hemphillian	7.5–6.7	7.1	63	55	29446.7
Miocene	Early early Hemphillian	9–7.5	8.25	65	47	31455.8
Miocene	Clarendonian	12.5–9	10.75	104	90	36139.8
Miocene	Late Barstovian	14.8–12.5	13.6	195	194	33789.1
Miocene	Early Barstovian	15.9–14.8	15.5	150	168	51753.3
Miocene	Late Hemingfordian	17.5–15.9	16.7	100	83	25478.4
Miocene	Early Hemingfordian	18.8–17.5	18.15	107	105	45531.3
Miocene	Late late Arikareean	19.5–18.8	19.15	108	123	38307.2
Oligocene/Miocene	Early late Arikareean	23.8–19.5	21.65	71	67	37892.2
Oligocene	Late early Arikareean	27.9–23.8	25.85	95	65	20927.8
Oligocene	Early early Arikareean	30–27.9	28.95	116	124	15382.3
Oligocene	Late Orellan	33.1–32	32.55	38	36	17725.7
Oligocene	Early Orellan	33.7–33.1	33.4	88	130	5579.8
Eocene	Middle Chadronian	35.7–34.7	35.3	88	37	10349.7

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we created taxon-by-locality occurrence matrices for extant and fossil mammals at the species taxonomic level excluding *Homo sapiens* [20,22]. In all cases, taxa and localities with fewer than two occurrences were removed from the dataset. Final numbers of localities and species are summarized in Table 1.

To make direct comparisons with modern mammals, we created occurrence matrices for extant mammals by pseudo fossil localities, which were generated using an iterative procedure in R with the maptools, sp, gpclib, ggplot2, rgeos, and MASS packages [48–54] (contact corresponding author for R code). To generate pseudo fossil localities and to ensure that we created pseudo fossil localities with the same spatial distributions as the fossil localities, we fit frequency distributions (normal, gamma, or β) to fossil localities for each NALMA subdivision (Fig. S1). We then generated point samples based on the frequency distributions and the number of fossil localities from which we created occurrence matrices (taxon-by-pseudo locality), repeating the procedure 100 times for each NALMA sub-age for a total of 2100 occurrence matrices. Fossil localities do not record the entire community and so show reduced richness compared to the actual communities (however, note that time averaging also increases richness at fossil localities). Further, most fossil localities, unless intensively screen washed, are biased against small species. Therefore, we also intentionally tested for the effects of sampling bias by removing 25%, 50%, and 75% of species from the extant mammal occurrence matrices for a total of 6300 occurrence matrices. Further, we tested for the effects of body mass bias by 25%, 50%, and 75% of species smaller than 5 kg for a total of 6300 occurrence matrices.

Climate space models

To create climate space models, we sampled the ranges of extant North and South American mammals at a series of 5066 points corresponding to a 1° grid (which we only used to project mammal occurrences under climate change models, but not to calculate biodiversity). Due to the focus on North America, we omitted any species with southern hemisphere ranges that did not cross the equator ($n = 602$; Table S2). We also excluded rare species (present in <20 cells) for which accurate species distribution models could not be generated ($n = 361$), leaving 706 species for the climate change projections. We extracted mean annual and winter (December, January, February) temperature and mean annual precipitation data from Climate Wizard (www.climatewizard.org) for the period of 1951–2006 and the following SRES scenarios and time periods: B1 2050s, A1b 2050s, A1b 2080s, A2 2050s, and A2 2080s [55] (Table S1). Each of these projections is based on an ensemble of 16 global circulation models [56]. However, to ensure that we sampled a range of potential warming, we also extracted the ensemble lowest B1 2050s projection (hereafter “B1 2050s low”) and the ensemble highest A2 2080s projection (hereafter “A2 2080s high”). This gave a range of warming in North America from 1.49°C (B1 2050s low) to 6.78°C (A2 2080s high, see Table S1 for the full range).

We modeled species' ranges with the BIOMOD package in R using generalized linear models, generalized boosted models, classification tree analysis, artificial neural networks, surface range envelopes, flexible discriminant analysis, multiple adaptive regression splines, and random forests [57] (contact corresponding author for R code). We then used these models to make consensus forecasts for each of the projections described above, as well as current climate to evaluate the performance of the models. We

tested model performance using area under the receiver operating curve (AUC), true skill statistic (TSS), and proportion correct classification (PCC, Fig. S2). Species and generic presences were determined across the 1° latitude-longitude grid to give presence or absence in each location at each time and SRES scenario.

Using the projections described above, we created pseudo localities, as before. From this, we created occurrence matrices as described above. We repeated this process 100 times for each projection for a total of 16,800 occurrence matrices.

Latitudinal turnover gradients (LTGs) and β diversity

We calculated β diversity as the change in mammalian communities across the North American landscape using multivariate dispersion and the Jaccard index for each NALMA sub-area, for modern mammals, and for the climate projections [58]. We calculated Euclidean distances from the centroid for localities using the R package vegan [59]. Larger distances from the centroid indicate greater spatial community turnover and thus higher β diversity. We did not regress the Jaccard index values against distance, as has been used for modern species [2] because we have found such an approach to be highly influenced by species-area relationships.

To estimate ancient, modern, and projected LTG strength for North American mammals, we calculated the amount of community change with latitude using detrended correspondence analysis (DCA; an ordination technique) in the vegan R package [59]. We used explained variance (R^2 ; how much of the variation in community change is explained by latitude) as a measure of LTG strength [13]. High values of explained variance indicate strong LTGs [60]. We did not compute latitudinal richness gradients because sampling bias (e.g. loss of taxa, body mass bias) is too great (Fraser, D. unpub.).

Sampling bias control

Although we have chosen methods that minimize the effects of sampling bias, we still used multiple methods to control for the non-independence of β diversity from the number of localities, the geographic area sampled, and the number of sampled taxa. We used three approaches. Firstly, we used a re-sampling approach wherein we sub-sampled (without replacement) each NALMA 100× using a standardized number of localities (thirty) and limited to localities occurring between 30° and 50° North latitude. We also re-sampled the extant mammal ranges under various conditions of bias (taxonomic bias through the removal of 25%, 50%, 75% of taxa and body mass bias where we removed 25%, 50%, and 75% of species with a body mass lower than 5 kg) as above to test for direct causality of sampling bias. We also used a method of detrending whereby we regressed LTG strength and β diversity against statistically significant sampling bias metrics and further analyzed the residuals from the model. Finally, we used multivariate linear models to simultaneously account for the model variance explained by sampling and biological phenomena. The last multivariate method is similar to [61] and [62] (also addressed in [63]) who combine the predictive properties of models of biodiversity change and taphonomic bias.

Correlation with climate

We tested for correlations of β diversity and LTG strength with stable oxygen isotopes from benthic foraminifera ($\delta^{18}\text{O}$ %) [64,65], mean annual precipitation estimated from paleosols [66], number of localities, sampling area (km^2), number of species, latitudinal range (degrees), and length of the sampled interval (Ma) of the fossil localities using generalized least squares and using an autocorrelation structure of order one (corAR1) to account for

temporal autocorrelation in R [67,68]. Best fit models were selected using automated model selection in the MuMIn R package [69] and the Akaike Information Criterion (ΔAIC).

Results

Fossil mammal β diversity showed considerable variation with the warmest intervals (late Eocene, mid-late Oligocene, mid Miocene, and mid Pliocene), but showing generally higher β diversity than with cooler intervals (early Oligocene, late Miocene) (Fig. 1C). The best fit model includes mean annual precipitation (MAP squared), length of the NALMA subdivision, and number of taxa, which together accounts for 67% of model variance (Table 2). β diversity is statistically significant for all three predictors ($p < 0.05$). Residual β diversity is significantly explained by MAP only (Table 2; Fig. 2B). Re-sampling did not alleviate the effects of sampling bias; re-sampled β diversity is significantly explained by MAP-squared, number of taxa, and NALMA subdivision length (Table 2). The remainder of the manuscript will discuss the results from the analyses of raw and residual β diversity only.

Mammalian latitudinal turnover gradients (LTGs) are weak prior to the late Miocene (Fig. 1D). Raw LTG strength (i.e. not detrended) peaks during late Miocene (Hemphillian) and late Pleistocene (Rancholabrean) (Fig. 1D). The best fit model includes mean annual precipitation (MAP) [66], number of taxa, area (km^2) and an interaction of area and the number of taxa, which explains 47% of the model variance (Table 2; Fig. 2C). LTG strength of late Cenozoic mammal species is statistically significantly explained by all four metrics ($p < 0.001$; Table 2). Residual LTG strength is significantly explained only by MAP ($p < 0.05$; Table 2; Fig. 2D). As above, re-sampling did not alleviate the effects of sampling bias on LTG strength (Table 2). In other words, even accounting for variables that describe potential sources of bias, a climatic variable (MAP) still explains a significant proportion of the variance.

β diversity is much lower for extant mammals than for extinct mammals (Fig. 3A). LTG strength for extant mammals is also greater than for early to mid Cenozoic fossil mammals, but similar to the values for the late Miocene and Pleistocene (Fig. 3B). Extant mammal β diversity shows a slight decrease under incomplete sampling and a slight increase under body-mass-bias sampling (Fig. 3A), but the change is much smaller than observed for fossil mammals. LTG strength does not appear to be significantly affected by the sample size reduction.

Our forecast models (which showed a strong fit to modern mammalian distributions, see Fig. S2A–C) show a slight increase in β diversity for extant mammals (Fig. 3C), but no substantial change in LTG strength compared to the present (Fig. 3D).

Discussion

Spatiotemporal patterns of β diversity remain poorly studied despite being potentially very useful in conservation biology [17,18,70] and linkage to well-studied biogeographic phenomena such as latitudinal richness gradients [4]. Using an extensive analysis of past and present mammalian communities, we demonstrate that, over the past 36 Ma, spatiotemporal patterns of mammal community composition have varied by orders of magnitude in North America. Specifically, Cenozoic spatial turnover of mammal communities is explained by continental mean annual precipitation (MAP) (Fig. 2A–B), broadly supporting predictions drawn from published studies of modern terrestrial organisms [2,70,71] and our predictions outlined above.

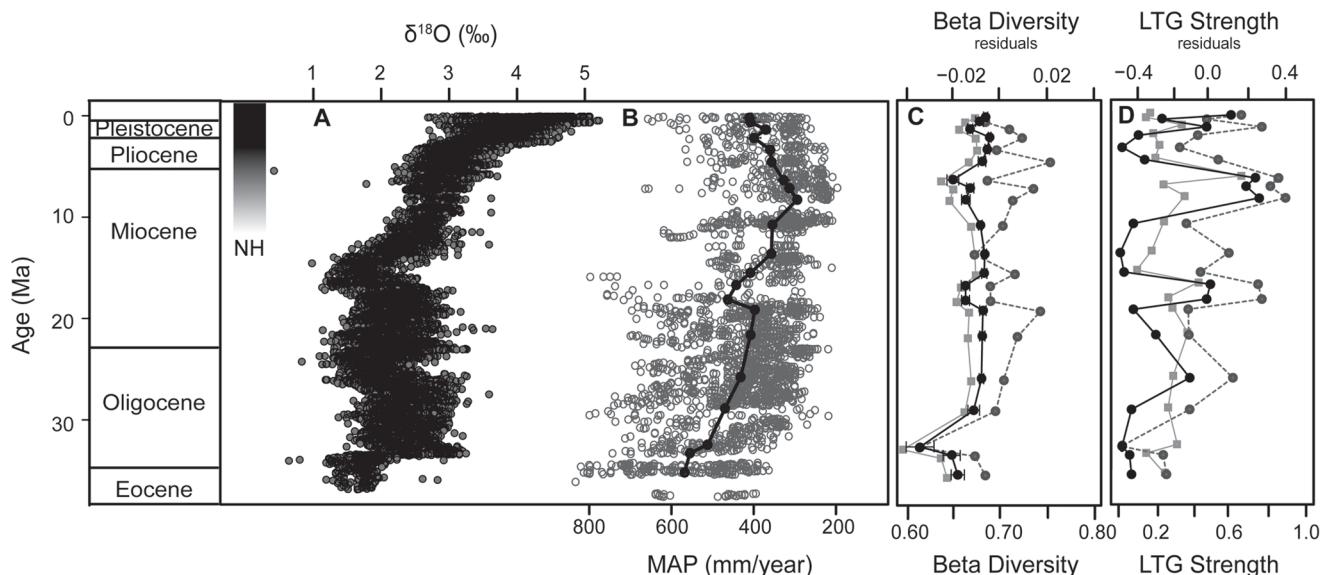


Figure 1. Mid to late Cenozoic trends of (A) $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Zachos et al. 2008), (B) mean annual precipitation estimated from paleosols (Retallack, 2007), (C) β diversity of North American mammal species measured using multivariate dispersion (average distance from the centroid), and (D) strength of latitudinal turnover gradients (LTGs) measured as gradient strength for North American fossil mammals. Black lines are raw values, gray lines are residuals from significant sampling bias predictors, and gray dashed lines are re-sampled. Standard errors for re-sampled data are too small to display.

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Contemporary ecological theory predicts that mammal diversity either declines monotonically with productivity or shows a unimodal pattern, declining with both low and high productivity [1,2,70,72]. Further, stronger latitudinal diversity gradients are associated with cooler, less productive environments [71] and steeper latitudinal climate gradients [1,70]. Both sets of predictions assume that changes in climate, productivity, and seasonality influence rates of origination and extinction [72,73], niche breadths [74], as well as the carrying capacity of the ecosystem

[75], all factors that change the spatial turnover of terrestrial faunas [70]. Specifically, terrestrial organisms in low latitude, high productivity environments show low rates of speciation and extinction [73], high β diversity [2,76], and weak or absent latitudinal diversity gradients [71]. In contrast, high latitude organisms show high rates of speciation and extinction [73], low β diversity [2,76], and strong latitudinal diversity gradients [71]. Evolutionary history also plays a role in determining rates of spatial community turnover. Modern tropical organisms show

Table 2. Results of best fit generalized least squares models relating β diversity and latitudinal turnover gradient (LTG) strength to mean annual precipitation from paleosols (Retallack, 2007), $\delta^{18}\text{O}$ (‰) from benthic forams (mm/year; Zachos et al. 2001; 2008), length of North American Land Mammal Age subdivision, number of taxa sampled, sampling area (km^2), and number of fossil localities.

Dependent Variable	Parameters of Best Fit Model	Variance explained by model (%)	t value	p
Beta Diversity	Mean annual precipitation (quadratic)	66.51	-3.25	0.005
	Length of NALMA subdivision		2.43	0.027
	Number of taxa		5.30	<0.001
Beta Diversity Residuals	Mean annual precipitation (quadratic)	26.48	-3.50	0.002
Beta Diversity Re-sampled	Mean annual precipitation (quadratic)	66.04	-2.39	0.029
	Length of NALMA subdivision		2.51	0.023
	Number of taxa		5.47	<0.001
Latitudinal Turnover Gradient Strength (LTGs)	Mean annual precipitation (quadratic)	46.76	-5.65	<0.001
	Area		-4.62	<0.001
	Number of taxa		-4.36	<0.001
	Area : Number of taxa		4.85	<0.001
LTG Residuals	Mean annual precipitation (linear)	37.48	-3.79	0.001
LTG Re-sampled	Number of taxa	28.59	-2.55	0.020

doi:10.1371/journal.pone.0106499.t002

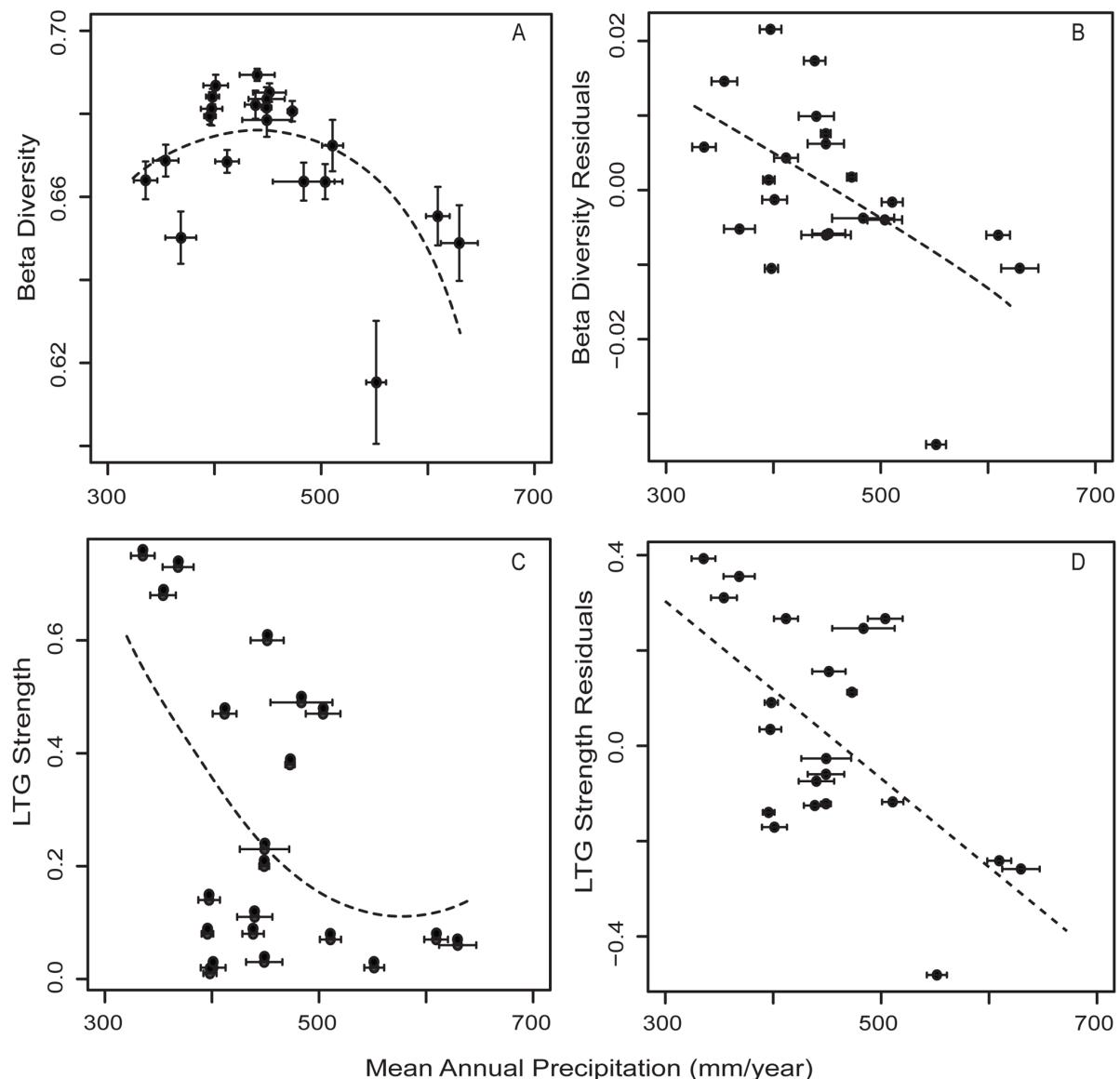


Figure 2. Relationship of mean annual precipitation estimated from paleosols (Retallack, 2007) with North American fossil mammal (A) raw β diversity ($R^2 = 0.43$), (B) residual beta diversity ($R^2 = 0.26$) and (C) raw latitudinal turnover gradient (LTG) strength ($R^2 = 0.25$), and (D) residual LTG strength ($R^2 = 0.37$).

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faster turnover than their temperate counterparts regardless of the rate of environmental change [70]. Spatial and, by extension, temporal patterns of β diversity are the result of a mosaic of ecological and evolutionary processes.

Cenozoic fossil mammal β diversity peaked at intermediate values of mean annual precipitation and declined under both drier and wetter conditions (MAP; ~450 mm per year; Fig. 2B), showing a similar shape to latitudinal diversity curves for modern mammals [71]. Mammal β diversity was similarly lowest during periods of relative cooling, including the early Oligocene and late Miocene, coincident with declining atmospheric CO₂ [77–80] and, in the latter case, the expansion of ice sheets in the Northern Hemisphere [27,36], strengthening of thermohaline circulation [27,37,81–84], and transition from C₃ to C₄ dominated ecosystems at middle latitudes [66,85,86]. Declining β diversity during the late Miocene is also coincident with increased maximum body

mass [87], an ecologically relevant characteristic linked to lower ecosystem energy [88,89]. Water is a key component in photosynthesis and therefore net primary productivity (NPP) and MAP are correlated at a global scale, showing an asymptotic relationship [90]. Our results therefore suggest that putatively lower energy ecosystems (e.g. early Oligocene, late Miocene) supported more spatially homogenous mammal faunas than putatively higher energy ecosystems (e.g. late Eocene, mid Miocene, mid Pliocene). Temporal changes in fossil mammal β diversity (this study) are therefore conceptually similar to spatial patterns observed in extant mammals.

Early Oligocene mammals had lower β diversity than expected based on MAP (Fig. 1C; Fig. 2A). The early Oligocene is associated with rapid global cooling [64] and expansion of open grassy ecosystems [91], which may have resulted in lower ecosystem energy. However, our taxonomic sample is the poorest

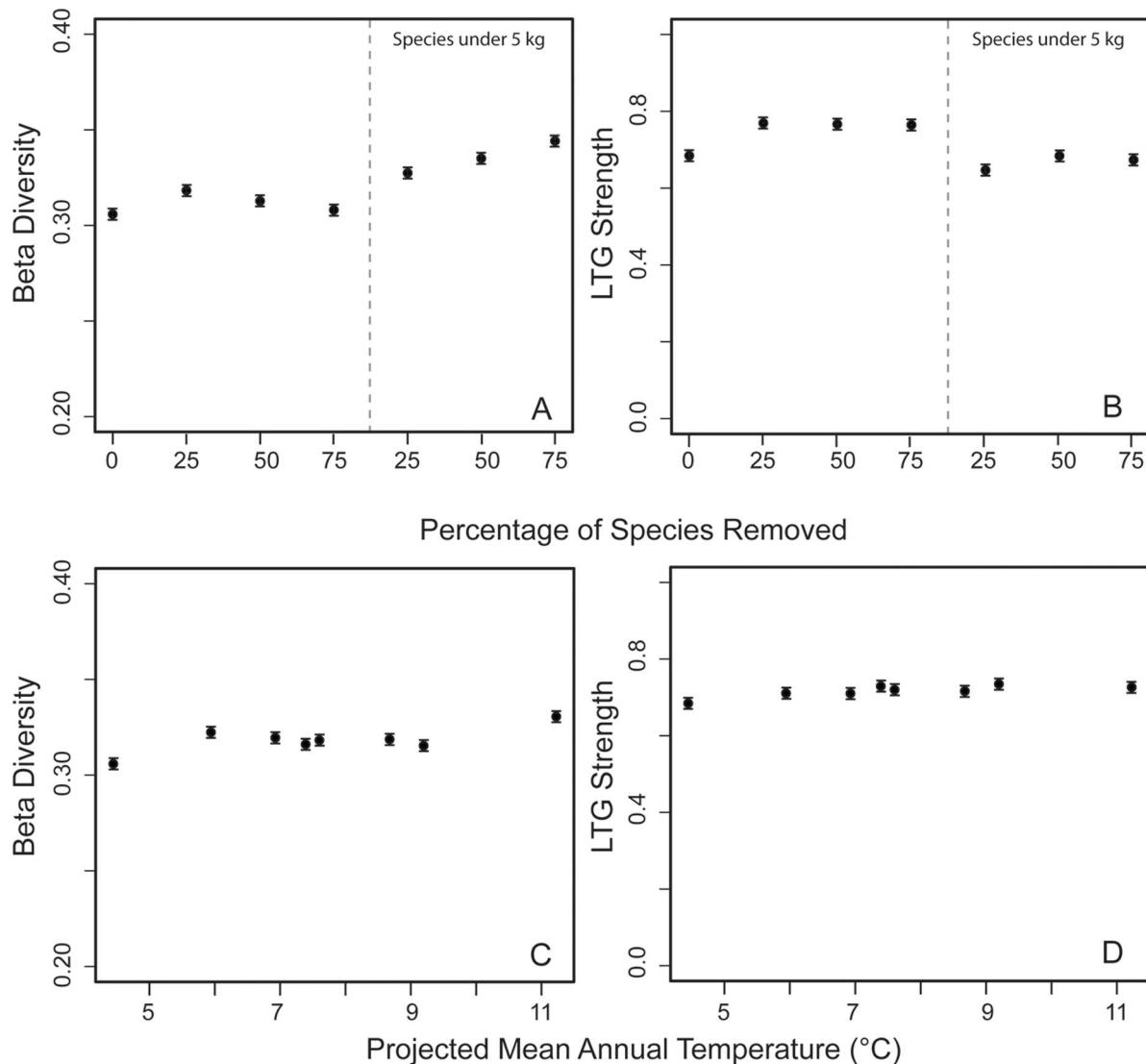


Figure 3. (A) β diversity (distance from centroid) and (B) latitudinal turnover gradients (LTG) strength of extant North American mammals under incomplete taxonomic sampling (removal of 25, 50, and 75% of species in sample) and body mass bias (removal of 25, 50, 75% of species smaller than 5 kg) and (C) β diversity (distance from centroid) and (D) latitudinal turnover gradients (LTG) strength of extant North American mammals under several International Panel on Climate Change scenarios (Special Reports on Emissions Scenarios).

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for the early Oligocene; number of taxa is a significant predictor of fossil mammal β diversity (Table 2), suggesting some variation in preservation of species among NALMA subdivisions. Rarefied diversity also shows little change from the late Eocene to the early Oligocene [10]. However, our incomplete sampling trials show that removing even 75% of species reduces β diversity by a negligible amount (Fig. 3A), suggesting that at least some (but not all) of the observed decline in early Oligocene β diversity may have been climatically driven.

The magnitude of the latitudinal turnover gradient (LTG) for fossil mammals shows a temporally cyclic pattern that increases in amplitude during the late Cenozoic as well as a general trend toward stronger LTGs (Fig. 1D), coincident with the formation of ice on Svalbard at ~15 Ma and perennial Arctic sea ice at ~14 Ma, declining atmospheric CO₂ [37], and declining terrestrial MAP (Fig. 2B). Specifically, LTGs are strongest when precipitation is lowest (putatively lower productivity environments)

and weakest at when precipitation is highest (putatively high productivity environments; Fig. 2B), similar to modern mammals that show weak or absent latitudinal diversity gradients in the tropics and strong diversity gradients at mid to high latitudes [71]. Climate gradients are steeper at mid to high latitudes in North America due to the albedo of high latitude glaciation. Northern glaciation is an important means by which solar radiation is reflected from high latitudes, resulting in cool, low productivity Arctic environments [92,93]. Mammal communities are sorted along a latitudinal axis according to their climatic tolerances and the process of abiotic filtering, whereby taxa meet the limits of their environmental tolerances and are excluded from communities farther north [94]. Although late Miocene sea and land ice thickness and extent were reduced compared to the modern, increasing northern albedo and strengthening of thermohaline circulation are coincident with that strengthening of mammal

LTGs during the late Miocene (25–60% stronger than for any preceding NALMA; Fig. 1D) [27,81–84].

At first glance, the Pliocene appears to be anomalous because the magnitude of the mammalian LTG declines dramatically (60–70% reduction in the magnitude of the LTG; Fig. 1D). However, evidence from fossil deposits on Ellesmere Island show that approximately 3.5 Ma the Pliocene Arctic was ~14–22°C warmer than present [83,95,96] with an associated reduced volume of Arctic sea ice [27,82]. Pliocene Arctic warming is similarly coincident with reduced richness gradients of marine zooplankton [81]. The Pliocene might therefore be the “exception” that proves the rule.

Under modern global warming, Arctic winter temperatures have increased at a greater rate than at southern latitudes [97]. Long-term projections suggest boosts in high latitude net primary productivity due to increasing nitrogen fertilization and increases in mean annual precipitation of 100–150 mm per year or 5–20% at middle to high latitudes [98]. From our analyses of fossil North American mammals and published studies of beta diversity [18], we therefore expect weakened climate gradients and thus weakened LTGs due to northward range shifting, and, in the long-term, declining β diversity under the influence of modern anthropogenic climate change. β diversity decline may be facilitated by the homogenization of communities due to any of the following (note the lack of mutual exclusivity): i) extinction of species with small geographic ranges and replacement with wide-ranging species, ii) evolution toward larger range sizes within species, and, iii) invasion by wide-ranging species even without the extinction of residents [18]. However, our climate space models that are based on SRES scenarios corresponding to absolute mean annual temperatures of 4.4–11.2°C (averaged across North and South America) did not show changes in mammal LTGs or β diversity (Fig. 3C–D). We suggest that climate space models (CSMs) are unlikely to accurately forecast the outcomes of anthropogenic climate change for modern mammals because current CSM algorithms do not incorporate microevolutionary, macroevolutionary, or ecological processes, such as niche shifts, niche creation, and differences in dispersal abilities that are inherent in the response of animals to climate change. However, even on modern ecological timescales, rapid evolutionary changes and niche shifts have been observed in native and invasive populations [41], and this local adaptation complicates the prediction of range shifts. On longer timescales, taxa adapt to new climates and the processes of speciation and extinction help form new terrestrial communities. Without the explicit inclusion of evolutionary parameters and historical data for the taxa of interest, we are unlikely to accurately predict long-term changes in terrestrial biodiversity patterns.

We have shown here that macroecological patterns of North American mammal community composition varied considerably over the past 35 million years in response to changes in global climate change and Arctic glaciation (Fig. 1C–D). Furthermore, our comparison of fossil evidence with climate-space forecast models (CSMs) suggests that CSMs (in which species are modeled

to simply track climate variables) may distort the degree of community composition change we should expect in the future. A unifying ecological theory relating diversity to climate must address both the spatial and temporal dimensions of diversity, as well as both richness and community composition. However, studies of organismal richness are far more common than studies of community composition (β diversity), despite the importance of the latter in conservation and their vast potential for contributing to our understanding of the processes underlying modern biodiversity. Studying the community composition of fossil animals represents a new frontier in paleontological research with potential to truly inform modern conservation.

Supporting Information

Figure S1 Maps of North America showing the distribution of fossil localities for all sampled North American Land Mammal Age subdivisions.

(TIF)

Figure S2 Model fit statistics for climate space models of extant North American mammals. Model performance was tested using area under the operating curve (A; AUC), the true skill statistics (B; TSS), and the proportion of correct classification (C).

(TIF)

Table S1 Summary of Special Emissions Report Scenarios (SERs) to which we fit climate models for extant mammalian species.

(DOCX)

Table S2 List of mammalian taxa included and excluded from the species distribution models.

(DOCX)

Appendix S1 Sources for the majority of mammal occurrence data downloaded from the Fossilworks database.

(DOCX)

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Author Contributions

Conceived and designed the experiments: DF CH NR. Performed the experiments: DF. Analyzed the data: DF. Contributed reagents/materials/analysis tools: CH RG. Contributed to the writing of the manuscript: DF. Manuscript copyediting: CH RG NR.

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Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals

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Animal richness, community composition, and phylogenetic community structure (PCS) vary across the modern landscape. Animal communities vary from phylogenetically clustered (i.e. higher relatedness amongst co-occurring species than is expected by chance) to phylogenetically even (i.e. co-occurring taxa are more distantly related than expected by chance), which is explained by abiotic or climatic filtering and competitive exclusion, respectively. Under this model, the contribution of historical origination and extinction events to modern animal PCS remains relatively unknown. Because origination and extinction determine the make-up of the terrestrial community, the study of historical changes in animal PCS is tantamount to understanding formation of modern communities. In the present study, we test the effects of macroevolution and climate changes on 'hoofed mammals' (i.e. perissodactyl and artiodactyl) PCS from the late Cenozoic of North America because they experience large, phylogenetically dispersed extinctions of browsing species and phylogenetically dispersed originations of grazing species associated with the evolution of grassland ecosystems during the late Miocene. We show that the loss of numerically dominant nonhypodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale that is well explained by global climate changes. Phylogenetic evenness and a reduced richness during the late Cenozoic may have facilitated reduced niche overlap among co-occurring hoofed mammal species as global climates cooled. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 114, 485–494.

ADDITIONAL KEYWORDS: Artiodactyla – composition – extinction – net relatedness index – origination – Perissodactyla.

INTRODUCTION

The richness and composition of modern animal communities changes vastly across space, a phenomenon that is attributed to geographical variation in climate and topography (Rosenzweig, 1995). Spatial diversity patterns are also associated with changes in phylogenetic composition of communities; animal

communities vary across the landscape with respect to the degree of relatedness among species (Buckley & Jetz, 2008; Qian *et al.*, 2013). Studying the phylogenetic structure of modern communities is revealing the proximate factors that structure geographical diversity patterns (Hardy & Senterre, 2007; Kraft *et al.*, 2007; Emerson & Gillespie, 2008; Vamosi *et al.*, 2009; Swenson *et al.*, 2012). Most studies of modern phylogenetic community structure (PCS) invoke contemporary drivers such as abiotic or climatic filtering and competition (Vamosi *et al.*, 2009) to the exclusion

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of historical macroevolutionary events. However, understanding the contribution of macroevolution and historical factors to community assembly is required to test hypotheses about the formation of modern communities. Studying trends in PCS through time using the fossil record might reveal the effects of macroevolutionary processes on PCS, as well as the role of long-term climate changes in the formation of modern communities.

Modern species assemblages comprise populations of species drawn from the regional source pool (i.e. from the entire complement of species in a region). The identity and relatedness of species in a local assemblage are determined by a variety of factors, including but not limited to abiotic filtering, dispersal, and competition (Webb *et al.*, 2002; Kraft *et al.*, 2007; Emerson & Gillespie, 2008). Abiotic filtering is a process where species with different environmental tolerances are filtered out of terrestrial communities along environmental gradients (Swenson *et al.*, 2012). Assuming niche conservatism (closely-related species share similar niches), low rates of dispersal and abiotic filtering are associated with high phylogenetic relatedness among species or phylogenetic clustering. Conversely, competitive exclusion and high rates of dispersal can lead to phylogenetic evenness or species being less phylogenetically related than expected by chance (Cavender-Bares *et al.*, 2004; Losos, 2008). Thus, local species assemblages occupy a point on a spectrum between phylogenetically clustered and even. Note that myriad conditions such as low rates of phylogenetic niche conservatism and trait convergence can result in communities that show every condition from phylogenetic evenness to phylogenetic clustering (Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007). However, the theoretical framework outlined above generally excludes the fossil record and thus excludes the contribution of historical factors such as extinction events.

Over long time scales of thousands to millions of years, origination and extinction are two of the dominant processes driving changes in organismal diversity (Benton & Pearson, 2001; Blois & Hadly, 2009; Dobrovolski *et al.*, 2012; Mayhew *et al.*, 2012; Price *et al.*, 2012). The composition of regional species pools and local assemblages through time are likely dependent upon numerous factors, including history of clades (e.g. species composition in preceding time intervals), patterns of origination and extinction across the phylogenetic tree (e.g. whether they are phylogenetically clumped or dispersed), climate, and tectonic changes. Whether extinction and origination are phylogenetically clumped or dispersed will largely depend on the distribution of ecologically relevant traits across the phylogenetic tree (i.e. whether those traits are conserved or convergent)

(Green *et al.*, 2011). Thus, both phylogenetically clumped and dispersed patterns of extinction and origination can result from abiotic filtering (Janis, Damuth & Theodor, 2000, 2004; Barnosky, 2005; Green *et al.*, 2011; Figueirido *et al.*, 2012). However, phylogenetically dispersed extinction should result in a trend of increasing phylogenetic evenness through time as the mean phylogenetic distance among surviving taxa increases. Conversely, if extinction is phylogenetically clumped, there should be a trend of increasing phylogenetic clustering through time as the mean phylogenetic distance between surviving taxa decreases. The effects of origination on PCS are more complex because they change throughout the history of a clade. For example, under an adaptive radiation model, early in the evolutionary history of a clade, the appearance of new species should result in increasing phylogenetic evenness as new branches are added to the phylogenetic tree. Later in the history of a clade, the origination of new species within well-established genera (i.e. adding new 'leaves' to the tree) should result in increasing phylogenetic clustering. Through time, local assemblages might mirror the changes in the regional species pool (i.e. follow the same trajectory) or show a different temporal trajectory related to more proximate drivers such as spatial abiotic filtering, dispersal, and competition. A comparison of PCS at regional and local scales might therefore reveal the extent to which local assemblages are influenced by macroevolutionary processes and changes in the regional species pool through time.

Over geological time, the diversity and composition of animal communities has changed dramatically, especially during the transition from the warm equitable climates of the early and mid Cenozoic to the cool temperate climates of the late Cenozoic (Alroy, Koch & Zachos, 2000; Janis *et al.*, 2000, 2004; Mayhew, Jenkins & Benton, 2008; Mayhew *et al.*, 2012; Fraser *et al.*, 2014). Therefore, the phylogenetic structure of regional species pools and local species assemblages has likely also been temporally variable. Evolution of late Cenozoic (Miocene to Pleistocene) North American ungulates is marked by a decline in richness, particularly of browsers (feeding on parts of woody plants, not herbaceous plants), associated with the expansion of open grassland habitats (Janis *et al.*, 2000, 2004; Fox & Koch, 2004; Fraser & Theodor, 2013). Furthermore, ecologically relevant traits such as tooth crown height and body size show significant changes among North American hoofed mammals as the ecosystems shifted away from woodland savannahs and primary productivity consequently declined (Janis *et al.*, 2000; Janis *et al.*, 2004; Smith *et al.*, 2010; Raia *et al.*, 2011; Cantalapiedra *et al.*, 2013). In the present study, we tested for effects of

late Cenozoic (15–0.01 Mya) extinction and global climate changes on North American ‘ungulate’ PCS at the regional and local-scales.

MATERIAL AND METHODS

We downloaded fossil occurrence data for the Miocene, Pliocene, and Pleistocene, which we partitioned by subdivisions of the North American Land Mammal Ages (NALMAs; see Supporting information, Table S1) because they delineate relatively stable community assemblages. The dates for all NALMA subdivisions are based on Woodburne (2004). Fossil ungulate (Perissodactyla and Artiodactyla) occurrence data for the Pliocene, and Pleistocene were downloaded from the Paleobiology Database (<http://paleodb.org/>) in July and August 2012, using the group name ‘mammalia’ and the parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial. Miocene ungulate occurrence data were downloaded from the Miocene Mammal Mapping Project (Carrasco *et al.*, 2005) in March 2011 using the NALMA subdivision as our search criterion. We then created taxon-by-NALMA subdivision occurrence matrices for perissodactyls and artiodactyls separately at the species level (Davis, 2005; Atwater & Davis, 2011). We removed all taxa that had equivocal species identifications (e.g. *Equus* sp.) unless they were the only occurrence for a genus. We assumed all occurrences of open nomenclature (e.g. *Equus* cf. *simplicidens*) were correct identifications.

We created composite phylogenies for fossil artiodactyls and perissodactyls primarily *sensu* Janis, Scott & Jacobs (1998) and Maguire & Stigall (2009). The backbone of the artiodactyl phylogeny is based on Price, Bininda-Emonds & Gittleman (2005). For comparison, we created two composite phylogenies each for the artiodactyls and perissodactyls, one better resolved tree based on published hypotheses (see Supporting information, Fig. S1) and one poorly resolved tree (see Supporting information, Fig. S2) where we assumed nothing about inter- and intra-generic relationships. For both sets of composite trees, we used taxonomy as a guide (i.e. we assumed species from the same genus were sister taxa with notable exceptions such as *Merychippus*, which is a known polyphyletic genus). Although fossil phylogenies inevitably include many polytomies, they are not problematic (Finarelli, 2007; Raia *et al.*, 2010). As such, our composite phylogenies may contain as yet unknown polyphyletic genera but reflect the current state of knowledge. Furthermore, all equivocal interfamilial and intergeneric relationships were represented by polytomies, and species that we could not place phylogenetically were removed from the analysis. We

created a third set of composite phylogenies for the artiodactyls from which we excluded the Bovidae and Cervidae, which comprise Eurasian immigrants. We used first and last occurrences of perissodactyl and artiodactyl taxa from the taxonomic range tool on the Paleobiology database with NALMAs as our time model and default settings to create dated composite phylogenies using the paleotree R package (Bapst, 2012).

We calculated the net relatedness index (NRI), which is a standardized measure of mean pairwise phylogenetic distance among co-occurring species, using the picante R package (Webb, 2000; Webb *et al.*, 2002; Kembel *et al.*, 2014). Positive values of NRI indicate that species in an assemblage (i.e. species that co-occur within a specific NALMA) are more closely related than expected by chance. Negative values of NRI indicate that species in an assemblage are more distantly related than expected by chance. NRI values of zero indicate phylogenetic randomness (Webb, 2000; Webb *et al.*, 2002; Raia, 2010). We calculated the NRI for each NALMA subdivision considered in the present study (see Supporting information, Table S1) at both the regional and locality scales. At the regional scale, we used the entire phylogeny (i.e. the total diversity of North American perissodactyls and artiodactyls) as the source pool from which communities (i.e. assemblages of species present in each NALMA subdivision) were drawn (Raia, 2010). At the locality scale, we calculated the mean NRI for all localities within each NALMA subdivision (i.e. assemblages of species present at each locality in each NALMA subdivision). Critically, we used a time slicing approach when analyzing locality scale NRI using the paleotree R package (Bapst, 2012). The time slice approach involves shortening the branch lengths to the youngest boundary for each NALMA subdivision to preclude overestimation of phylogenetic distance and thus to exclude species with temporal ranges outside the selected time interval.

To evaluate the relationship between dietary traits and extinction, we used stochastic character mapping to visualize the distribution of tooth crown traits (hypodont, mesodont, submesodont, and brachydont) across the artiodactyl and perissodactyl composite phylogenies (Huelsenbeck, Neilsen & Bollback, 2003; Paradis, Claude & Strimmer, 2004; Bollback, 2006; Revell, 2011). We assigned tooth crown types to fossil taxa using published sources (Janis *et al.*, 2004; Mihlbachler *et al.*, 2011). Where tooth crown types were unknown, we assumed similarity within genera. However, taxa for which tooth crown type is equivocal were excluded.

We tested for significant temporal trends in artiodactyl and perissodactyl NRI by regressing NRI

against the midpoint age of each NALMA subdivision using generalized least squares (GLS) regression in R (Dornelas *et al.*, 2013; R Development Core Team, 2014). We also tested for a climatic filter by regressing NRI for both groups of hoofed mammals against stable oxygen isotopes from benthic foraminifera ($\delta^{18}\text{O} (\text{\textperthousand})$) (Zachos, Dickens & Zeebe, 2008), atmospheric carbon dioxide (CO_2 ; Zhang *et al.*, 2013), and mean annual precipitation estimated from paleosols (as inferred from degree of weathering and depth of carbonate nodules; Retallack, 2007) using the GLS approach. We also included several proxies for sampling bias in our GLS models, including the number of localities, number of species, and length of the sampled interval (Myr) of the fossil localities. The number of localities broadly correlates with amount of available rock record and sampling effort. Similarly, the number of species accounts for sampling effort but may also represent true changes in richness (Benton *et al.*, 2011). The length of NALMA subdivisions is a metric for the amount of time averaging in each sample; sample species richness should tend to increase with higher time averaging. Best fit models were selected using an information theoretic approach in the MUMIN R package (Bartoń, 2013), which is superior to the commonly employed stepwise regression approach (Whittingham *et al.*, 2006). Furthermore, the multivariate approach used in the present study allows for the combination of climate proxies and taphonomic biases into a single model, thereby partitioning their explanatory power (Mannion *et al.*, 2011; Benson & Mannion, 2012; Dornelas *et al.*, 2013). We did not use detrending

methods such as first differences or extraction of residuals because the GLS method simultaneously deals with both temporal autocorrelation and bias.

RESULTS

Both artiodactyls and perissodactyls show phylogenetically dispersed extinction and origination through time (see Supporting information, Fig. S1, S2). Both clades also show dietary trait convergence (see Supporting information, Fig. S3). Furthermore, our composite phylogenies reflect declining browser (black) and mixed feeder (green and blue) diversity through time, in agreement with Janis *et al.* (2000, 2004) (see Supporting information, Fig. S3).

At the regional scale, both artiodactyls and perissodactyls show significant increases in phylogenetic evenness or decreases in the NRI through time when using both poorly resolved and better resolved composite phylogenies (Fig. 1B, Table 1; see also Supporting information, Fig. S3). Artiodactyl NRI shows a significant correlation with $\delta^{18}\text{O} (\text{\textperthousand})$ from benthic foraminifera (Fig. 2A, B; Table 2). Perissodactyl NRI is best fit by models of NALMA length and $\delta^{18}\text{O} (\text{\textperthousand})$ from foraminifera (Fig. 2C, D; Table 2).

Locality-scale NRI also shows a significant increase in phylogenetic evenness through time for artiodactyls (Fig. 1C; Table 1) when using both composite phylogenies, but shows strong dependence on the number of taxa in the sample (Table 2). Perissodactyl locality-scale NRI varies between phylogenetically even and clumped (Fig. 1C). There

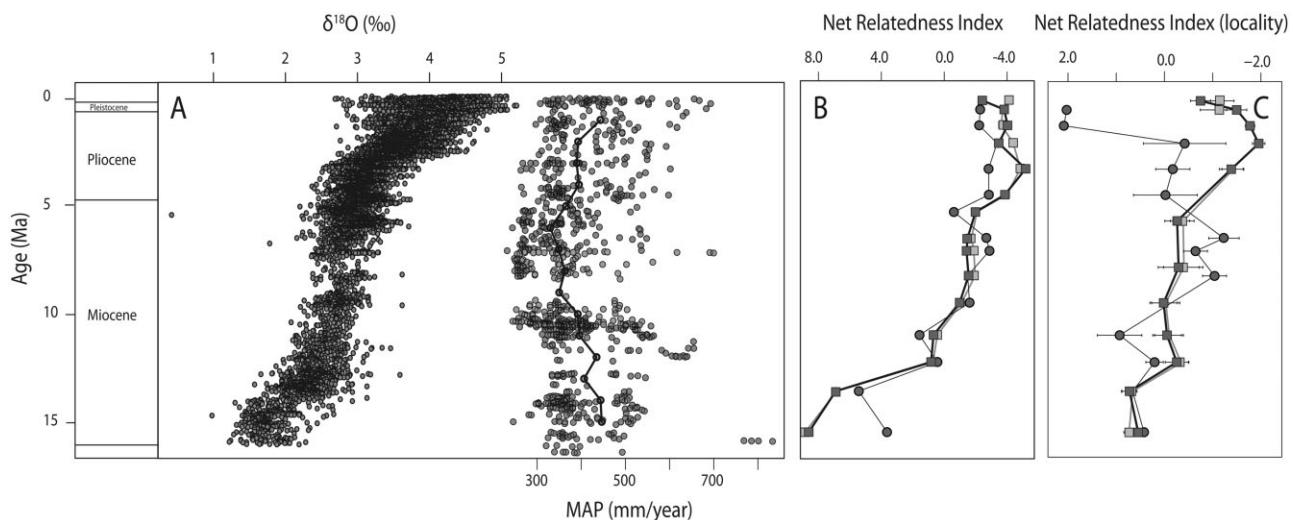


Figure 1. Relationships of artiodactyl (squares; black with immigrants and grey without immigrants) and perissodactyl (circles) phylogenetic community structure (PCS) (net relatedness index; NRI) with (A) $\delta^{18}\text{O} (\text{\textperthousand})$ from benthic foraminifera (Zachos *et al.*, 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the well resolved artiodactyl and perissodactyl phylogenies.

Table 1. Generalized least squares regression of phylogenetic community structure against North American Land Mammal Age subdivision midpoint age

Order	Dependent variable	<i>t</i> -value	<i>P</i> -value
Artiodactyla	NRI (resolved)	4.98	< 0.001
	NRI (unresolved)	2.63	0.020
	NRI without immigrants (resolved)	3.60	0.003
	NRI without immigrants (unresolved)	3.38	0.005
	NRI local scale (resolved)	3.29	0.008
	NRI local scale (unresolved)	3.23	0.009
	NRI local scale without immigrants (resolved)	5.50	< 0.001
	NRI local scale without immigrants (unresolved)	7.29	< 0.001
Perissodactyla	NRI (resolved)	4.06	0.001
	NRI (unresolved)	4.23	0.001
	NRI local scale (resolved)	-0.59	0.570
	NRI local scale (unresolved)	-0.35	0.730

NRI, net relatedness index.

were no significant regression coefficients for perissodactyl locality-scale NRI (Tables 1, 2).

At the regional and local scales, artiodactyls still show increasing phylogenetic evenness through time after the removal immigrant taxa; with and without immigrant taxa artiodactyl PCS show an almost identical trend (Fig. 1B; see also Supporting information, Fig. S4). We have not analyzed these data further as a result of model nonconvergence, although we are confident that our interpretations will remain unaffected.

DISCUSSION

Neontological studies of PCS often invoke the proximate processes of abiotic filtering and competition to explain phylogenetic clustering and evenness, respectively (Webb, 2000; Losos, 2008; Vamosi *et al.*, 2009). However, there has been limited focus on how historical events have influenced the PCS of modern communities, even though macroevolutionary events determine the number and identity of taxa in regional source pools from which local assemblages are drawn (McPeek, 2008). We therefore specifically test for the effects of North American ‘ungulate’ macroevolution on PCS because ungulate extinction rates are high after the warm mid Miocene climatic optimum (Janis *et al.*, 2000, 2004).

At the regional scale, assemblages of species emerge from the cumulative effects of origination, extinction, immigration, and emigration (McPeek, 2008). Thus, climatic filtering, insofar as climate influences patterns and rates of extinction and origination (Mayhew *et al.*, 2008), are more likely to explain long-term temporal changes in the regional pool than competition. We made two predictions about the PCS of

regional species pools based on the distribution of extinction events throughout the phylogenetic tree: (1) phylogenetically dispersed extinction and origination should result in a trend toward phylogenetic evenness and (2) phylogenetically clumped extinction and origination should lead to increased phylogenetic clustering through time. We also suggest that (3) local assemblages might follow the same trajectory as the regional species pool if they are drawn at random from the regional pool or, alternatively, that changes in local assemblages might diverge from the regional pattern as a result of other proximate mechanisms (e.g. abiotic filtering, dispersal, competition).

The evolution of late Cenozoic North American ungulates is typified by both a dramatic decline in richness and a dramatic loss of browsing species (i.e. woody plant specialists) within both the artiodactyl and perissodactyl clades (Janis *et al.*, 2000, 2004). Large, dominant clades of browsers were replaced by comparatively depauperate faunas comprised primarily of larger bodied grazers and mixed feeders (Janis *et al.*, 2004). One of the drivers of declining browser richness may have been the mid latitude transition from productive woodland savannah during the mid Miocene to grassland savannah from the latest Miocene through the Pliocene that was facilitated by climatic cooling and declining atmospheric CO₂ (Jacobs, Kingston & Jacobs, 1999; Janis *et al.*, 2000, 2004; McInerney, Strömberg & White, 2011; Strömberg & McInerney, 2011; Fox *et al.*, 2012; Fraser & Theodor, 2013; Zhang *et al.*, 2013). We showed that, contemporaneous with declining browser richness, regional ungulate PCS increased in phylogenetic evenness through time (Fig. 1B). At the regional scale, artiodactyls and perissodactyls show

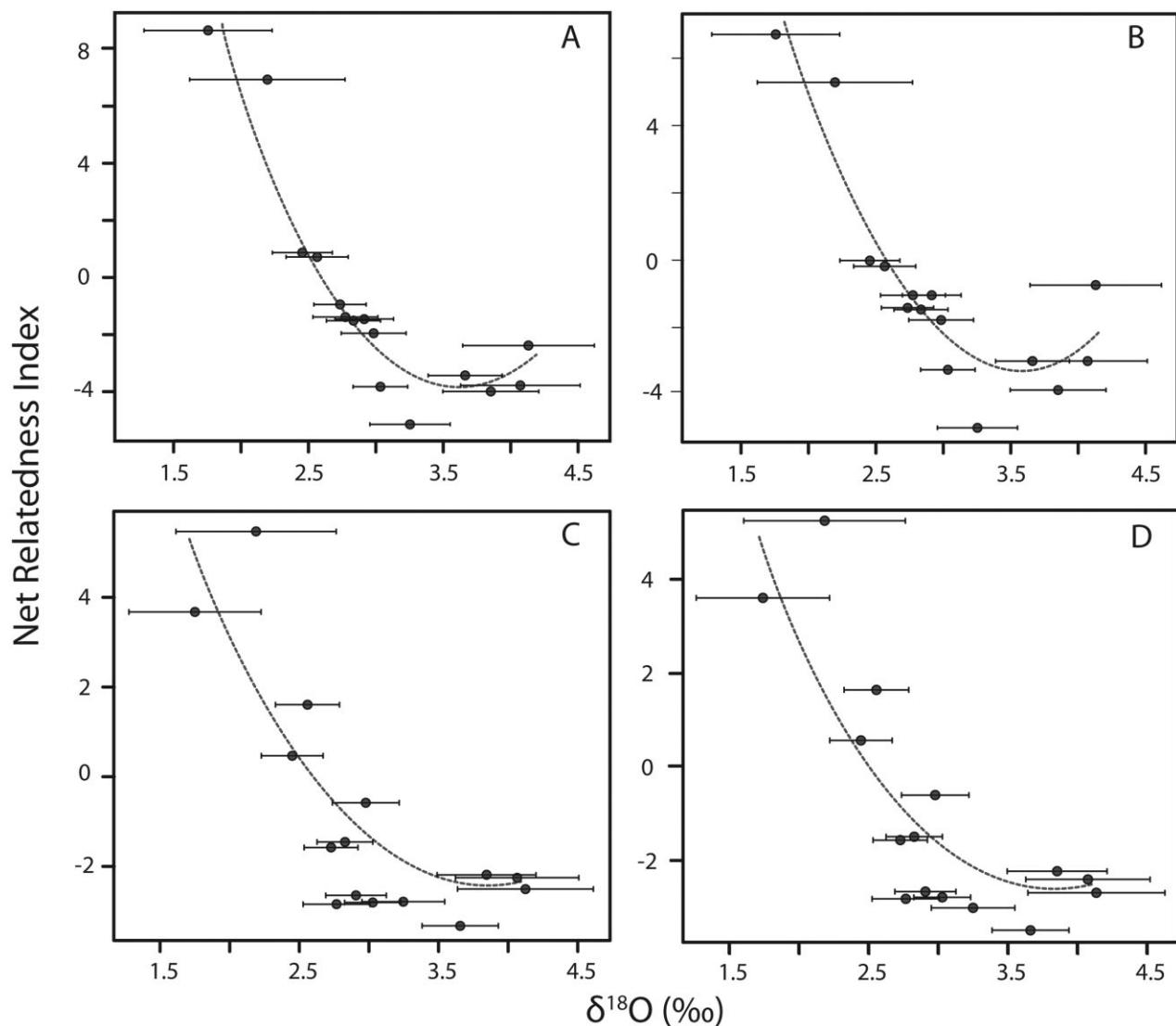


Figure 2. Relationship of $\delta^{18}\text{O}$ (‰) from benthic foraminifera with (A) artiodactyl regional phylogenetic community structure (PCS) (net relatedness index; NRI) calculated from the resolved, (B) unresolved composite phylogeny, (C) perissodactyl regional NRI calculated from the resolved, and (D) unresolved composite phylogeny.

significant decreases in the NRI when using the poorly resolved and better resolved phylogenies (Fig. 1B; Table 1). A declining ungulate NRI is explained by changes in global temperatures ($\delta^{18}\text{O}$ from benthic foraminifera) (Fig. 2; Table 2). However, perissodactyl NRI does show dependence on the length of the NALMA subdivision (Table 2), which might reflect a lack of precision in first and last occurrence dates used to timescale the composite phylogeny; some first and last occurrences correspond to NALMA boundaries in the absence of chemical dating.

Among North American ungulates, increased tooth crown height (i.e. hypsodonty) or a tendency toward open habitat living and consumption of herbaceous

plants has evolved multiple times (see Supporting information, Fig. S3) (i.e. feeding specialization is phylogenetically dispersed). We show that the loss of numerically dominant nonhypodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale. Strong correlation with global climate proxies ($\delta^{18}\text{O}$ from benthic foraminifera and mean annual precipitation; Fig. 2; Table 2) is likely indirectly driven by the effects of declining global temperatures and possibly declining atmospheric CO₂ on the evolution of grassland ecosystems (Zachos *et al.*, 2001, 2008; Zhang *et al.*, 2013), consistent with the

Table 2. Results of best fit generalized linear models relating phylogenetic community structure to mean annual precipitation (MAP) from paleosols (Retallack, 2007), $\delta^{18}\text{O}$ (‰) from benthic forams (mm year⁻¹; Zachos *et al.*, 2008), length of North American Land Mammal Age subdivision, number of taxa sampled, and number of fossil localities

Order	Dependent variable	Best fitted model	Pseudo r^2	Independent variable	t-value	P-value
Artiodactyla	NRI (resolved)	$\delta^{18}\text{O}$ (‰) (quadratic)	0.93	$(\delta^{18}\text{O})^2$	6.11	< 0.001
				$\delta^{18}\text{O}$	-7.43	< 0.001
	NRI (unresolved)	$\delta^{18}\text{O}$ (‰) (quadratic)	0.88	$(\delta^{18}\text{O})^2$	4.99	< 0.001
				$\delta^{18}\text{O}$	-6.02	< 0.001
	NRI local scale (resolved)	Number of taxa	0.43	-	3.33	0.008
	NRI local scale (unresolved)	Number of taxa	0.51	-	3.23	0.009
Perissodactyla	NRI (resolved)	$\delta^{18}\text{O}$ (‰) (quadratic), length of NALMA subdivision	0.88	$(\delta^{18}\text{O})^2$	3.57	0.002
				$\delta^{18}\text{O}$	-4.18	0.004
	NRI (unresolved)	$\delta^{18}\text{O}$ (‰) (quadratic), length of NALMA subdivision	0.87	Length of NALMA	4.53	0.001
				$(\delta^{18}\text{O})^2$	3.35	0.007
	NRI local scale (resolved)	Null	-	$\delta^{18}\text{O}$	-3.96	0.002
	NRI local scale (unresolved)	Null	-	Length of NALMA	4.20	0.002

NALMA, North American Land Mammal Age; NRI, net relatedness index.

proposition of Janis *et al.* (2000, 2004). Our analysis therefore adds a phylogenetic component to the findings of Janis *et al.* (2000, 2004), revealing that loss of diversity during the late Miocene resulted in phylogenetic evenness and probably reduced niche overlap, as had been suggested.

At the local scale, trends in artiodactyl and perissodactyl phylogenetic community structures are divergent (Fig. 1C). Artiodactyl PCS shows a similar, albeit dampened, increase in phylogenetic evenness, as is also the case at the regional scale (Fig. 1C; Table 1), suggesting that local assemblages are partly reflecting macroevolutionary dynamics rather than other proximate processes (e.g. competition and dispersal limitation) (Raia *et al.*, 2012), at least at this scale of analysis. However, local artiodactyl PCS is not well explained by global climate ($\delta^{18}\text{O}$ from benthic foraminifera) (Table 2) but rather by the number of taxa in the sample. Artiodactyl local-scale PCS might therefore reflect the combined effects of phylogenetically dispersed extinctions and originations, as well as sampling effort. Even with the possible influence of sampling bias, our result is significant because we show that the extinctions noted by Janis *et al.* (2000, 2004) resulted in larger phylogenetic distances amongst surviving species, lending circumstantial support to their model of reduced niche overlap among late Cenozoic ungulates.

Perissodactyl locality-scale PCS shows a contrasting pattern to the regional-scale, cycling between phylogenetic clustering and evenness throughout the late Cenozoic (Fig. 1C). There are two periods of large PCS changes among late Cenozoic perissodactyls: late Miocene and late Pliocene (Fig. 1C; see also Supporting information, Fig. S4C; circles). The late Miocene increase in phylogenetic evenness (i.e. decrease in NRI) is coincident with the loss of small-bodied, nongrazing species from within *Merychippus*, *Archaeohippus*, and *Hypohippus* (see Supporting information, Fig. S3B) associated with the opening of grassland ecosystems and loss of woodland savannah in North America (Janis *et al.*, 2000, 2004). The late Pliocene increase in phylogenetic clustering is coincident with a loss of most perissodactyl diversity in North America, with the exception of a few grazing equid genera including *Equus* and *Nannippus*, as well as *Tapirus* (see Supporting information, Fig. S3B). Changes in perissodactyl locality-scale PCS therefore appear to have resulted from stepped extinction and origination events that were coincident with the closure of the Panama seaway, with consequent changes in the distribution of oceanic heat, declining atmospheric CO₂, and the intensification of Northern Hemispheric glaciation (Zachos *et al.*, 2001, 2008; Ballantyne *et al.*, 2006, 2010; Csank *et al.*, 2011; Zhang *et al.*, 2013).

CONCLUSIONS

The role of macroevolution in shaping the phylogenetic structure of animal communities is poorly known. We show that North American perissodactyl and artiodactyl communities increased in phylogenetic evenness at the regional scale, coincident with large extinctions of woody dicot specialists or browsers and their replacement by depauperate faunas of grazers and mixed feeders following the mid Miocene climatic optimum. We suggest that the phylogenetic community structure of both clades reflects the loss of speciose nongrazing clades because of climatic filtering as a result of global cooling trends and the encroachment of grasslands during the late Cenozoic of North America. Artiodactyl phylogenetic community structure following the mid Miocene climatic optimum is also explained by phylogenetically dispersed origination of large bodied, grazing species. Patterns of perrissodactyl community structure diverge, particularly at the locality scale, because origination is confined primarily to *Equus* during the late Cenozoic. Our results lend further support to studies of North American hoofed mammal richness, showing the effects of climatic filtering on ungulate phylogenetic community structure in North America.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Well-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

Figure S2. Poorly-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

Figure S3. Character maps of tooth crown height conditions in North American (A) Artiodactyla and (B) Perissodactyla. Black lines show the brachydont or low crowned tooth conditions, green shows the mesodont condition, blue shows the submesodont condition, and red shows the hypsodont or high crowned tooth condition.

Figure S4. Relationships of artiodactyl (squares) and perissodactyl (circles) PCS (NRI) with (A) δ¹⁸O (‰) from benthic foraminifera (Zachos *et al.*, 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the poorly resolved artiodactyl and perissodactyl phylogenies. PCS, phylogenetic community structure; NRI, net relatedness index.

Table S1. Summary of North American Land Mammal Age subdivisions and associated sample sizes.

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