

Abiotic and Biotic Drivers of Turnover and Community Assembly in African Mammals

by

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A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved August 2018 by the
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December 2018

ABSTRACT

Climate and environmental forcing are widely accepted to be important drivers of evolutionary and ecological change in mammal communities over geologic time scales. This paradigm has been particularly influential in studies of the eastern African late Cenozoic fossil record, in which aridification, increasing seasonality, and C₄ grassland expansion are seen as having shaped the major patterns of human and faunal evolution. Despite the ubiquity of studies linking climate and environmental forcing to evolutionary and ecological shifts in the mammalian fossil record, many central components of this paradigm remain untested or poorly developed. To fill this gap, this dissertation employs biogeographical and macroecological analyses of present-day African mammal communities as a lens for understanding how abiotic change may have shaped community turnover and structure in the eastern African Plio-Pleistocene. Three dissertation papers address: 1) the role of ecological niche breadth in shaping divergent patterns of macroevolutionary turnover across clades; 2) the effect of climatic and environmental gradients on community assembly; 3) the relative influence of paleo- versus present-day climates in structuring contemporary patterns of community diversity. Results of these papers call into question many tenets of current theory, particularly: 1) that niche breadth differences (and, by extension, their influence on allopatric speciation) are important drivers of macroevolution, 2) that climate is more important than biotic interactions in community assembly, and 3) that communities today are in equilibrium with present-day climates. These findings highlight the need to critically reevaluate the role and scale-dependence of climate in mammal evolution and community ecology and to carefully consider potential time lags and disequilibrium dynamics in the fossil record.

To my parents, Linda and John

and Robyn

this is for you

ACKNOWLEDGMENTS

First, I would like to thank my dissertation chair, Kaye Reed. Kaye has been the best advisor anyone could ask for and she has played a significant role in all of my successes in graduate school. Whether it was answering emails at midnight, providing a letter of support at last minute notice, funding a research visit to Ethiopia or a week-long safari in South Africa – Kaye was there. I will never be able to thank her enough for her generosity, patience, and friendship over the last six years. Likewise, I am indebted to my committee members Chris Campisano, Janet Franklin, and Curtis Marean, who have encouraged and supported me every step of the way. They have been invaluable mentors, and I thank them for sharing their expertise with me and helping me to mature as a young researcher.

The camaraderie of the graduate student and postdoc community at IHO and ASU is unrivaled. I am thankful for the friendship of so many people I cannot possibly name them all here, but would like to mention Susanne Daly, Dominique Garello, Halszka Glowacka, Neysa Grider-Potter, Jake Harris, Gen Housman, Erick Lundgren, Amanda McGrosky, Maria-Nieves Colon, Andrew Ozga, Jon Paige, Terry Ritzman, Josh Robinson, Ben Schoville, Chalachew Seyoum, and Tim Webster. My labmates Ellis Locke and Irene Smail have been some of my closest graduate companions and I will always remember the laughs we shared. Finally, I would like to thank two best friends – Kathleen Paul and Ignacio Lazagabaster – for love, support, and good times.

For collaboration, guidance, and friendship over the past several years, I am indebted to Lydia Beaudrot, Kay Behrensmeyer, Faysal Bibi, Cécile Blondel, René Bobe, Jean-Renaud Boisserie, Dave Braun, Andrew Du, Tyler Faith, David Feary, John Fleagle, Yemane Gebru, Tomas Getachew, Ari Grossman, Jason Kamilar, Bill Kimbel, Margaret

Lewis, Mike Lague, Pietro Martini, Owen Middleton, Dave Patterson, Simon Schowanek, Gary Schwartz, Eric Scott, Sahle Selassie, Antoine Souron, Lillian Spencer, Brian Villmoare, Roger Wood, and Dr. Moges.

This dissertation would not have been conceivable without continuous love and support from my family. My parents Linda and John encouraged me to pursue a PhD and it would be impossible to list all the ways they helped to make it happen. I will never be able to thank them enough for all that they have given me. To my brothers Kevin and Chris, step-parents Marissa and Dave, Pillari brothers and sisters, the Merchants, and all of extended family – thank you.

Finally, I would like to thank my soon-to-be wife Robyn, who stuck by my side through the highs and lows as my career path and future unwound before me. Finishing this has been a long and tortuous process at times, and I could not have done it without you. Thank you for endless love, support, and encouragement. I look forward to the road ahead.

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CHAPTER 1. INTRODUCTION

Introduction

Hypotheses of climatically-driven evolution have been a central pillar of human origins research ever since Darwin's (1871) *The Descent of Man*, wherein he outlined a multi-stage model to account for the divergence of the human lineage from that of apes. Darwin's proposed model (formulated in the virtual absence of a hominin fossil record at the time) was initiated by a shift from arboreal to terrestrial habitats during environmental change, which in turn led to several positive feedback loops facilitating the emergence of familiar components of the *Homo* adaptive suite (e.g., bipedalism, brain enlargement, and stone tool use). Environmental hypotheses for human evolution were subsequently adopted and widely expanded upon by others as the hominin fossil record began to fill in (e.g., Dart, 1925; Jolly, 1970), eventually giving rise to the influential paradigm it is today (e.g., Behrensmeyer, 2006; deMenocal, 1995, 2004; Levin, 2015; Marean et al., 2015; Maslin et al., 2015; Potts, 2013). Although much research remains focused on explaining hallmark adaptations of the human lineage in the context of ancient climates or environments, such as the paleovegetational context of bipedalism (e.g., Cerling et al., 2011; White et al., 2009), the foci of hominin paleoecology have significantly broadened through time.

Today, a major focus of research of hominin paleoecology revolves around the role of climate change in driving macroevolutionary turnover (e.g., Behrensmeyer et al., 1997; Bibi and Kiessling, 2015; Vrba, 1980, 1987, 1995) and shifts in the functional structure of Plio-Pleistocene mammal communities as early humans evolved (e.g., Bobe and Leakey 2009; Cerling et al., 2015; Reed, 1996, 1997, 2008; Wynn et al., 2016). Such research interests, however, are not restricted to hominin paleoecologists. Indeed, studies

of the global Cenozoic fossil record of mammals are heavily reliant on climate and environmental change as explanatory variables for species turnover and ecological shifts in communities (e.g., Agustí and Antón, 2005; Blois and Hadly, 2009; Figueirido et al., 2012; Fraser et al., 2015; Janis et al., 2000, 2002). This includes, for example, the global replacement of perissodactyls by artiodactyls during the Paleogene (Janis 1989, 1993) and the replacement of hominoids by cercopithecids during the Neogene (Eronen and Rook, 2004), both of which have been linked to global cooling and increased aridity and seasonality (Zachos et al., 2001).

In both hominin and mammal paleoecology, research on the links between climate, macroevolutionary turnover, and community change have been mainly grounded in temporal correlations between these phenomena across geological time scales (Fritz et al., 2013; Marean et al., 2015). As such, paleontological studies have largely ignored newly developed methods for inferring the influence of climates and environments on present-day mammal diversity and community structure and assembly (e.g., Graham et al., 2012; Kraft and Ackerly, 2010; Webb et al., 2002). This divide between neo- and paleo- ecology has deep historical roots. Although paleontology was a major component of the 1940s modern evolutionary synthesis and informed studies of present-day ecological communities (e.g., Mayr, 1942; Simpson and Roe, 1939), these disciplines have diverged strongly and have operated in relative isolation over the last century. In hindsight, this divergence is somewhat puzzling, as these disciplines aim to understand the same fundamental abiotic and biotic processes governing the diversity and structure of ecological communities, whether today or in the past. Recent appeals to reintegrate neo- and paleo- ecological perspectives offers a promising venue for a holistic

understanding of the underlying drivers of biodiversity patterns and the structure of ecological communities (Fritz et al., 2013).

This dissertation casts a wide net by using biogeographical and macroecological analyses of present-day African mammal communities as a way of understanding how climatic- and environmental- change may have shaped community turnover and structure during the Plio-Pleistocene as humans evolved. The principal organization of the dissertation revolves around three papers, each of which tackles separate but related issues in the study of climatic- and environmental- influences on mammal community evolution:

Paper I ('Niche conservatism, niche breadth, and macroevolutionary turnover in the African fossil record of large-bodied mammals') tests the underlying assumptions of Elisabeth Vrba's (1987, 1999) widely influential resource-use hypothesis (RUH). Vrba's RUH posits that niche breadth contrasts between ecologically specialized and generalized mammal clades can largely account for differences in their rates of macroevolutionary turnover as documented by the fossil record and, by extension, their present-day diversity patterns. Because specialist clades have relatively narrow niches, they should experience higher rates of range fragmentation and contraction during climate change, thus increasing the likelihood of allopatric speciation and/or extinction. The opposite is true of generalist clades, whose relatively broad niches and high dispersal ability buffer them from vicariance and range contraction. Despite widespread discussion and application of this hypothesis in studies of the hominin and mammalian fossil record (e.g., see Bobe and Eck (2001), Cantalapiedra et al. (2011), Frost (2007), Kimbel (1995), Werdelin and Lewis (2005), and White (1995) for specific taxonomic groups), it has yet to be

rigorously tested. In Paper I, I combine measures of biomic, climatic, and dietary niche breadths with phylogenetic and fossil record data to test several underlying assumptions of the RUH (e.g., niche breadth is phylogenetically conserved) as well as its central tenet: clade-level niche breadths (measured for genera and tribes in Paper I) should predict rates of origination and extinction in the fossil record, with specialists having higher rates of turnover than generalists.

Paper II ('Climate and primary productivity modulate the relative influence of competition and abiotic filtering across African mammal communities') analyzes the influence of climatic and environmental gradients on community assembly across present-day African mammals. In the fossil record, climate and environmental change are widely accepted to be important drivers of community evolution through time, although the exact nature of their influence on assembly processes remains unclear. Fortunately, a relatively recent body of studies in community ecology have shown that analyzing the phylogenetic and functional trait structure of communities is a powerful way of inferring the assembly processes that have shaped them and how the strength of one process over the other changes across environmental gradients (e.g., Graham et al., 2009, 2012; Kraft and Ackerly, 2010). The basic question asked by phylogenetic and functional trait community ecology is: if the set of species found in a particular locality (i.e., a local community) is only a subset of the species found within the broader region (i.e., the regional species pool), are the processes that determine community composition predictable and deterministic, or are they neutral and stochastic? If assembly processes are largely deterministic, then communities shaped by different processes should have a predictable phylogenetic and functional trait structure deviating from randomness. If

species within a community are more distantly related or dissimilar in their traits than expected by chance, the community is inferred to have been assembled through competitive processes, such as competitive exclusion or niche partitioning. Conversely, if species within a community are more closely related or similar in their traits than expected by chance, dispersal limitation and abiotic filtering are inferred. The abiotic filter has favored similar ecological or physiological characteristics, assumed to be phylogenetically conserved, that are suited for a particular environment. Patterns of community overdispersion (competition) and clustering (abiotic filtering) can then be analyzed in relation to climatic and environmental gradients to determine how these forces shape community assembly. Studies of present-day communities, like Paper II in this dissertation, feed directly into our interpretations of the fossil record of community evolution in the context of paleo- climatic and environmental changes through deep time.

Paper III ('Strong influence of paleoclimate on the structure of modern African mammal communities') analyzes the relative influence of present-day versus paleo- climates in structuring modern African mammal communities. It is widely accepted by both neo- and paleo- ecologists that climate plays a major role in shaping the diversity and structure of ecological communities, and thus the relationship between climate and community structure patterns has emerged as a principal focus of ecological research. Most studies, however, implicitly or explicitly assume that: 1) species geographic ranges track climate change in real-time and thus 2) the structure of ecological communities is fundamentally in equilibrium with current climates (Franklin, 2010; Araújo and Peterson, 2012).

However, climate fluctuations over geologic time scales have influenced species dispersal and extinction, which in turn may affect community structure. The structure of

present-day ecological communities is therefore likely a product of both modern and paleo- climates, with their relative degrees of influence unknown. In Paper III, I combine community data from > 200 protected areas (e.g., national parks) across Africa with modern, mid-Holocene (~ 6,000 years ago), and Last Glacial Maximum (~ 22,000 years ago) climate models to test the relative influence of modern versus past climates. The results of this study bear directly on time lags between climate and community change, as well as the response of the world's biodiversity to anthropogenic climate change over the next century.

Together, these results are synthesized and discussed in the context of the Plio-Pleistocene record of paleo- climatic, environmental, and paleo- community change in eastern Africa as early hominins evolved. Additionally, these results bear on fundamental questions of climate-mammal community relationships and the response of the world's mammalian biodiversity to anthropogenic climate change and land alteration over the next century.

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CHAPTER 2: NICHE CONSERVATISM, NICHE BREADTH, AND MACROEVOLUTIONARY TURNOVER IN THE AFRICAN RECORD OF LARGE- BODIED MAMMALS

Title: Niche conservatism, niche breadth, and macroevolutionary turnover in the African fossil record of large-bodied mammals

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Abstract

Climate change has long been acknowledged as an important driver of mammalian evolution over geological timescales. E.S. Vrba's 'resource-use hypothesis' (RUH) posits that differences in niche breadth play a deterministic role in shaping divergent patterns of macroevolutionary turnover across clades, with ecologically specialized clades having higher incidences of range fragmentation and contraction, and therefore speciation and extinction, than generalist clades in the face of climatic change. Despite widespread application of the RUH in studies of mammalian evolution, many of its central tenets remain to be rigorously tested. Here, we combine present-day and fossil data from large-bodied African mammals to measure species' niche breadths, test the degree to which they are phylogenetically conserved, and analyze the relationship between clade-level niche breadth and origination and extinction rates in the fossil record. Our principal findings are: (1) species' dietary niche breadths are unrelated to their biomic and climatic niche breadths, failing to support an overall specialist-generalist dichotomy across mammals, and (2) although species' biomic, climatic, and dietary niche breadths show moderate to high phylogenetic conservatism, there is no relationship between clade-level measures of niche breadth and turnover rates in the fossil record. Our results indicate that the evolutionary trajectories of Eltonian and Grinnellian niche dimensions have been largely decoupled in African mammals and, perhaps as a consequence, had little to no influence in driving the diversification histories of clades. We suggest that future studies of turnover should begin to directly test Red Queen dynamics, such as shifting competitive landscapes, in driving mammalian evolutionary patterns over geological timescales.

Keywords: Court Jester, Red Queen, paleoclimate, phylogenetic niche conservatism

1. Introduction

Climate change is often causally linked to macroevolutionary and macroecological events in the Cenozoic fossil record of mammals (Badgley et al., 2008; Badgley and Finarelli, 2013; Barnosky, 2001; Barnosky and Kraatz, 2007; Blois and Hadly, 2009; Janis, 1989, 1993; Vrba, 1992, 1995a). The explicit or implicit assumption of such studies is that mammal species have climatic niche breadths, or a limited range of climatic conditions (e.g., precipitation, temperature) under which they can exist and maintain fitness (Quintero and Wiens, 2013a). Under this assumption, the mammalian fossil record is viewed as reflecting species tracking their niches across time and space (e.g., range shifts) or failing to do so (e.g., extirpation or extinction) as climates changed. Similar climate-related explanations of turnover have also been proposed for the fossil records of entire clades, under the assumption that species' climatic niches scale up to clade-level niches because of phylogenetic niche conservatism (Hadly et al., 2009). Phylogenetic niche conservatism is the pattern by which close relatives are more similar in their niches than distant relatives because of shared evolutionary history, which can be inferred from a strong relationship between degree of relatedness and niche similarity across taxa (Webb et al., 2002; Wiens and Graham, 2005; Wiens et al., 2010). Niche conservatism has been implicated in explanations of major events in the mammalian fossil record, such as the Paleogene replacement of perissodactyls by artiodactyls (Janis 1989, 1993) and the Neogene replacement of hominoids by cercopithecids (Eronen and Rook, 2004), both of which were coincident with global cooling and increasing aridity and seasonality (Zachos et al., 2001).

Despite the commonly made assumption of niche breadth conservatism in mammalian clades, few studies have directly tested for it. These include a handful of

studies on primates (Kamilar and Muldoon, 2010; Kamilar and Cooper, 2013; Duran et al., 2013; Duran and Pie, 2015) and mammals in general (Dormann et al., 2010; Cooper et al., 2011) that provide mixed results, with some finding weak niche conservatism (Kamilar and Muldoon, 2010; Kamilar and Cooper, 2013) and others finding strong niche conservatism (Duran et al., 2013). In addition to its importance for understanding the role of climate change in mammalian evolution, resolving the degree of niche conservatism also has conservation implications, for clades with highly conserved niches may find it difficult to track their preferred climates or adapt to new ones in the face of anthropogenic climate change (Wiens, et al. 2010). For example, Quintero and Wiens (2013b) showed that estimated rates of climatic niche evolution across vertebrates are vastly slower than projected rates of climate change over the next century, suggesting that clades with highly conserved niches are at an even greater extinction risk than more generalized clades with labile niches.

One of the most commonly made links between climate change and the mammalian fossil record concerns how paleoclimate influenced the timing and pattern of temporal turnover across clades that vary in ecology. Much of this work is grounded in ‘habitat theory’ and in particular Vrba’s (1980, 1987, 1992, 1995a, 1999) ‘resource-use hypothesis’ (hereafter, RUH), which posits that specialist lineages should have higher incidences of range fragmentation and contraction, and therefore higher speciation and extinction rates, than generalist lineages in the face of climate change. Furthermore, because specialist species are likely to have poorer dispersal potential by virtue of their narrower niches, populations of specialist species fragmented during climate change are unlikely to be reconnected even when favorable conditions return (Baselga et al., 2011; Rolland and Salamin, 2016), increasing temporal isolation and thus the likelihood of

allopatric speciation occurring. Likewise, the narrower niches of specialist species increase the likelihood of their preferred environments completely disappearing during climate change, which increases the probability of extinction (Baselga et al., 2011).

Although several studies have explored the theoretical framework of the RUH in explaining temporal turnover in the mammalian fossil record (e.g., Bibi and Kiessling, 2015; Hernandez-Fernandez et al., 2015), many of its central tenets remain to be formally tested. For example, if differences in niche breadth (i.e., specialists versus generalists) do in fact play a deterministic role with respect to variation in temporal turnover among clades, as suggested by the RUH, then niche breadth must be phylogenetically conserved. If this assumption of the RUH is not supported, even with a broad correlation between climate change and turnover, this suggests that there are likely other and more proximate influences at work, such as biotic pressures under a Red Queen view of evolution (e.g., Barnosky, 2001; Benton, 2009, 2010; Van Valen, 1973).

Here, we examine the relationship between climate change and mammalian evolution by characterizing modern species' niches and niche breadths, testing the degree to which these are phylogenetically conserved, and analyzing the relationship between clade niche breadth and turnover rates using the fossil record. We calculate niche breadth for biome, climate, and dietary data, following Vrba (1987), who characterized specialists and generalists based on both "...physical and biotic factors including temperature, moisture, substrate...food items, vegetation cover and any other environmental components that can be utilized by organisms or determine whether they can function in a habitat." Furthermore, most macroecological studies have utilized measures of habitat, climatic, and dietary niche breadths for addressing evolutionary questions (Slatyer et al., 2013). Using biomic, climatic, and dietary measures of niche breadth, we ask the

following questions and test their constituent hypotheses according to expectations based on the RUH:

(Q₁) Are biomic, climatic, and dietary dimensions of species' niche breadth related?

H₁: The breadth of niche dimensions are positively related to one another.

H₁ proposes that dietary specialists will also be biome and climate specialists because dietary specialization has been shown to be linked to habitat specialization (Greenacre and Vrba, 1984; Vrba, 1987), and habitat and biome distribution is largely controlled by climate. Conversely, dietary generalists can persist in a wide variety of biomes and therefore climates. Testing this hypothesis is critical as many studies broadly assign species into a specialist versus generalist dichotomy, although it is likely these terms are only useful when used in relation to a specific resource category. For example, armadillos (*Oryzomys afer*) exclusively consume ants and termites, but because these food items are widely distributed, they are found in a wide variety of habitats ranging from semi-desert to woodland-forest mosaics (Kingdon, 2015). Thus, armadillos are dietary specialists but habitat and climate generalists. Therefore, it is important to test the degree to which species' niche breadth is overall congruent across different aspects of their ecologies.

(Q₂) Is niche breadth correlated with range size?

H₂: All dimensions of niche breadth will be positively related to range size.

H₂ proposes that species with larger ranges will be biome, climatic, and dietary generalists, whereas specialists in these dimensions will have smaller ranges. Testing H₂ is important because most studies assume that generalist species have larger ranges than specialist species (e.g., Gomez-Rodriguez et al., 2015; Rolland and Salamin, 2016) and are therefore buffered from extinction in the face of climate or habitat change.

Alternatively, we propose that it is possible that the larger ranges of generalist species provide more opportunity for vicariance and allopatric speciation, which would likely increase both origination and extinction rates.

(Q₃) Is niche breadth phylogenetically conserved?

H₃: Niche breadth has a high phylogenetic signal.

H₃ proposes that niche breadth is phylogenetically conserved. Phylogenetic conservatism of niches is often proposed as the reason why clades exhibit synchronous responses to climate and habitat change (e.g., Vrba, 1987).

(Q₄) Is niche breadth related to turnover rates?

H₄: Specialists should have higher origination and extinction rates.

H₄ is the ultimate test of Vrba's RUH. We predict that specialist lineages should have both higher origination and extinction rates than generalist lineages when compared across an equal amount of time.

In asking these questions, we focus solely on orders of large-bodied mammals in sub-Saharan Africa (i.e., Africa below $\sim 15^{\circ}\text{N}$), hereafter Africa, for several reasons. First, large-bodied African mammals are ecologically diverse and have relatively complete fossil records, both of which are required to test our hypotheses. Second, African mammal faunas are among the least anthropogenically altered today and were only weakly impacted by late Quaternary extinctions (Barnosky et al., 2004; Faurby and Svenning, 2015a; Sandom et al., 2014). Therefore, measures of niches and niche breadth should be less influenced by anthropogenic impacts in Africa compared to other areas of the world. Third, Africa has an extraordinarily speciose mammal fauna compared to other similarly sized regions (Wilson and Reeder, 2005) and nearly 90% of its large mammals are endemic (Hernandez-Fernandez and Vrba, 2005), which limits potentially confounding factors from widely distributed species (i.e., those also found in Eurasia). Fourth, present-day African mammals have well-known distributions and ecological traits, and their phylogenies are well-resolved (e.g., Hassanin et al., 2012; Bibi, 2013; Faurby and Svenning, 2015b). Finally, many studies of turnover in relation to climate change have used the rich Plio-Pleistocene African fossil record of mammals (e.g., Behrensmeyer et al., 1997; Bibi and Kiessling, 2015; Bobe and Behrensmeyer, 2004; Bobe and Eck, 2001; Frost, 2007; Vrba, 1995b; Werdelin and Lewis, 2005), so our results bear directly on the late Cenozoic fossil record of the continent, including that of human evolution (e.g., Kimbel, 1995; White, 1995).

2. Materials and Methods

We combined data from the fossil record with present-day species ranges and biome, climatic, and dietary data, and a time-calibrated phylogeny to test our RUH-based

hypotheses. Fossil data on species' temporal durations were used to estimate turnover rates; extant species ranges, biome, climatic, and dietary data were used to calculate species' niche breadth; the phylogeny of extant species was used to measure the phylogenetic signal of species' niches. Correlations between turnover rates and niche breadth were assessed using linear models. We provide details for each of these steps below.

2.1 Taxon selection and fossil data collection

We systematically examined all genera of large-bodied African mammals with fossil records for inclusion in our analyses. We chose genera as our main units of analysis because: 1) species-level anagenetic lineages (i.e., fossil lineages leading directly to an extant species) are poorly resolved and/or controversial, whereas genus-level lineages (chronogenera) are well-established and widely accepted; 2) higher taxonomic levels (e.g., families or orders) vary widely in their ecologies and therefore do not provide ecologically cohesive units of analysis for our questions; 3) Vrba (1987) used mammalian genera as her main units of analysis in her original formulation of the RUH and therefore our separate tests of this hypothesis should be comparable. However, we also analyzed tribal-level turnover rates for the families Bovidae and Cercopithecidae because tribes in these families are virtually as ecologically cohesive as genera and have been the focus of many studies implicating the RUH (e.g., Cantalapiedra et al., 2011; Vrba, 1995b). We included all extant and extinct taxa for tribal-level analyses, whereas our genus-level analyses only included fossil taxa attributed to an extant genus. For example, the sole reduncin taxon in our genus-level analyses is the genus *Kobus*, while the genera *Kobus*,

Menelikia (†), *Redunca*, and *Zephyreduncinus* (†) are included in the tribe Reduncini for tribal-level analyses.

Fossil occurrence data for the last seven million years (Myr) were collected from published site-based species lists and used to build a binary presence-absence matrix; maximum and minimum absolute age estimates were collected for each site in millions of years (Ma) from the literature. We restricted our fossil database to records from eastern Africa (Ethiopia, Kenya, Tanzania) because this region contains the most continuous, temporally well-constrained, and fossiliferous sequence for the late Cenozoic of the continent; other regions have patchy fossil records (i.e., Central Africa) or have taxonomies in need of revision and poor temporal control of sites (i.e., South Africa). Genera analyzed for turnover-niche breadth relationships were limited to large-bodied mammalian orders (Artiodactyla, Carnivora, Perissodactyla, Primates, Proboscidea) because of well-known taphonomic and collection biases against smaller-bodied taxa (Behrensmeyer et al., 1979). Within these orders, we excluded genera with very poor fossil records (e.g., *Cephalophus*) or those that were considered in need of extensive revision (e.g., wastebasket ‘*Gazella*’). Our final dataset included 87 species, 17 genera (genus-level analyses) and 9 tribes (tribal-level analyses) of large-bodied mammals (Tables 1.1-1.2).

Table 1.1. Genera ($n=17$) used in genus-level analyses.

Order	Family	Genus
Artiodactyla	Bovidae	<i>Aepyceros</i>
Artiodactyla	Bovidae	<i>Connochaetes</i>
Artiodactyla	Bovidae	<i>Damaliscus</i>
Artiodactyla	Bovidae	<i>Kobus</i>
Artiodactyla	Bovidae	<i>Tragelaphus</i>
Artiodactyla	Giraffidae	<i>Giraffa</i>
Artiodactyla	Hippopotamidae	<i>Hippopotamus</i>
Artiodactyla	Suidae	<i>Hylo.-Kolpochoerus</i>
Artiodactyla	Suidae	<i>Phaco.-Metridiochoerus</i>
Carnivora	Felidae	<i>Panthera</i>
Carnivora	Hyaenidae	<i>Crocuta</i>
Carnivora	Hyaenidae	<i>Hyaena</i>
Perissodactyla	Equidae	<i>Equus</i>
Perissodactyla	Rhinocerotidae	<i>Ceratotherium</i>
Perissodactyla	Rhinocerotidae	<i>Diceros</i>
Primates	Cercopithecidae	<i>Theropithecus</i>
Proboscidea	Elephantidae	<i>Loxodonta</i>

Table 1.2. Tribes ($n=9$) used in tribal-level analyses.

Order	Family	Tribe
Artiodactyla	Bovidae	Aepycerotini
Artiodactyla	Bovidae	Alcelaphini
Artiodactyla	Bovidae	Antilopini
Artiodactyla	Bovidae	Bovini
Artiodactyla	Bovidae	Hippotragini
Artiodactyla	Bovidae	Reduncini
Artiodactyla	Bovidae	Tragelaphini
Primates	Cercopithecidae	Colobini
Primates	Cercopithecidae	Papionini

Some of our fossil taxa included open nomenclature (e.g., ‘aff.’, ‘cf.’), which may potentially inflate our estimates of turnover rates. To test for this, we generated two versions of our database: the first can be considered as taxonomically liberal, wherein all open nomenclature and indeterminate records were retained; the second can be considered taxonomically conservative, wherein ‘cf.’ taxa were lumped with their likely species (e.g., *Panthera cf. leo* = *Panthera leo*) and indeterminate records (e.g., *Panthera* sp., *Colobini* indet.) were deleted, but ‘aff.’ records were retained in the dataset with the understanding that this is most often used to denote a closely related but distinct species. Preliminary comparisons indicated that turnover rates estimated from the taxonomically

liberal and conservative databases were highly correlated ($r = 0.7-0.8$). Thus, we used a mixed database for final analyses in which we retained ‘aff.’ and ‘cf.’ records but removed indeterminate records.

2.2 Present-day taxon distribution data

We used present-day species range maps to calculate species’ range size and climatic and habitat niche breadths. Although the potential problems with range map data have been noted (Hurlbert and Jetz, 2007; Hurlbert and White, 2005), range maps have been successfully used in a variety of studies operating at large spatial scales (Cardillo, 2011; Cooper et al., 2011; Duran et al., 2013; Duran and Pie, 2015; Olalla-Tarraga et al., 2011; Marechaux et al., 2017). For this study, range maps were used for two primary reasons. First, many of the taxa in our dataset had little occurrence data (e.g., georeferenced occurrence data from the Global Biodiversity Information Facility) and therefore likely under-sampled the range size, climatic niche breadth, and habitat niche breadth of most taxa. Second, although range maps may slightly overestimate the range size and niche breadth of taxa because they are interpolations of data on species’ actual ranges, this overestimation may counterbalance recent range contraction due to human influence. For example, Martinez-Freiria et al. (2016) have shown that human encroachment on ranges in the last century alone leads to vastly smaller estimates of climatic niche breadth for African elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). Finally, it has been shown that range maps are congruent with well-sampled occurrence data at large spatial scales and may even provide a less-biased estimate of species distributions than occurrence data (Hawkins et al., 2008; Hurlbert and Jetz, 2007).

We obtained species distribution data from range maps from International Union for Conservation of Nature (IUCN) Red List assessments (IUCN, 2017). Shapefiles of species ranges were sampled using a 0.5 x 0.5° grid with the package *letsR* (Vilela and Villalobos, 2015). The number of points a species was sampled across was used as a proxy for range size in all analyses (e.g., African elephant *Loxodonta africana* = 2044 points, mountain nyala *Tragelaphus buxtoni* = 12 points). All species-level data were then aggregated for genus- and tribal- level analyses.

2.3 Biome and climate data

We used a modified version of White's (1983) physiognomic classification of African vegetation biomes to classify species' biomic niche breadth. White's (1983) classification was used because it is one of the most comprehensive biome maps made for the continent, was built over decades of fieldwork (versus interpolation from satellite imagery), and because it has similar spatial resolution to IUCN range maps. We used 17 physiognomically distinct natural vegetation units that also differ in regional climate, topography, and edaphic characteristics (Figure 1.1 A) to quantify species' biome niche breadth.

Rasters of climate data were downloaded from WorldClim (Hijmans et al., 2005) at 2.5' resolution for 19 climatic variables (<http://www.worldclim.org/bioclim>). Climate variables were extracted for each taxon's range based on their 0.5 x 0.5° grids using the packages *dismo* (Hijmans et al., 2017a) and *raster* (Hijmans et al., 2017b). All variables were then assessed for their relevance to mammal species distributions following Kamilar et al. (2015) and Rowan et al. (2016) and a final set of six was chosen (Figure 1.1 B, Table 1.3). The six variables capture averages and seasonality of temperature and

precipitation, as well as lower climate extremes that shape productivity (i.e., temperature of the coldest month, rainfall of the driest month). All temperature variables are measured in 1/10th degrees Celsius (°C) and precipitation variables in millimeters (mm). We note that the seasonality variables are measured differently for temperature and precipitation: temperature seasonality is measured as the standard deviation of temperature throughout the year multiplied by 100 and precipitation seasonality is measured as the coefficient of variation of rainfall throughout the year (Hijmans et al., 2005). For each taxon, these climate data were used to calculate its climatic niche breadth.

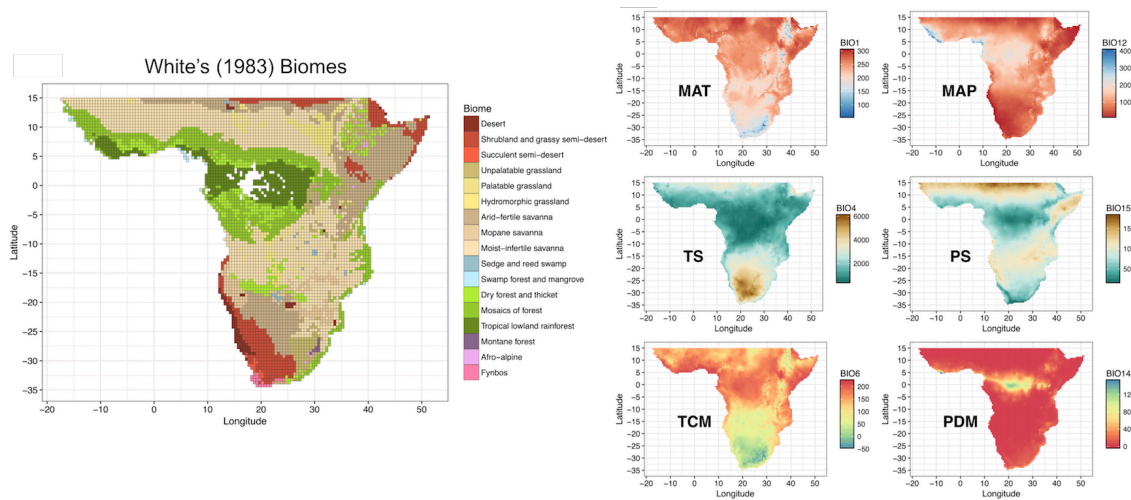


Figure 1.1 A, Map of modified biomes based on White (1983) used to calculate biome niche breadth of species. White points in Central Africa are ‘anthropogenic landscapes’, which were not used for analyses. B, climate variables used to calculate climatic niche breadth: mean annual temperature (MAT), temperature seasonality (TS), temperature of the coldest month (TCM), mean annual precipitation (MAP), precipitation seasonality (PS), and precipitation of the driest month (PDM). See text for details.

Table 1.3. Climate variables from WorldClim (Hijmans et al., 2005) used in a principal components analysis (PCA) to characterize the climatic niche breadth of African mammal species. Temperature variables are measured in degrees Celsius (°C) and precipitation variables in millimeters (mm).

Acronym	Variable Description	WorldClim Code
MAT	Mean annual temperature	BIO1
TS	Temperature seasonality (standard deviation*100)	BIO4
TCM	Temperature of the coldest month	BIO6
MAP	Mean annual precipitation	BIO12
PS	Precipitation seasonality (coefficient of variation)	BIO15
PDM	Precipitation of the driest month	BIO14

2.4 Phylogenetic and dietary trait data

We used the species-level phylogeny of mammals compiled by Faurby and Svenning (2015b) for all phylogenetic analyses. This phylogeny includes all extant species of mammals and was compiled based on a novel heuristic-hierarchical Bayesian algorithm using genetic data. The Faurby and Svenning (2015b) phylogeny was used because it includes species-level data for all genera and tribes within our dataset and because it is the most recent and comprehensive estimate of mammalian phylogeny. Although some robust order-level phylogenies have been recently published (e.g., Hassanin et al., 2012), these trees have sparse species-level sampling and are focused more on broad relationships across each clade. Visual examination of the Faurby and Svenning (2015b) topology for different groups was consistent with recently published phylogenies focusing on lower taxonomic levels.

Diet was recorded as an ordinal variable for 10 food groups (e.g., seed, fruit, invertebrate) (Table 1.4) roughly following the MammalDIET system of Kissling et al. (2014). Food groups were recorded for each species as follows: 0 = not consumed, 1 = rarely consumed, 2 = often consumed, 3 = primary food resource. Dietary data were collected from Butynski et al. (2013), Kingdon (1971, 1977, 1979, 1982a, 1982b), Kingdon et al. (2013), Kingdon and Hoffmann (2013a, 2013b), and Skinner and Chimimba (2005).

Table 1.4. Dietary classifications for mammal species. An ordinal rank (0 = ‘not consumed’, 1 = ‘rarely consumed’, 2 = ‘often consumed’, 3 = ‘primary food resource’) was assigned for each diet category for each species based on published sources (see Materials and Methods).

Diet Category	Description
Mammal	Consumes mammalian prey
Bird	Consumes avian prey
Herptile	Consumes reptile or amphibian prey
Fish	Consumes fish prey
Invertebrate	Consumes invertebrate prey
Seed	Consumes seeds
Fruit	Consumes fleshy fruits
Root	Consumes roots
Woody	Consumes leaves of woody plants (e.g., tree leaves)
Herbaceous	Consumes leaves of herbaceous plants (e.g., grasses)

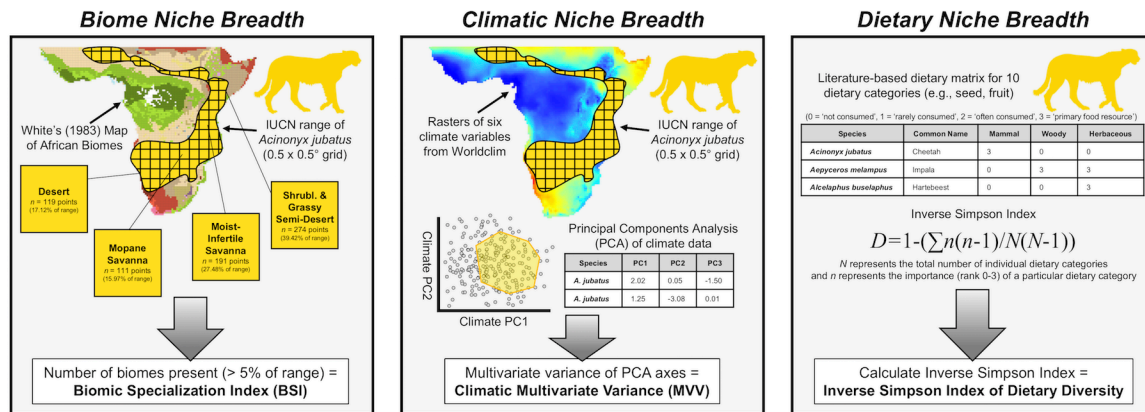


Figure 1.2. Schematic overview of niche breadth metrics for biome, climatic, and dietary data using cheetah *Acinonyx jubatus* as an example. Biome niche breadth was calculated following the Biomic Specialization Index (BSI) of Hernandez-Fernandez and Vrba (2005a, 2005b), which is simply a count of the number of biomes a species is present in; we imposed a 5% cutoff for a biome to count towards a species’ BSI. Climatic niche breadth was calculated by measuring the weighted multivariate variance (MVV) of a species’ principal component scores (e.g., PC1, PC2...) from a principal components analysis of six climate variables (see Table 3). Dietary niche breadth was calculated using the Inverse Simpson Index on a matrix of dietary data.

2.5 Quantifying taxon niche breadth

Species-level niche breadths were calculated for biome, climatic, and dietary data using separate methods (Figure 1.2). Species’ scores were averaged to generate genus- and tribal- level niche breadths.

Biome niche breadth—Biome niche breadth was calculated following the Biomic Specialization Index (BSI) of Hernandez-Fernandez and Vrba (2005), which is a count of the number of biomes a species is present in. For example, a BSI score of 1 indicates a species present in only a single biome, whereas a BSI score of 5 indicates a species present in five biomes. As both White's (1983) biomes and IUCN range maps have coarse spatial resolution, we used a 5% cutoff for biome presence (i.e., 5% of a species' range had to present within a biome to count towards its BSI). Based on this threshold, for example, the range of impala *Aepyceros* (BSI = 4) occupies 55.6% moist-infertile savanna, 20.2% arid-fertile savanna, 14.9% Mopane savanna, and 9.6% mosaics of forest, which is consistent with literature- and handbook- based accounts of the habitat preferences of this genus (Fritz and Bourgarel, 2013).

Climatic niche breadth—To calculate climatic niche breadth, we first used a principal components analysis (PCA) to reduce the dimensionality of the climate data. Species points for the six climate variables (Table 1.3) were log-transformed and used in a correlation matrix-based PCA using the *prcomp* function in R. For each species, we then calculated an intraspecific weighted multivariate variance (MVV) from the resulting PCA axes as a measure of climatic niche breadth. To calculate MVV, we adopted a morphological disparity method from Wills et al. (1994), wherein we weighted each principal component score by its respective axis' eigenvalue, calculated the variance of weighted principal component scores for each species, and then summed weighted component variances for each species to generate an MVV value of climatic niche breadth. This method has been widely applied for interspecific studies of both morphological (e.g., Foth and Joyce, 2016) and ecological (e.g., Kamilar and Baden, 2014) data.

Dietary niche breadth—We calculated dietary niche breadth from our ordinal diet matrix using the Inverse Simpson Index following Pineda-Munoz et al. (2016). The Inverse Simpson Index is calculated as

$$D=1-(\sum n(n-1)/N(N-1))$$

where N represents the total number of individual dietary categories and n represents the importance (rank 0-3) of a particular dietary category. An Inverse Simpson score of 0.00 indicates a specialized dietary niche (e.g., obligate grazer blue wildebeest *Connochaetes taurinus* = 0.00), whereas a score closer to 1.00 indicates a species with a diverse dietary niche (e.g., omnivorous Chacma baboon *Papio ursinus* = 0.83). Inverse Simpson Indices were calculated using PAST v3.18 (Hammer et al., 2017).

2.6 Phylogenetic conservatism of niche breadth

We tested the degree to which BSI and climatic and dietary niche breadths were phylogenetically conserved across mammals by analyzing their phylogenetic signal. Phylogenetic signal is essentially a measure of the covariance between trait similarity (niche breadth) and phylogenetic relatedness across a clade (Cadotte and Davies, 2016). We used Pagel's λ to measure the phylogenetic signal in mammal species' niches following Pagel (1999). Pagel's λ is bounded from 0-1 and assumes a Brownian motion model of evolution, with the null hypothesis (no phylogenetic signal) $\lambda=0$, whereas a high λ value close to 1 indicates a high phylogenetic signal and that the trait of interest is conserved across the phylogeny of species. Here, we adopt the view that a high phylogenetic signal is evidence for phylogenetic niche conservatism (following Cooper et

al., 2010, Kamilar and Cooper, 2013, and Olalla-Tarraga et al., 2016), although this interpretation has been debated (Losos, 2008). Pagel's λ was calculated using the function *phylosig* in the package *phytools* (Revell et al., 2012) and 1,000 simulations of a randomization test were used to judge its significance. Because Pagel's λ is a traditional parametric test, all niche breadth variables were log-transformed to ensure normality when measuring their phylogenetic signal.

As two of our niche breadth variables (BSI, MVV) are inherently geographic in nature, a high phylogenetic signal may be simply due to significant range overlap between closely related species instead of a biologically meaningful result. To test for this, we generated a series of sister pairs from the Faurby and Svenning (2015b) phylogeny and calculated their geographic distances (measured as degree of range overlap and median range distance). We calculated range overlap between sister species following Chesser and Zink (1994), in which range overlap is calculated as the percentage of the smaller range that overlaps the larger range (i.e., 100% overlap = 100% of the smaller range falls within the larger range). Median range distances were calculated as Euclidean distances between the median latitude and longitude of each sister's range. BSI distances were calculated as an anomaly by subtracting the smaller BSI value from the larger BSI value. Climatic MVV distances were calculated by generating pairwise Euclidean distances for climate data (see Table 1.3) of each species. BSI and MVV distances were then plotted against range overlap for sister pairs to assess the degree to which biomic and climatic niche breadth similarity may be the result of geography alone.

2.7 Estimating taxon turnover rates

Turnover rates (origination, extinction) can be calculated from both molecular phylogenies and the fossil record. Here, we focus only on fossil datasets because previous studies have demonstrated the shortcomings of molecular phylogenies based solely on living taxa for estimating macroevolutionary rates, especially extinction (e.g., Rabosky, 2010; Quental and Marshall, 2010; Pyron and Burbink, 2013). Furthermore, although Cantalapiedra et al. (2015) showed that turnover rates from molecular phylogenies and fossil records were broadly congruent, their results were based on higher taxa (suborder Ruminantia) and therefore may not apply to our genus- and tribal- level analyses.

We calculated genus- and tribal- level turnover rates over the last 7 Myr using 250,000-year intervals (e.g., 3.5-3.25 Ma, 3.25-3.0 Ma) with Foote's (2000) turnover metrics. Foote's metrics were calculated for each 250,000-year interval using four fundamental groups of taxa (Figure 1.3): 1) taxa with first and last appearances within the interval (*FL*); 2) taxa that cross the lower boundary but make their last appearance within the interval (*bL*); 3) taxa that make their first appearance within the interval and cross its upper boundary (*Ft*); and 4) taxa that range through the entire interval (*bt*). From these groups, turnover rates are calculated as

$$\hat{p}: -\ln(N_{bt}/N_t)/\Delta t$$

$$\hat{q}: -\ln(N_{bt}/N_b)/\Delta t$$

where \hat{p} and \hat{q} are per-capita origination and extinction rates, respectively, N_t is the total number of taxa crossing the top boundary ($N_t = N_{Ft} + N_{bt}$), N_b is the total number of taxa crossing the bottom boundary ($N_b = N_{bl} + N_{bt}$), and Δt represents an interval of time.

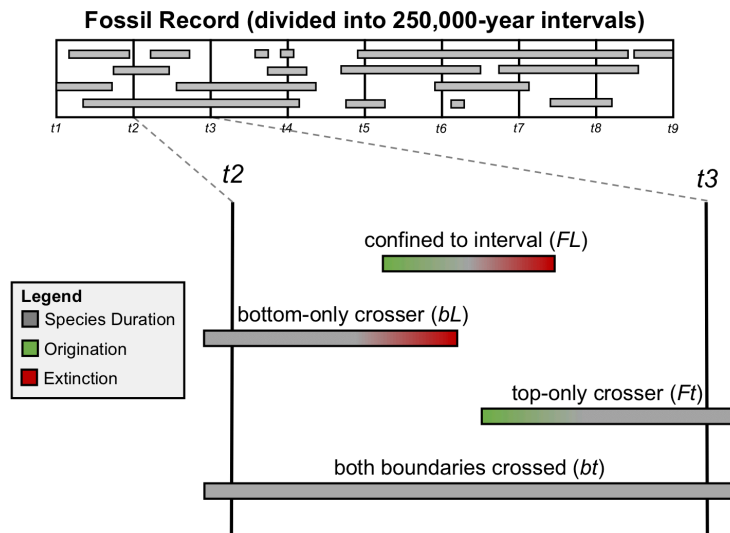


Figure 1.3. Schematic overview of the calculation of Foote's (2000) turnover metrics from four fundamental groups of taxa: 1) taxa with first and last appearances within the interval (*FL*); 2) taxa that cross the lower boundary but make their last appearance within the interval (*bL*); 3) taxa that make their first appearance within the interval and cross its upper boundary (*Ft*); and 4) taxa that range through the entire interval (*bt*).

2.8 Linear models and correlation analyses

We analyzed the relationship between niche breadth measures (BSI, MVV, Inverse Simpson Indices) using scatter plots and Pearson correlation coefficients (r). Range size-niche breadth relationships were analyzed using Ordinary Least Squares (OLS) models, with range size as the predictor and BSI, MVV, and Inverse Simpson Indices as the response variables. Models were judged based on their coefficient of determination (r^2).

We analyzed the relationship between origination and extinction rates and niche

breadth measures using multiple regression and the corrected Akaike Information Criterion (AICc) (Burnham and Anderson, 2002) in the package *MuMIn* (Bartoń, 2018). As two of our niche breadth measures, BSI and MVV, were highly correlated ($r = 0.78-0.83$), we only used MVV in models to avoid the potentially confounding effects of multicollinearity. MVV was chosen over BSI because it is a continuous variable, whereas BSI is a count. For both genus- and tribal- level analyses, models were specified as

$$\log(\text{Origination Rate}) \sim \log(\text{MVV}) + \log(\text{Inverse Simpson Index})$$

$$\log(\text{Extinction Rate}) \sim \log(\text{MVV}) + \log(\text{Inverse Simpson Index})$$

with origination/extinction rates as the response and MVV and Inverse Simpson Indices as the predictors; all variables were log-transformed to ensure normality. From these models, we generated AICc weights for each predictor variable as a measure of its overall importance using the function *dredge* (Bartoń, 2018). Overall model fit was judged based on the coefficient of determination (r^2).

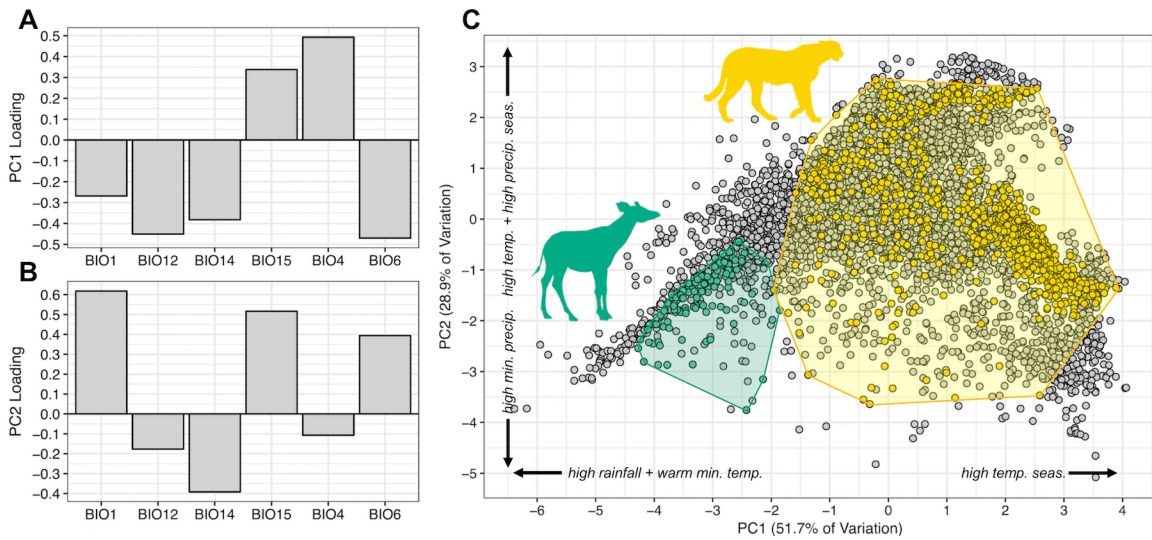


Figure 1.4. A-B, Principal components analysis (PCA) loadings for PC1 (A) and PC2 (B) based on six climatic variables (see Table 3). C, PCA biplot of PC1 (51.7% of variation) against PC2 (28.9% of variation), with species points for cheetah *Acinonyx jubatus* (yellow) and okapi *Okapia johnstoni* (green) connected by minimum convex polygons as examples; gray points represent those from all other species.

3. Results

3.1 PCA of climate data

The PCA generated six principal component axes (PC1-PC6) summarizing species' climate data (Table 1.5), which were all used to calculate species' climate MVV values. Most variation, however, was captured on PC1 (51.7% of variation) and PC2 (28.9% of variation), which collectively explain ~ 80% of the variation in the climate data. PC1 was mainly driven by BIO4 (temperature seasonality) loading positively and BIO6 (temperature of the coldest month) and BIO12 (mean annual precipitation) loading negatively (Figure 1.4 A). PC2 was mainly driven by BIO1 (mean annual temperature) and BIO15 (temperature seasonality) loading positively and BIO14 (precipitation of the driest month) loading negatively (Figure 1.4 B). Together, these axes separate species points with high precipitation and weak seasonality (negative on PC1 and PC2) from

those with high temperature and strong seasonality (positive on PC1 and PC2) (Figure 1.4 C).

Table 1.5. Eigenvalues, proportion of variation explained, and cumulative variation explained for principal component analysis (PCA) axes PC1-PC6 from a PCA of six climate variables (see Table 1.3).

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	3.100	1.734	0.520	0.355	0.252	0.038
Proportion of Variation	0.517	0.289	0.087	0.059	0.042	0.006
Cumulative Variation	0.517	0.806	0.893	0.952	0.994	1.000

3.2 Species-, genus-, and tribal- level niche breaths

Species-level BSI scores varied widely, although a BSI score of 3 is the most common (26.7% of species). Species with the lowest BSI values (BSI value = 1) tended to be restricted to extreme biomes, especially those from shrubland and grassy semi-desert in the Horn of Africa (e.g., beisa oryx *Oryx beisa*, dibatag *Ammodorcas clarkei*, and Grevy’s zebra *Equus grevyi*). Only four taxa – white rhino *Ceratotherium simum*, Guereza colobus *Colobus guereza*, African elephant *Loxodonta africana*, and greater kudu *Tragelaphus strepsiceros* – have BSI scores of 7, which was the highest BSI score in the dataset (Figure 1.5 A). Among genera considered here (see Table 1.1), *Equus* (3.5 ± 2.08), *Giraffa* (3.00), and *Kobus* (3.60 ± 1.34) have the lowest average BSI scores, while *Ceratotherium* (7.00) and *Loxodonta* (7.00) have the highest (Figure 1.6 A, Table 1.6). The remainder of genera have BSI scores between 4 and 6, with apex carnivores (*Crocuta*, *Panthera*) and large-bodied herbivores (*Diceros*, *Hippopotamus*) having higher BSI scores on average than medium-sized bovids and suids (e.g., *Aepyceros*, *Phacochoerus*). For tribes (Figure 1.6 D, Table 1.7), Antilopini and Hippotragini had the lowest average BSI scores (2.36 ± 1.21 and 2.50 ± 1.00 , respectively) and Bovini, represented only by the eurytopic African buffalo *Syncerus caffer*, had the highest

average BSI score (6.00). All other tribes have average BSI scores between 3 and 5, with primate tribes (Colobini, Papionini) being slightly more specialized in their biome niche breadth than bovid tribes (Aepycerotini, Alcelaphini, Reduncini, Tragelaphini).

Table 1.6. Genus-level niche breadth means and standard deviations (StDev) for the Inverse Simpson index, Biomic Specialization Index (BSI), and climatic multivariate variance (MVV).

Genus	Inv. Simpson		BSI		MVV	
	Mean	StdDev	Mean	StdDev	Mean	StdDev
<i>Aepyceros</i>	0.5	-	4	-	13.68	-
<i>Connochaetes</i>	0	0	4.5	0.71	9.19	6.53
<i>Damaliscus</i>	0	0	5	0	13.38	8.58
<i>Kobus</i>	0.08	0.17	3.6	1.34	8.26	5.8
<i>Tragelaphus</i>	0.47	0.19	4	1.94	14.94	9.7
<i>Giraffa</i>	0	-	3	-	25.07	-
<i>Hippopotamus</i>	0	-	5	-	20.49	-
<i>Hylo.-Kolpochoerus</i>	0.48	-	5	-	15.21	-
<i>Phaco.-Metridiochoerus</i>	0	0	4	1.41	13.12	9.09
<i>Panthera</i>	0.19	0.27	6	0	26.03	11.45
<i>Crocuta</i>	0	-	6	-	19.78	-
<i>Hyaena</i>	0.65	-	4	-	13.69	-
<i>Equus</i>	0.1	0.19	3.5	2.08	9.61	6.59
<i>Ceratotherium</i>	0	-	7	-	29.37	-
<i>Diceros</i>	0	-	6	-	25.94	-
<i>Theropithecus</i>	0.5	-	4	-	6.36	-
<i>Loxodonta</i>	0.65	-	7	-	29.23	-

Table 1.7. Tribal-level niche breadth means and standard deviations (StDev) for the Inverse Simpson index, Biomic Specialization Index (BSI), and climatic multivariate variance (MVV).

Tribe	Inv. Simpson		BSI		MVV	
	Mean	StdDev	Mean	StdDev	Mean	StdDev
Aepycerotini	0.5	-	4	-	13.68	-
Alcelaphini	0	0	4	1.55	12.25	9.66
Antilopini	0.39	0.2	2.36	1.21	5.56	3.35
Bovini	0.38	-	6	-	38.16	-
Hippotragini	0.33	0.24	2.5	1	9.55	3.76
Reduncini	0.04	0.13	4.22	1.3	11.95	8.63
Tragelaphini	0.47	0.19	4	1.94	14.94	9.7
Colobini	0.51	0.18	3	1.79	12.42	7.98
Papionini	0.72	0.1	3.12	1.54	9.43	5.15

Species-level climatic niche breaths based on MVV values varied from narrow-niche desert- (sand cat *Felis margarita* MVV = 0.09) and forest- (dryad monkey *Cercopithecus dryas* MVV = 0.20) specialists, to species widely distributed across Africa

(e.g., ratel *Mellivora capensis* MVV = 36.06, armadillo *Dasypus novaeboracae* MVV = 34.92).

The most common MVV values are between ~ 5-10, which accounts for ~ 35% of species (Figure 1.5 B). Genus-level MVV values ranged from montane specialist *Theropithecus* (6.36) to megaherbivores and apex carnivores with MVV values above 20: *Ceratotherium* (29.37), *Loxodonta* (29.23), *Panthera* (26.03 ± 11.45), *Diceros* (25.94), *Giraffa* (25.07), and *Hippopotamus* (20.49) (Figure 1.6 B, Table 1.6). Tribal MVV values ranged from specialist Antilopini (5.56 ± 3.35) to generalist Bovini (38.16), with all other tribes having MVV values between 9 and 15 (Figure 1.6 E, Table 1.7).

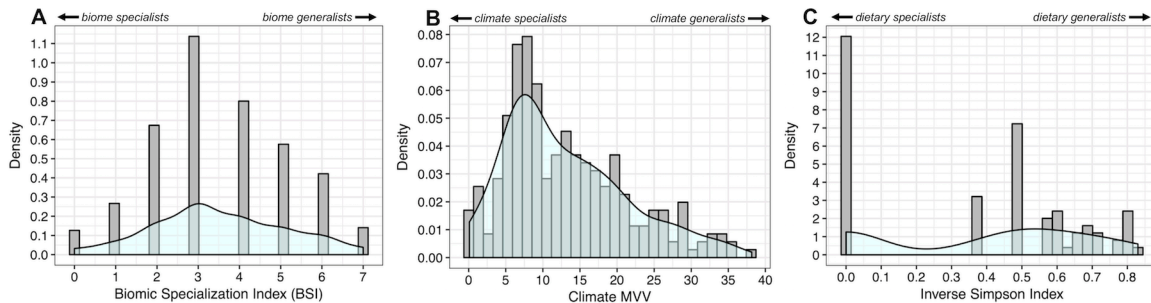


Figure 1.5. Density plots of species-level niche breadth data: A, Biomic Specialization Index (BSI); B, climatic multivariate variance (MVV); C, Inverse Simpson Index.

Species-level Inverse Simpson Indices were dominated by taxa with specialized diets, as 34.5% of species have Inverse Simpson values of 0.00 (Figure 1.5 C). These species are mainly herbivores that are obligate grazers (e.g., hartebeest *Alcelaphus buselaphus*, hirola *Beatragus hunteri*) or browsers (e.g., gerenuk *Litocranius walleri*, giraffe *Giraffa camelopardalis*), although apex predators (e.g., lion *Panthera leo*) that specialize on large-bodied prey also have Inverse Simpson values of 0.00. *Papio* spp. have the highest Inverse Simpson values (yellow baboon *Papio cynocephalus* = 0.81, Guinea baboon *P. papio* = 0.81, Chacma baboon *P. ursinus* = 0.83), followed closely by other papionin species such as agile mangabey *Cercocebus agilis* and mandrill

Mandrillus sphinx. All remaining species have Inverse Simpson values from 0.38-0.80 and have mid-range dietary niche breadths. Genera show similar patterns to species-level results (Figure 1.6 C, Table 1.6), with genera having Inverse Simpson Index values of 0.00 being mainly obligate grazing or browsing herbivores. Mixed-feeding *Loxodonta* (0.65) and generalist *Hyaena* (0.65) had the highest Inverse Simpson values among genera. For tribes (Figure 1.6 F, Table 1.7), grazing Alcelaphini (0 ± 0.00) and Reduncini (0.04 ± 0.13) had the lowest Inverse Simpson Index value (0.00), while dietarily generalized Papionini had the highest (0.72 ± 0.10) followed by Colobini (0.51 ± 0.18).

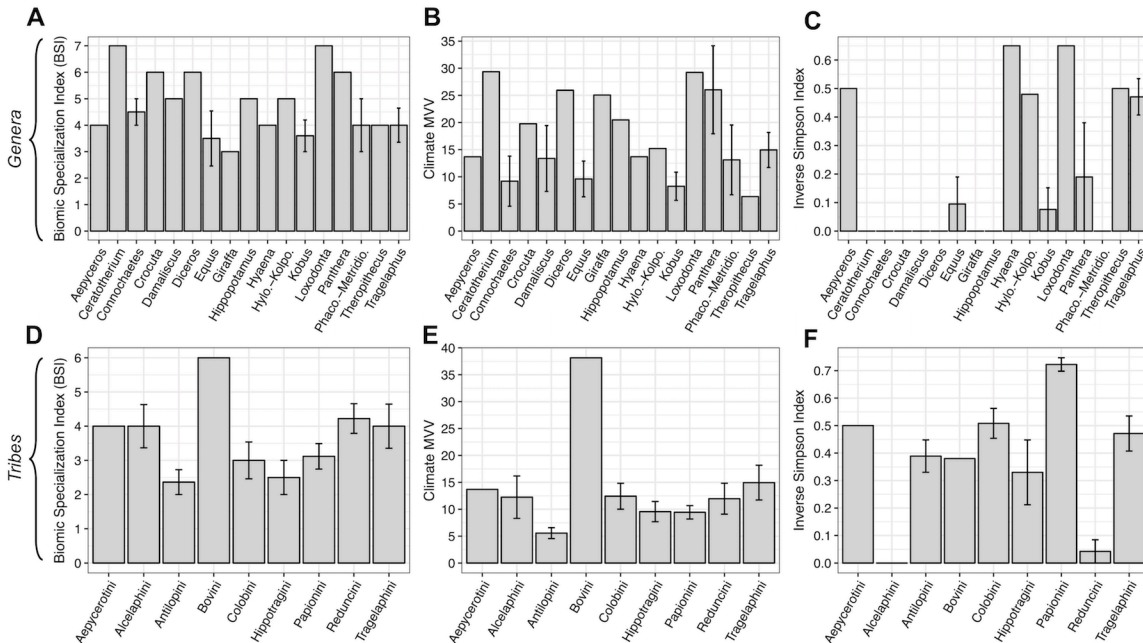


Figure 1.6. Genus- (A-C) and tribal- (D-F) level barplots of niche breadth data. Error bars on barplots represent standard errors (SEs).

3.3 Niche breadth relationships (Q₁)

Genus-level BSI has a strong positive relationship with MVV (Figure 1.7 A), while both BSI ($r = 0.02$) and MVV ($r = 0.35$) are weakly related to Inverse Simpson Indices (Figure 1.7 B-C). Genera that have narrow BSI values (< 4.0) have narrow

Inverse Simpson values (< 1.5), but above a BSI of 4.0 Inverse Simpson values are highly variable. Tribal-level patterns are broadly similar (Figure 1.7 D-F), with BSI and MVV having a strong positive relationship ($r = 0.78$) and Inverse Simpson Indices being weakly related to BSI ($r = -0.5$) and MVV ($r = -0.17$).

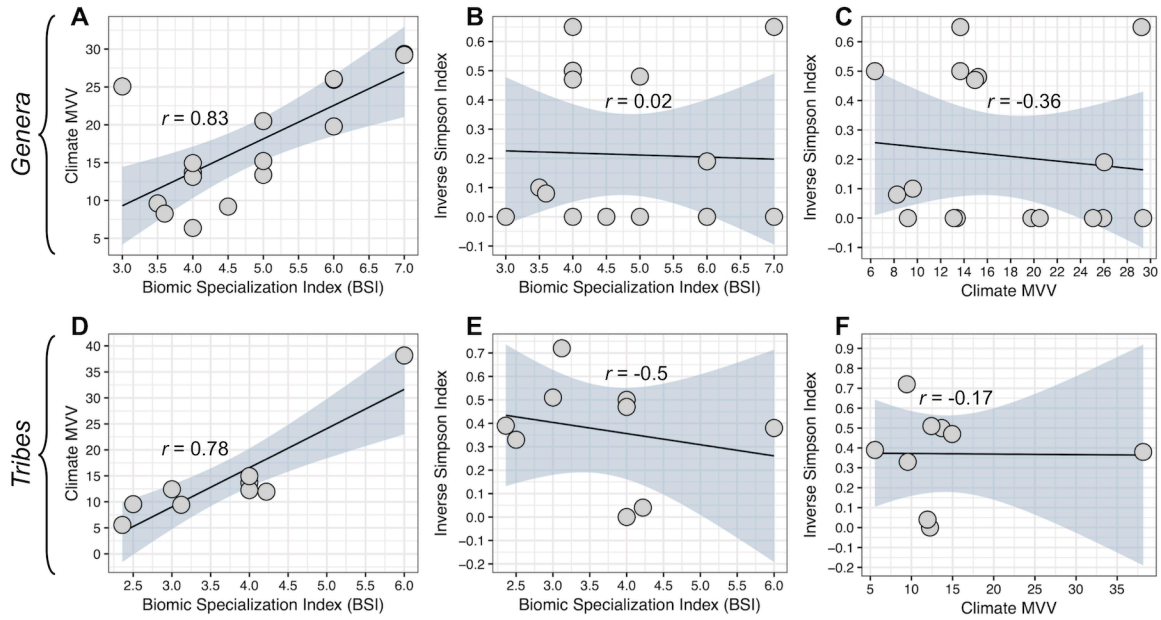


Figure 1.7. Genus- (A-C) and tribal- (D-F) level scatterplots for mean niche breadth correlations. For both genera and tribes, the Biomic Specialization Index (BSI) and climatic multivariate variance (MVV) are highly correlated, but both have weak relationships to the Inverse Simpson Index. Blue shading represents 95% confidence intervals.

3.4 Range size-niche breadth relationships (Q_2)

Genus-level range size-niche breadth relationships are shown in Figure 1.8 (B-D) and Table 1.8. Range size is a significant positive predictor of both BSI ($r^2 = 0.423$, $p = 0.005$) and MVV ($r^2 = 0.388$, $p = 0.008$). Inverse Simpson Indices are unrelated to range size ($r^2 = 0.036$, $p = 0.468$). Tribal-level range size-niche breadth relationships are shown in Figure 1.8 (F-H) and Table 1.9. As with genus-level results, range size is a significant

positive predictor of both BSI ($r^2 = 0.765, p = 0.002$) and MVV ($r^2 = 0.873, p < 0.001$), while Inverse Simpson Indices are unrelated to range size ($r^2 = 0.081, p = 0.785$).

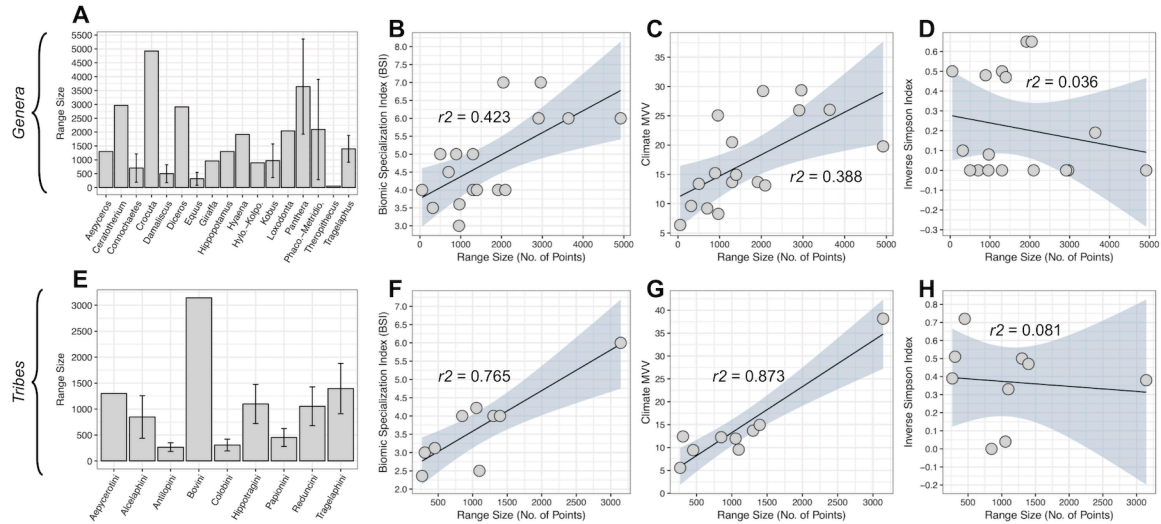


Figure 1.8. Genus- (A-D) and tribal- (E-H) level barplots of range size and scatterplots of mean range size-niche breadth correlations. For both genera and tribes, the Biomic Specialization Index (BSI) and climatic multivariate variance (MVV) are highly correlated with range size; the Inverse Simpson Index has a weak relationship to range size. Error bars on barplots represent standard errors (SEs); blue shading represents 95% confidence intervals.

Table 1.8. Genus-level OLS models predicting niche breadth measures from geographic range size (number of points sampled used as range size proxy).

Model	Estimate	Std. Error	t-value	p-value	r^2
BSI~Range Size	0.001	0.000	3.316	0.005	0.423
MVV~Range Size	0.004	0.001	3.082	0.008	0.388
Inv. Simpson~Range Size	0.000	0.000	-0.744	0.468	0.036

Table 1.9. Tribal-level OLS models predicting niche breadth measures from geographic range size (number of points sampled used as range size proxy).

Model	Estimate	Std. Error	t-value	p-value	r^2
BSI~Range Size	0.001	0.000	4.770	0.002	0.765
MVV~Range Size	0.010	0.001	6.943	0.000	0.873
Inv. Simpson~Range Size	0.000	0.000	-0.284	0.785	0.081

3.5 Phylogenetic signal of niche breadths (Q₃)

Niche breadth metrics showed significant moderate to high phylogenetic signal (Figure 1.9, Table 1.10), with BSI ($\lambda = 0.429$, $p = 0.019$) and MVV ($\lambda = 0.504$, $p = 0.021$) being less conserved than Inverse Simpson Indices ($\lambda = 0.876$, $p < 0.001$). Phylogenetic signals of BSI and MVV data are unlikely to be driven solely by geographic effects, as comparisons of sister pairs from our dataset indicate weak relationships between range overlap (BSI $r = 0.086$, MVV $r = 0.090$) and median range distances (BSI $r = 0.314$, MVV $r = 0.554$) and niche similarity (Figure 1.10 A-D).

Table 1.10. Phylogenetic signal based on Pagel’s λ for niche breadth measures. For Pagel’s λ , the null hypothesis (no phylogenetic signal) $\lambda=0$, whereas a high λ value close to 1 indicates a high phylogenetic signal and that the trait of interest is conserved across the phylogeny of species.

Niche Breadth Metric	λ	Log. likelihood	p-value
Biomic Specialization Index (BSI)	0.429	236.133	0.019
Climatic multivariate variance (MVV)	0.504	106.006	0.021
Inverse Simpson Index	0.876	408.800	0.000

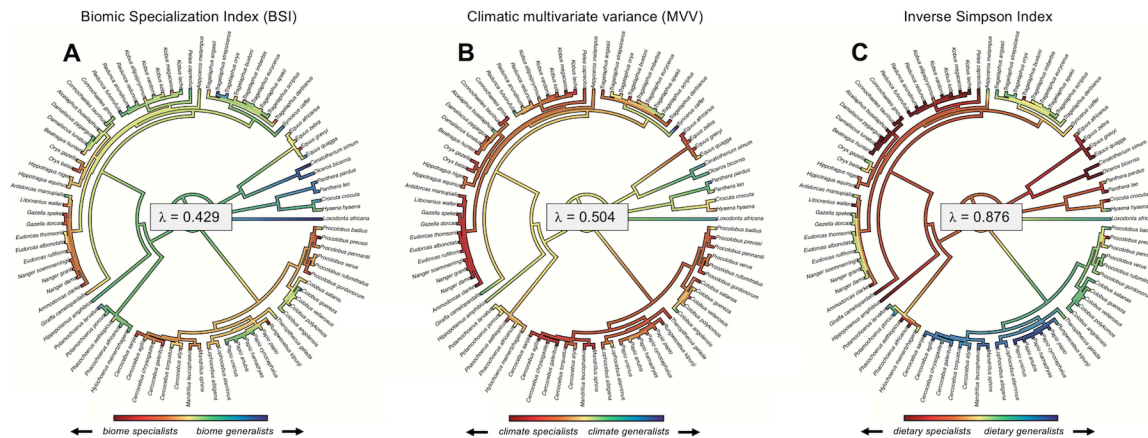


Figure 1.9. Phylogenetic signal (Pagel’s λ) of the Biomic Specialization Index (A), climatic multivariate variance (B), and Inverse Simpson Index (C) for species used in genus- and tribal-level analyses. For Pagel’s λ , the null hypothesis (no phylogenetic signal) $\lambda=0$, whereas a high λ value close to 1 indicates a high phylogenetic signal and that the trait of interest is conserved across the phylogeny of species. Among niche breadth measures, the Inverse Simpson Index has the highest phylogenetic signal ($\lambda = 0.876$).

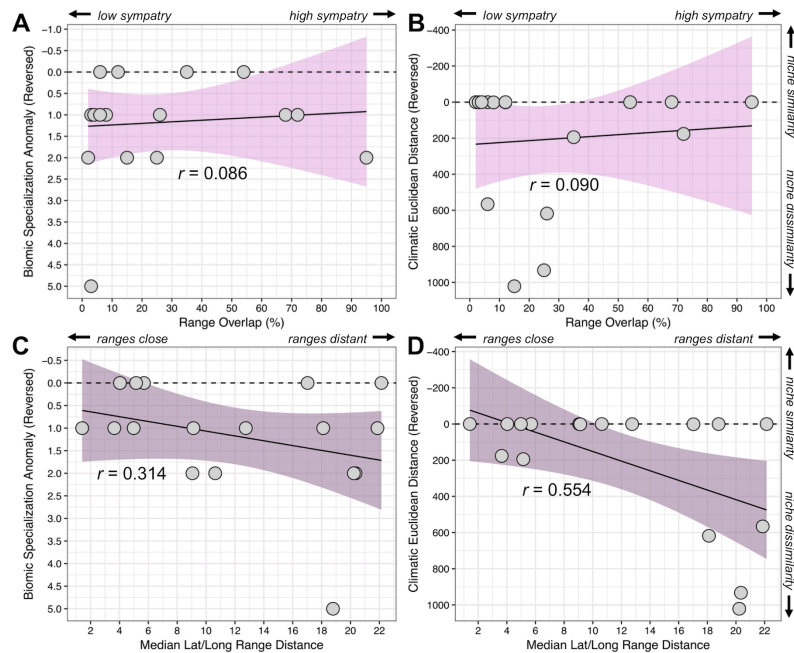


Figure 1.10. Scatter plots of range overlap (A-B) and median range distances (C-D) against niche breadth distances for sister species pairs based on the Faurby and Svenning (2015b) phylogeny. Purple shading represents 95% confidence intervals; black dotted lines represent complete niche similarity between sister species. Note that y-axes are reversed so that the null expectation is a positive relationship between niche similarity and range overlap (A-B) or a negative relationship between niche similarity and range distance (C-D).

3.6 Genus- and tribal- level turnover rates

Genus-level origination rates varied significantly (Figure 1.11 A, Table 1.11), with *Theropithecus* (0.10 ± 0.41) having low rates and *Equus* (1.19 ± 1.48) and *Tragelaphus* (0.83 ± 1.05) having high rates. Among tribes (Figure 1.11 C, Table 1.12), Alcelaphini has by far the highest origination rate (1.43 ± 1.51), with Hippotragini (0.28 ± 0.88) having the lowest. All other tribes have origination rates ~ 0.40 - 0.80 . For genera, *Equus* (0.79 ± 1.10) has the highest extinction rate, while *Diceros* (0.20 ± 0.74) has the lowest. All other genera have extinction rates ~ 0.20 - 0.70 . Tribal-level extinction rates are highest for Alcelaphini (1.16 ± 1.02) and lowest for Hippotragini (0.28 ± 0.88). All other tribes have extinction rates ~ 0.30 - 0.66 .

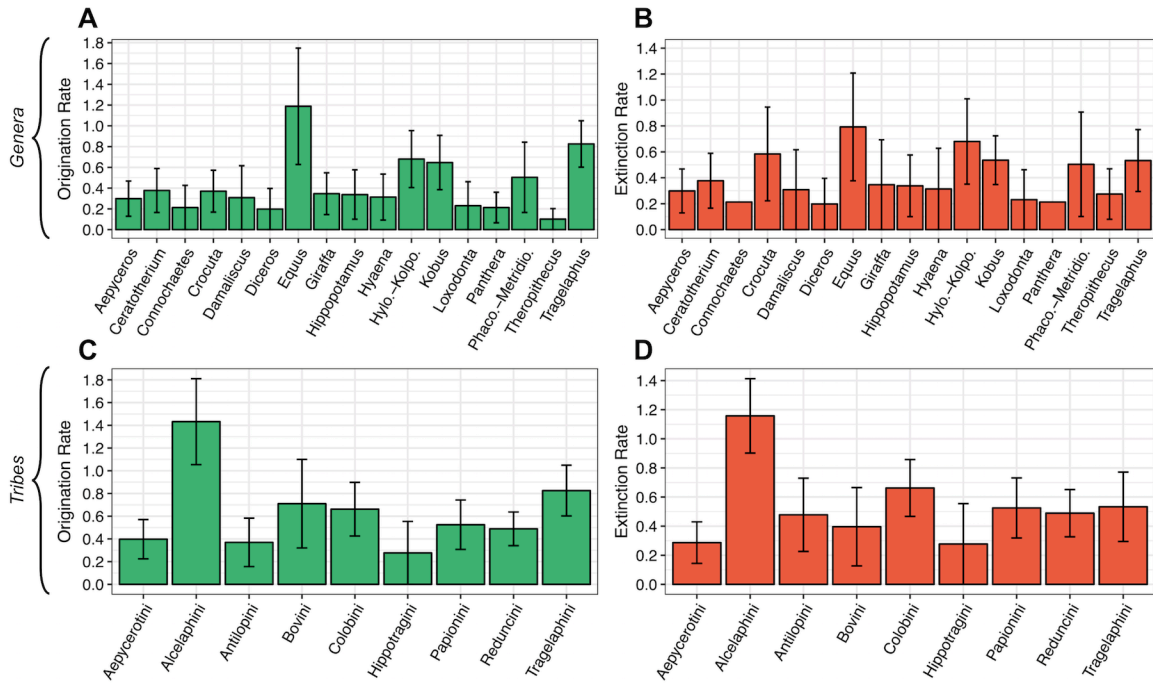


Figure 1.11. Genus- (A-B) and tribal- (C-D) level barplots of origination and extinction rates based on Foote’s (2000) metrics. Error bars on barplots represent standard errors (SEs).

Table 1.11. Genus-level mean origination (Orig) and extinction (Ext) rates and their standard deviations (StdDev) based on a 7-Myr record from eastern Africa.

Genus	Orig. Mean	Orig. StdDev	Ext. Mean	Ext. StdDev
<i>Aepyceros</i>	0.30	0.83	0.30	0.83
<i>Connochaetes</i>	0.21	0.77	0.21	0.77
<i>Damaliscus</i>	0.31	0.92	0.31	0.92
<i>Kobus</i>	0.65	1.31	0.54	0.94
<i>Tragelaphus</i>	0.83	1.05	0.53	1.12
<i>Giraffa</i>	0.35	0.80	0.35	1.39
<i>Hippopotamus</i>	0.34	0.86	0.34	0.86
<i>Hylo.-Kolpochoerus</i>	0.68	1.13	0.68	1.36
<i>Phaco.-Metridiochoerus</i>	0.50	1.12	0.50	1.34
<i>Panthera</i>	0.21	0.53	0.21	0.77
<i>Crocuta</i>	0.37	0.73	0.58	1.30
<i>Hyaena</i>	0.31	0.83	0.31	1.17
<i>Equus</i>	1.19	1.48	0.79	1.10
<i>Ceratotherium</i>	0.38	0.92	0.38	0.92
<i>Diceros</i>	0.20	0.74	0.20	0.74
<i>Theropithecus</i>	0.10	0.41	0.27	0.78
<i>Loxodonta</i>	0.23	0.80	0.23	0.80

Table 1.12. Tribal-level mean origination (Orig) and extinction (Ext) rates and their standard deviations (StdDev) based on a 7-Myr record from eastern Africa.

Tribe	Orig. Mean	Orig. StdDev	Ext. Mean	Ext. StdDev
Aepycerotini	0.40	0.87	0.29	0.71
Alcelaphini	1.43	1.51	1.16	1.02
Antilopini	0.37	0.83	0.48	0.97
Bovini	0.71	1.46	0.40	1.01
Hippotragini	0.28	0.88	0.28	0.88
Reduncini	0.49	0.74	0.49	0.81
Tragelaphini	0.83	1.05	0.53	1.12
Colobini	0.66	1.13	0.66	0.94
Papionini	0.53	1.00	0.53	0.94

3.7 Turnover rates and turnover-niche breadth relationships (Q4)

Genus-level turnover rates were poorly predicted from niche breadth measures (Figure 1.12 A-B, Table 1.13). Origination rates ($r^2 = 0.112$) were negatively related to both MVV (coeff. est. = -0.014, AICc = 0.089) and Inverse Simpson Indices (coeff. est. = -0.152, AICc = 0.185), although Inverse Simpson Indices are a better overall predictor than MVV. Extinction rates ($r^2 = 0.159$) were negatively related to MVV (coeff. est. = -0.009, AICc = 0.316) and Inverse Simpson Indices (coeff. est. = -0.151, AICc = 0.204), with MVV being the better predictor overall.

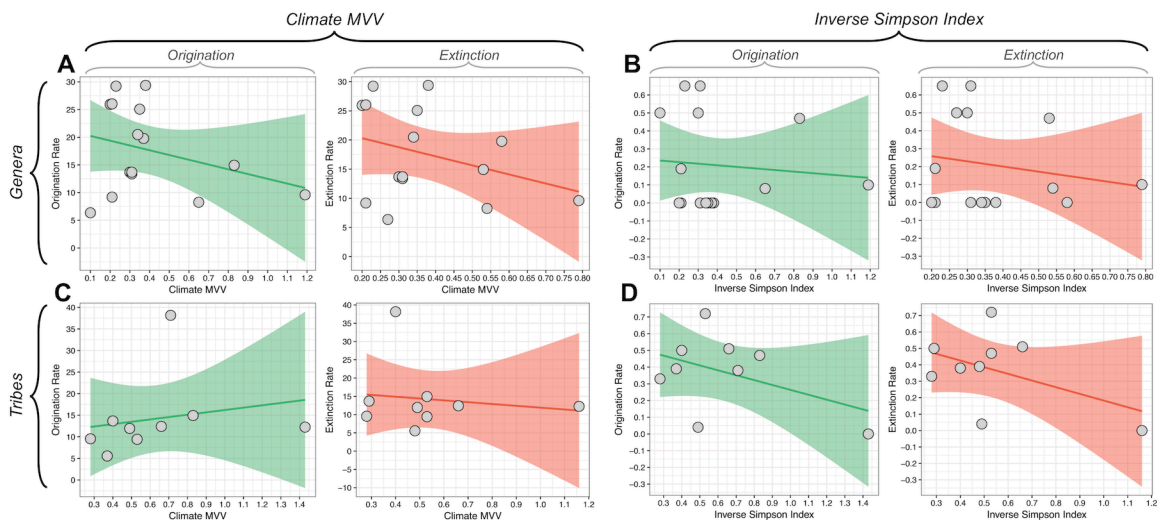


Figure 1.12. Genus- (A-B) and tribal- (C-D) level scatterplots of origination and extinction rates as a function of niche breadth measures (MVV, Inverse Simpson Index); green and red shading represent 95% confidence intervals.

Table 1.13. Genus-level multiple regression results and AICc weights (i.e., overall importance) built from models in the package *MuMIn* (Bartoń, 2018).

Origination Model	Estimate	Std. Error	t-value	p-value	AICc weight
Climatic multivariate variance (MVV)	-0.014	0.012	-1.180	0.261	0.089
Inverse Simpson Index	-0.152	0.298	-0.511	0.618	0.185
Overall model: adj. r^2 =-0.036, r^2 = 0.112, F =0.758, p =0.489					
Extinction Model	Estimate	Std. Error	t-value	p-value	AICc weight
Climatic multivariate variance (MVV)	-0.009	0.007	-1.340	0.205	0.316
Inverse Simpson Index	-0.151	0.172	-0.878	0.397	0.204
Overall model: adj. r^2 =0.019, r^2 =0.159, F =1.142, p =0.352					

Table 1.14. Tribal-level multiple regression results and AICc weights (i.e., overall importance) built from models in the package *MuMIn* (Bartoń, 2018).

Origination Model	Estimate	Std. Error	t-value	p-value	AICc weight
Climatic multivariate variance (MVV)	0.009	0.016	0.586	0.579	0.089
Inverse Simpson Index	-0.665	0.537	-1.238	0.262	0.185
Overall model: adj. r^2 =-0.013, r^2 =0.240, F =0.949, p =0.438					
Extinction Model	Estimate	Std. Error	t-value	p-value	AICc weight
Climatic multivariate variance (MVV)	-0.005	0.012	-0.390	0.710	0.077
Inverse Simpson Index	-0.541	0.409	-1.321	0.235	0.206
Overall model: adj. r^2 =-0.015, r^2 =0.239, F =0.941, p =0.441					

As with genera, tribal-level turnover rates were poorly predicted from niche breadth measures (Figure 1.12 C-D, Table 1.14). Origination rates ($r^2 = 0.240$) were positively related to MVV (coeff. est. = 0.009, AICc = 0.089) and negatively related to the Inverse Simpson Index (coeff. est. = -0.665, AICc = 0.185), with the latter being the best predictor. Extinction rates ($r^2 = 0.239$) were negatively related to both MVV (coeff. est. = -0.005, AICc = 0.077) and Inverse Simpson Indices (coeff. est. = -0.541, AICc = 0.206), with Inverse Simpson Indices being the best predictor.

4. Discussion

Overall, our analyses of niche breadth-turnover relationships fail to support Vrba's (1980, 1987, 1992, 1995a, 1999) RUH. We find no evidence to support the claim that climatic or dietary niche breadth is significantly related to origination and extinction rates across several genera and tribes of large-bodied African mammals (Tables 1.13-14;

Figure 1.12). This may be due to the fact that niche breadth is unimportant in driving divergent diversification histories of clades, or that different dimensions of niche breadth interact antagonistically and more or less cancel out one another. Indeed, we found that dietary niche breadth (measured by the Inverse Simpson Index) is poorly predicted by measures of biomic specialization (BSI) or climatic niche breadth (climate MVV) (Figure 1.7). Despite failure to support the RUH overall, several important results have emerged from our study that we discuss below.

4.1 Niche breadth correlates

We predicted that different dimensions of ecological niche breadth would be positively related to one another. That is, dietary generalists would also be biome and climatic generalists, whereas dietary specialists would be biome and climate specialists. In contrast to our predictions, we found that dietary and biomic/climatic dimensions of niche breadth were decoupled from one another (the latter are related because they are inherently geographic in nature). Our finding is significant because many studies broadly assign species into a specialist versus generalist dichotomy. For example, Baselga et al. (2011), Gomez-Rodriguez et al. (2015), and Rolland and Salamin (2016) used climatic niche breadth (often the range (maximum-minimum value) of climate variables across a species' distribution) as an overall measure of ecological niche breadth. Our results suggest that estimates of climatic niche breadth do not fully capture the overall breadth of a species' ecological niche and this should caution against using one dimension as a proxy for others, at least for large-bodied mammals.

The mismatch between dietary and biomic/climatic measures of ecological niche breadth may be due to differing limits on Grinnellian and Eltonian dimensions of a

species' niche (Soberón, 2007). The Grinnellian dimension of a species' niche emphasizes non-interactive environmental conditions necessary for species survival, such as large-scale climatic variables (Grinnell, 1917). Grinnellian niche dimensions influence species distributions directly through thermoregulation and indirectly through controls on the distribution of preferred habitats. For endothermic large-bodied mammals, thermoregulatory constraints are unlikely to be a major influence on species distributions (Khaliq et al., 2014), although this is undoubtedly important for ectothermic vertebrates, such as amphibians and reptiles (Sunday et al., 2012). Therefore, Grinnellian dimensions of niche breadth for mammals are most likely controlled by the distribution of preferred habitats or biomes, which results in abiotic filtering of species and shapes the size and geometry of their geographical ranges (Slatyer et al., 2013). On the other hand, the Eltonian dimension of a species' niche is defined as a species' "relation to food and enemies" and resource-consumer dynamics, therefore emphasizes its interactions with other co-occurring species in a community (Elton, 1927). Thus, Eltonian niche dimensions are primarily influenced by competitive processes such as competitive exclusion over ecological timescales and niche partitioning and divergence over evolutionary timescales (Holt, 1987; Pianka, 1981).

It is possible that the different drivers of Grinnellian and Eltonian niche dimensions, which in our study were captured by BSI and Climate MVV measures and Inverse Simpson Indices, respectively, are responsible for the mismatch between these niche breadth measures. Likewise, it is also important to consider the potential offset between species realized and fundamental niches: the realized niche is the set of climatic or environmental conditions within which a species is currently found or its current breadth of diet, whereas the fundamental niche is the full range of conditions within

which it could persist or the full range of dietary food items it could consume (Wiens et al., 2010). Limitations on a species' realized niche are well-known to be shaped by a variety of factors, including dispersal limitation (Beaudrot and Marshall, 2011) and interspecific competition (Dormann et al., 2010). For example, if abiotic filtering and dispersal limitation are weaker than competitive processes in structuring species distributions for large-bodied mammals, species may fill more of their fundamental climatic/environmental niches but occupy only a subset of their fundamental dietary niches. The species' realized dietary niche may only expand when a competitor becomes removed from the community (either through extirpation or extinction), an ecological phenomenon known as 'trophic release' (Estes et al., 2011). Trophic release has been extensively well-documented in large-bodied mammals, such as coyote (*Canis latrans*) dietary niche breadth expansion during wolf (*Canis lupus*) extirpation in Yellowstone National Park, Wyoming (Ripple et al., 2014). Likewise, another study of coyotes in California showed significant differences in niche breadth and prey preferences between populations in wildland versus human settlements. In wildlands, coyotes consumed relatively larger prey such as mule deer (*Odocoileus hemionus*), whereas those in human settlements focused on a wider range of micromammal prey (Smith et al., 2018). Such studies of dietary plasticity underscore the fact that our observations may be gross underestimates of their fundamental dietary niches and therefore bias our interpretations of this important ecological aspect of a species.

With respect to climatic and environmental niche breadth, Varela et al. (2009, 2010) used the fossil record of spotted hyenas (*Crocuta crocuta*) to show that extant species may only occupy a small subset of their realized climatic niches today. They found that species distribution models (SDMs) built on the present-day sub-Saharan

African distribution of *Crocuta* failed to hindcast its paleo-distribution, which included much of Eurasia during the Last Interglacial ~ 126,000 years ago (Varela et al., 2009, 2010). In a similar study, Davis et al. (2014) found that SDMs of present-day small-bodied North American mammals poorly predicted their known Last Glacial Maximum (~ 22,000 years ago) fossil records, suggesting that present-day distributions may not encompass the full range of climatic or environmental conditions within which a species can survive. Rowan et al. (2015) also showed similar biases in hindcast Last Glacial Maximum species distributions for plains zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) in Africa. Collectively, these results suggest that mammal species may have very wide climatic and environmental fundamental niches and that analyses of abiotic niche breadths based on present-day distributions may systematically undersample a species' true niche breadth.

The factors that determine why a species range does not fully fill environmentally suitable areas are likely multilayered and multiplicative. First, as in the case of spotted hyenas, extinctions and other deep-time processes play a major role in shaping current distributions and therefore niche estimates from them (Pulliam, 2000). It is well documented for Pleistocene glaciation events that, despite the return of suitable climatic conditions, species may not recolonize their former ranges because of dispersal limitation, such as bands of unsuitable climates, or the appearance of novel biotic interactions, such as new competitors in the region (Svenning and Skov, 2007; Svenning et al., 2015). In a similar vein, human-induced extirpations may also lead to species occupying a smaller subset of their fundamental niche. Martinez-Freiria et al. (2016) showed that anthropogenic encroachment on species ranges since the 1970s leads to much smaller estimates of the climatic niche breadth of African elephants (*Loxodonta*

africana) and giraffes (*Giraffa camelopardalis*) than their historical distributions (pre-1970).

4.2 Niche breadth-range size relationships

Many macroecological studies of niche breadth assume that ecologically generalized species have larger ranges than ecological specialists (Gaston and Blackburn, 2000; Gomez-Rodriguez et al., 2015; Rolland and Salamin, 2016). This oft-made assumption is largely rooted in an influential paper by Brown (1984), who argued that the broad niches of generalist species allow a greater array of resources to be utilized and that this, in turn, allows viable populations to persist in a greater number of environments. These population- and habitat- level processes ‘scale up’ to regional- and continental- levels and result in generalist species having larger geographic ranges than specialist species (Brown, 1984). In contrast to these predictions, we found that only geographically-based niche breadth variables (BSI and Climate MVV) were positively related to range size, which is intuitive: a larger range is likely to span a greater variety of biomes or climates than a smaller one. On the other hand, Inverse Simpson Indices had no relationship to range size (Figure 1.8), with both dietary generalists and specialists having small to large ranges.

Although there are few studies of mammals that consider multiple aspects of niche breadth to which we can compare our results, our findings are congruent with those of Laube et al. (2013) for European passerine birds. They found that although habitat niche breadth had a strong positive relationship to range size, dietary niche breadth was unrelated. Laube et al. (2013) proposed that dietary niche breadth may play a lesser role in species’ ranges because different food resources can be found within a single habitat,

whereas multiple habitat types do not often co-occur within the same area. This is similar to Vrba's (1987) example for armadillos (*Oryzomys afer*), which exclusively consume ants and termites (and are therefore towards the most extreme of dietary specialists) but are found in a wide variety of habitats ranging from semi-desert to woodland-forest mosaics because these food items are widely distributed across sub-Saharan Africa (Kingdon, 2015). Thus, armadillos are dietary specialists but habitat and climate generalists. Such anecdotal data suggest that it is important to test the degree to which measures of species' niche breadths are congruent across different dimensions of their ecologies and that different niche breadth axes (e.g., diet, habitat, climate) may not necessarily correlate to one another, as we found.

Likewise, a meta-analysis of studies by Slatyer et al. (2013) across multiple plant and animal groups found that different axes of niche breadth had divergent relationships to range size. Across 64 studies, they found that measures of climatic ($z = 0.49$) and habitat ($z = 0.45$) breadths had large and significant effect sizes on geographic range size (measured by Fisher's z), whereas dietary breadth was poorly and non-significantly predicted by range size ($z = 0.28$). For the only major study of African mammals, Hernandez-Fernandez and Vrba (2005) found a strong relationship between BSI and range size (measured as the latitudinal extent of a species' range following Stevens (1989)), but no relationship between body mass and latitudinal range, further suggesting differential drivers of niche breadth on range size. Their correlation between BSI and latitudinal range size is somewhat unsurprising, as biomes in Africa are mainly determined by latitudinal climatic gradients (White, 1983). Although in our analyses (which are more precise because they consider both latitudinal and longitudinal aspects of

a taxon's range and overall area), we also found a strong correlation between BSI and range size.

4.3 Niche breadth conservatism

Based on previous studies (Wiens and Graham, 2005; Wiens et al., 2010), we predicted that measures of species' niche breadths would have a high phylogenetic signal, meaning that they have been conserved throughout the evolutionary history of clades. Clades must satisfy the assumption of phylogenetic niche conservatism if niche breadth differences are to be used to explain synchronous turnover patterns in the face of climatic- or environmental- change in the fossil record (Vrba, 1987). Here, we found that climatic, biomic, and dietary dimensions of large-bodied African mammal niche breadths show moderate to high phylogenetic conservatism, with dietary niche breadth conservatism being the strongest ($\lambda = 0.876$) followed by climatic ($\lambda = 0.504$) and biomic ($\lambda = 0.429$) niche breadths (Figure 1.9).

Olalla-Tarraga et al. (2016) provides the only other study that tests for phylogenetic niche conservatism in mammalian dietary niche breadth. Using two major mammal dietary databases, EltonTraits (Wilman et al., 2014) and MammalDIET (Kissling et al. 2014), they calculated dietary niche breadth using two measures: 1) the total number of dietary categories consumed (a discrete measure of dietary diversity) and 2) the standardized Levin's Index of dietary diversity, which is a continuous measure and analogous to the Inverse Simpson Index. Although Olalla-Tarraga and colleagues (2016) found that dietary niche breadths were similar among closely related species, their statistical measure of phylogenetic signal (Blomberg's K) failed to support niche conservatism, which contrasts with the results of our study wherein we found mammalian

dietary niche breadths to be highly conserved. We believe these differences, however, are likely methodological in nature and relate to disparities in: 1) the taxonomic scope of analysis; 2) the source and accuracy of dietary data; 3) the phylogenetic signal metric used.

First, Olalla-Tarraga et al. (2016) considered all extant mammal species for which they could obtain dietary data (1730 species shared between EltonTraits and MammalDIET datasets). Our dataset, given our focus on sub-Saharan Africa and tribes and genera largely endemic to it, is considerably smaller (87 species). From random sampling alone, it is possible for differences to arise in the results from our datasets. Furthermore, our measures of dietary niche breadth show varied correspondence to those generated from the EltonTrait and MammalDIET datasets of Olalla-Tarraga et al. (2016) as shown in Figure 1.13. A species-by-species comparison of our Inverse Simpson Indices of dietary breadth most closely matches dietary breadth metrics generated from EltonTraits, whether these be Levin's Indices (Figure 1.13A) or counts of the number of dietary categories consumed (Figure 1.13B); most of the differences between our dataset and EltonTraits come from species with very low dietary diversity (Inverse Simpson Indices = 0.00). Dietary breadth data from MammalDIET, however, were poorly congruent with our Inverse Simpson Indices (Figure 1.13C), suggesting that differences among dietary databases may account for the divergent results between our study and that of Olalla-Tarraga et al. (2016). We consider our estimates of niche breadth to be more precise as they were compiled from the literature by hand versus error-prone 'big data' databases (e.g., Borries et al., 2013) that often contain a significant amount of imputed trait data. Similarly, the particular phylogenetic signal metric chosen may also underlie differences in the results of the studies. Here, we used Pagel's λ , whereas Olalla-Tarraga

and colleagues (2016) used Blomberg’s K . Although these metrics are related (e.g., they estimate phylogenetic signal relative to a Brownian Motion evolution), their efficacy in inferring phylogenetic niche conservatism differs (Cadotte and Davies, 2016), with Pagel’s λ often outperforming other metrics (Münkemüller et al., 2012). Given these differences between our study and that of Olalla-Tarraga et al. (2016), we conclude that mammalian dietary niche breadth is characterized by a relatively high phylogenetic signal.

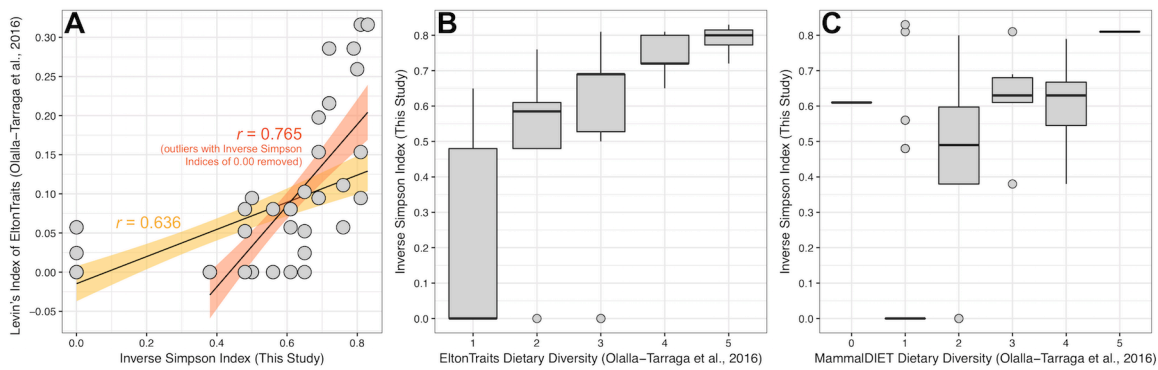


Figure 1.13. Comparisons of Inverse Simpson Indices of mammalian dietary niche breadth calculated for this study with different niche breadth datasets and measures from Olalla-Tarraga et al. (2016). For EltonTraits data, a species-by-species comparison of Levin’s Index of dietary diversity (A) and counts of the number of dietary categories consumed (B) are broadly similar to our Inverse Simpson Indices; the few outliers are mainly species with Inverse Simpson Indices of 0.00 but higher estimates of dietary diversity based on EltonTraits. Measures of dietary niche breadth based on MammalDIET were poorly congruent with our Inverse Simpson Indices (C).

The moderate phylogenetic signal ($\lambda = 0.429-0.504$) in BSI and Climate MVV requires special consideration because of the geographical nature of these variables – it is possible that a phylogenetic signal in BSI and MVV may arise simply as a product of distributional overlap and may therefore be an artifact of geography and not a real ecological signal (Freckleton and Jetz, 2009). In our study, however, we showed that closely related species share similar biomic and climatic niche breadths despite having

distant and largely non-overlapping ranges (Figure 1.10). We therefore propose that the moderate phylogenetic niche conservatism in mammalian environmental niches is a ‘true’ ecological pattern, as found in other studies (e.g., Cooper et al., 2011; Duran et al., 2013; Olalla-Tarraga et al., 2011). The lower phylogenetic signal for BSI and MVV data compared to Inverse Simpson Indices may indicate more heterogeneity in filling of environmental fundamental niche space than dietary niche space. If so, this suggests that the evolutionary trajectories of Eltonian and Grinnellian niche dimensions in mammals have been largely decoupled (e.g., Larson et al., 2010).

4.4 Turnover-niche breadth relationships

Following Vrba’s (1987) RUH, we predicted that specialist species would have higher rates of macroevolutionary turnover (origination and extinction) than generalist species, because the broad niches of the latter have buffered them from range fragmentation and extinction during environmental change. Our analyses of large-bodied African mammals found no support for this hypothesis. This may be because niche breadth is unimportant in shaping the diversification histories of clades, or that the different dimensions of niche breadth (dietary, biomic, and climatic) and range size interact antagonistically and/or counteract one another. For example, in contradiction to Vrba’s (1987) hypothesis, it is possible that the larger ranges of generalist species provide greater opportunities for vicariance and allopatric speciation, which increases both origination and extinction rates (Rolland and Salamin, 2016). Likewise, niche breadth might positively influence diversification rates if wider niches buffer species from extinction and therefore permit greater opportunity to speciate, whereas higher extinction rates in specialist species impede diversification (Gomez-Rodriguez et al., 2015). We

consider the latter scenario unlikely, however, because we found origination rates (and extinction rates) to be unrelated to niche breadth measures.

There are a handful of studies with which we can compare our results. For dietary niche breadth, Price et al. (2012) analyzed the impact of trophic mode on macroevolutionary rates across all extant mammals and found that herbivores diversified the fastest and omnivores the slowest, with carnivores being intermediate. Dietary transitions towards omnivory were related to lower diversification rates, as predicted by the RUH, suggesting that omnivory may be a macroevolutionary sink in mammals. Burin et al. (2016) found a similar result for a global database of birds, suggesting potential universality of this pattern among vertebrates. For climatic and biomic data, Rolland and Salamin (2016) found that climatic specialization was positively related to diversification rates across three major vertebrate clades (amphibians, birds, mammals), and similar results were reported for ruminants (Cantalapiedra et al., 2011), amphibians (Gomez-Rodriguez et al., 2015), and beetles (Baselga et al., 2011) in smaller studies. Together, these studies support the central tenets of the RUH while our analyses do not. We discuss several potential explanations for this difference below.

First, it is important to note that the previous studies relied solely on molecular estimates of diversification, whereas our study estimated turnover rates from the fossil record. Major discrepancies in diversification estimates from molecular versus fossil data are well-known (Hunt and Slater, 2016). For example, molecular estimates of diversification from time-calibrated phylogenies may be highly influenced by present-day species richness patterns as they are solely based on the relationship between clade age and clade diversity (Rabosky, 2009). On the other hand, turnover rates estimated from fossil data are independent of present-day richness patterns but suffer from preservational

and collection biases inherent in the fossil record and its sampling (Patzkowsky and Holland, 2012).

Second, while the previous analyses have often been global in scope, our study is considerably smaller and focuses specifically on sub-Saharan Africa but uses only the fossil record of eastern Africa to calculate turnover rates. Because our fossil record is restricted to a particular region of sub-Saharan Africa, we concede that our turnover metrics may be downwards biased and underestimate actual diversification rates. Such biases, however, should not affect our results if they are randomly distributed across the taxonomic groups used in our analyses. For example, previous work has demonstrated similar genus-level diversity patterns for Bovidae, Felidae, and Hyaenidae in eastern and southern Africa over the last 3 Myr (Patterson et al., 2013), suggesting minimal differences in fossil preservation across these major taxonomic groups in the two regions of the continent.

Third, it is possible that extant species differ from their fossil congeners and tribemates in their ecology, confounding the relationship between niche breadth and turnover rates. For example, although most extant tragelaphins (genus *Tragelaphus*, tribe Tragelaphini) are C₃-browsers, isotopic and dental wear data for Plio-Pleistocene fossil species shows significant dietary variability and that many species consumed significant quantities of C₄ grasses (Blondel et al., 2018). For the vast majority of mammalian taxa, however, paleobiological data are consistent with the present-day ecology of genera and tribes considered here (e.g., Cerling et al., 2015). Furthermore, we found that biomic, climatic, and dietary niche breadth dimensions of extant species show moderate to high phylogenetic signal, suggesting that they have been conserved throughout the entire

history of the clade. We therefore consider it unlikely for opposing patterns of niche conservatism to underlie differences between our study and others.

Finally, it is possible that differences in taxonomic units of analysis are responsible for conflicting results between our study and others. Taxonomic units are arbitrary to a degree, as there are a number of possible ways to partition species into clades. Here, we have used genera and tribes as units of analysis following Vrba (1987), although most other studies have analyzed family-level patterns (e.g., Gomez-Rodriguez et al., 2015). It is perhaps likely that differences in taxonomic and, by extension, phylogenetic scale are important factors – e.g., tribes and genera may not be dissimilar enough in their niches to detect niche breadth-turnover relationships, while these relationships may only emerge when analyzing coarser, family-level ecological differences. The importance of considering multiple taxonomic and phylogenetic scales in ecological studies was recently reviewed by Graham et al. (2018) and should be incorporated into future studies of niche breadth-turnover relationships.

5. Conclusions

Vrba's (1980, 1987, 1992, 1995a, 1999) RUH has been widely influential in studies of macroevolutionary turnover in the mammalian fossil record. The RUH posits that differences in the ecological niche breadths of clades play a deterministic role in shaping divergent patterns of macroevolutionary turnover, with specialized clades having higher incidences of vicariance and range contraction, and therefore speciation and extinction, than generalist clades in the face of climatic or environmental change. We combined present-day and fossil data from large-bodied African mammals to measure species' niche breadths, test the degree to which they are phylogenetically conserved, and

analyze the relationship between clade-level niche breadth and origination and extinction rates in the fossil record. These analyses bear directly on the central tenets of the RUH. In contrast to predictions derived from the RUH, we found that: (1) species' dietary niche breadths are unrelated to their biomic and climatic niche breadths, failing to support an overall specialist-generalist dichotomy across mammals, and (2) although species' biomic, climatic, and dietary niche breadths show moderate to high phylogenetic conservatism, there is no relationship between clade-level measures of niche breadth and turnover rates in the fossil record. Our results indicate that the evolutionary trajectories of Eltonian and Grinnellian niche dimensions have been largely decoupled in African mammals and had little to no influence in driving the diversification histories of clades. Future studies of turnover in mammals should begin to directly test Red Queen dynamics, such as shifting competitive landscapes, in driving mammalian evolutionary patterns over geological timescales (Benton, 2009; Strotz et al., 2018).

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CHAPTER 3: CLIMATE AND PRIMARY PRODUCTIVITY MODULATE THE RELATIVE INFLUENCE OF COMPETITION AND ABIOTIC FILTERING ACROSS AFRICAN MAMMAL COMMUNITIES

Title: Climate and primary productivity modulate the relative influence of competition and abiotic filtering across African mammal communities

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Abstract

The influence of different assembly processes in shaping mammal communities is poorly understood. Although observation of community assembly over experimental timescales is improbable, linking pattern to process permits inference of community assembly: if species in a community are more distantly related (and therefore ecologically dissimilar) than expected by chance, competition was likely strong; conversely, if a community contains more closely related (ecologically similar) species than expected by chance, abiotic filtering is likely to have played a stronger role. Here, we use mammal communities in sub-Saharan Africa to address how the relative influence of assembly processes differs across taxonomic groups and how the strength of assembly processes is modulated by abiotic gradients. We quantified the phylogenetic and functional trait structure for three groups (macromammals, micromammals, bats) and three orders (Artiodactyla, Carnivora, Primates) and predicted their structure from climatic and environmental variables using linear models. We find that macromammal and micromammal communities are primarily shaped by dietary competition, whereas abiotic filtering of body mass and diets is high in bat communities. Artiodactyl communities are randomly structured, carnivoran communities are shaped by abiotic filtering of diets, and primate communities are shaped by weak body mass competition. The relative strength of assembly processes is strongly related to climatic gradients across most groups and orders, with dietary competition being the most important assembly process overall and elevated in high productivity forest biomes.

Keywords: Community assembly, community ecology, phylogenetic structure, functional trait structure

1. Introduction

The relative influence of the different assembly processes that shape mammal community composition are poorly known. One view is that competitive processes are the dominant control (Holt, 1987; Hutchinson, 1957; Pianka, 1981; Van Valkenburgh, 1996), wherein community structure is modulated by species vying for similar resources and outcompeting one another (e.g., competitive exclusion) or by species evolving ways to limit competition (e.g., niche partitioning or differentiation). As niche similarity is a precondition for competition, communities shaped by competitive processes should not contain species with substantial niche overlap. An alternative view to competition is that abiotic filtering of niches across environmental gradients (e.g., climate, topography) is the primary determinant of community structure (Cornwell et al., 2006; Kraft et al., 2008, 2015). Abiotic filtering results in the co-occurrence of taxa that have similar niches because only those species, equipped with particular ecological and/or physiological adaptations, can persist in a given environment. Therefore, a community shaped by abiotic filtering should contain species that are overall ecologically similar.

Though it is likely that both competition and abiotic filtering act in tandem in shaping mammal community structure, observing them over experimental timescales is improbable because assembly processes play out over relatively large spatial and temporal scales. There is therefore great need to infer community assembly processes from present-day community patterns. Recent studies have shown that analyzing the phylogenetic and functional trait structure of communities is a powerful way of inferring the assembly processes that shaped them (Figure 2.1) and how the strength of competition and abiotic filtering changes across environmental gradients (Graham et al.,

2009, 2012; Kraft and Ackerly, 2010; Webb, 2000; Webb et al., 2002).

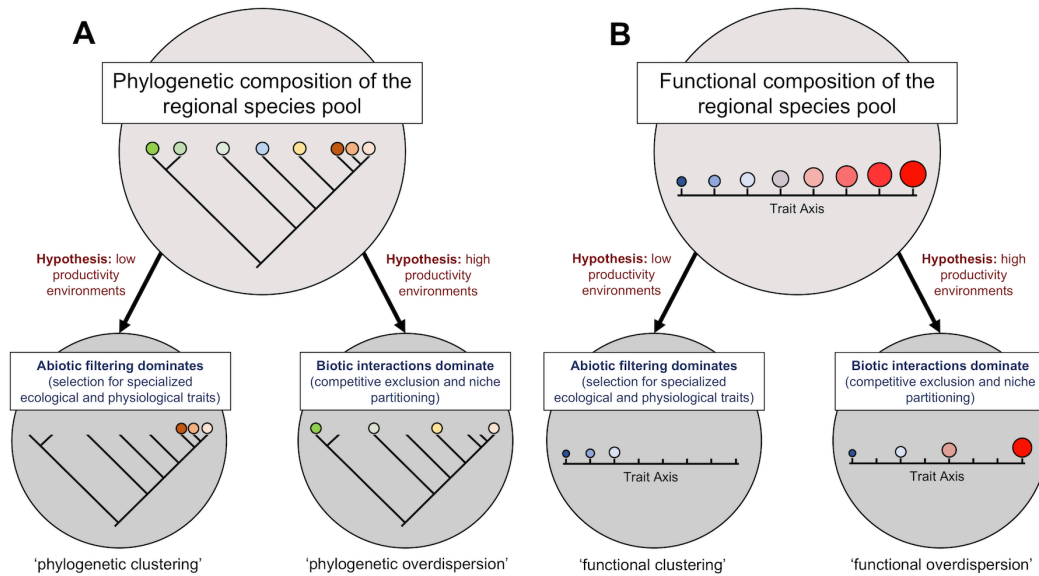


Figure 2.1. Schematic of the conceptual background to using the phylogenetic and functional trait structure of ecological communities to determine what community assembly processes have shaped them. Analyses of phylogenetic community structure (A) assume that closely related species have similar niche requirements, which is the hypothesis of phylogenetic niche conservatism. If niches are conserved among species, then it is hypothesized here that abiotic filtering will dominate in low productivity environments because climatic and environmental gradients ‘filter’ for particular ecological or physiological traits. Conversely, I predict that biotic interactions such as competitive exclusion and niche partitioning should dominate in high productivity environments as species compete for resources. Analyses of functional trait community structure (B) are conceptually similar but analyze traits directly versus inferring them from phylogenetic relatedness.

Webb (2000) and Webb et al. (2002) pioneered the field of phylogenetic community ecology to understand the relative influence of different assembly processes on community structure. As summarized by Cardillo (2011), the basic question asked by phylogenetic community ecology is: if the set of species found in a particular locality (i.e., a local community) is only a subset of the species found within the broader region (i.e., the regional species pool), are the processes that determine community composition predictable and deterministic, or are they neutral and stochastic? This question is

addressed by determining whether a community's composition significantly deviates from a null expectation under which species are drawn randomly from the regional pool. If a community does significantly deviate, then the nature of this deviation permits inference of the assembly processes that have shaped community composition (Webb, 2000; Webb et al., 2002; Cardillo, 2011). Specifically, if species within a community are more distantly related than expected by chance, the community is said to be 'phylogenetically overdispersed' and is inferred to have been assembled through competitive processes (e.g., competitive exclusion, niche partitioning). Conversely, if species within a community are more closely related than expected by chance, the community is said to be 'phylogenetically clustered' and is inferred to have been assembled through abiotic filtering and dispersal limitation, wherein similar ecological or physiological traits are favored in that particular environment. Thus, phylogenetic overdispersion implies a strong influence of biotic interactions on community composition, whereas phylogenetic clustering implies a strong influence of abiotic filtering on community composition.

The fundamental assumption of phylogenetic community ecology is phylogenetic niche conservatism, wherein ecological traits are conserved among close relatives (Wiens and Graham, 2005; Wiens et al., 2010). If traits are phylogenetically conserved, then closely related species are likely to compete more intensely than distantly related ones, as first proposed by Darwin – 'As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera' (Darwin, 1859). Recent evidence for widespread phylogenetic niche conservatism, however, on

which analyses of phylogenetic community structure are contingent on, is equivocal (Losos, 2008). The mismatch between relatedness and ecological similarity can be attributed to both convergent evolution across distantly related species (Losos, 2008) and rapid niche divergence between sister taxa (Cooper et al., 2011; Dormann et al., 2011).

In response to mixed evidence for phylogenetic niche conservatism, measures of the functional trait structure of communities have been proposed as an alternative method for inferring community assembly processes (Kraft and Ackerly, 2010; Laliberté and Legendre, 2010; Schleuter et al., 2010). Functional traits are measurable properties of species that strongly influence organismal performance and species' interactions (McGill et al., 2006), such as body size and diet, and therefore reflect fundamental aspects of a species' ecology. Analyses of community functional trait structure are conceptually similar to those of phylogenetic community structure but examine traits directly rather than use phylogenetic relatedness as a proxy for ecological similarity. The overdispersion or clustering of traits within a community relative to regional species pool is used to infer the influence of biotic versus abiotic processes in determining community composition, as in phylogenetic community ecology.

As analyses of community phylogenetic and functional trait structure are used to infer the assembly processes shaping community composition, there has been much interest in the climatic and environmental correlates of community structure metrics (e.g., Graham et al., 2009, 2012; Kamilar et al., 2015; Rowan et al., 2016). Establishing the relationship between climatic and environmental gradients and community structure permits investigation of how these gradients modulate the influence of abiotic and biotic forces on community assembly. For example, Neotropical communities of hummingbirds (Graham et al., 2009) and rodents (Dreiss et al., 2015) show clear elevational influences

on community structure. In both cases, lowland communities in high productivity environments were overdispersed, reflecting strong competition, whereas those in high altitude low productivity environments were clustered, reflecting strong abiotic filtering across local environments. How assembly processes shape communities at larger spatial scales, however, is poorly understood – most analyses of community structure have focused on local assemblages, with few exceptions (e.g., Cardillo, 2011; Cantalapiedra et al., 2013).

Here, we analyze the phylogenetic and functional trait structure of three groups of African mammals: macromammals (non-volant orders > 500g on average), micromammals (non-volant orders < 500g on average), and bats. We also further divide macromammals into three order-level groups, artiodactyls (Artiodactyla), carnivorans (Carnivora), and primates (Primates). Using these groups and orders, we address four major questions:

Q₁: If ecological traits are phylogenetically conserved, do phylogenetic and functional trait structure metrics mirror one another?

H₁: We predict that if ecological traits are phylogenetically conserved across mammals, then community phylogenetic and functional trait structure metrics should be highly correlated. Failure to support this expectation would suggest that the phylogenetic and functional trait structure of communities are determined by different processes, or that the traits analyzed (body mass, diet) are not important in community assembly.

Q₂: Does the relative influence of community assembly processes differ across mammal groups and, if it does, how so?

H₂: We predict that the relative influence of different community assembly processes will vary across mammal groups. Macromammal communities are predicted to be overdispersed overall, while micromammal and bat communities should be largely clustered or randomly structured. This is based on the premise that dispersal limitation weakens with increasing body mass (Bowman et al., 2002), and therefore macromammal communities have been more strongly shaped by biotic interactions (e.g., competitive exclusion, niche partitioning), whereas smaller-bodied micromammal and bat communities have been subject to stronger abiotic filtering because they are dispersal-limited. Carnivoran communities are expected to be overdispersed, reflecting competition between secondary consumers (Creel and Creel, 1996; Durant, 1998). Primates and artiodactyls are mostly primary consumers and are therefore more directly tied to their local environments; these orders are expected to be primarily clustered or random, reflecting abiotic filtering or a mix of assembly processes.

Q₃: Within mammal groups, how does the relative influence of community assembly processes differ across biomes?

H₃: For Q₃, we predict that the relative influence of biotic versus abiotic factors within a given group will vary along a gradient based on the biome's overall productivity: biomes with high net primary productivity (NPP) are expected to be overdispersed, reflecting strong competition for resources, whereas those with low NPP are expected to be

clustered, reflecting specialized ecological and physiological adaptations to low productivity environments (Graham et al., 2009; Dreiss et al., 2015).

Q4: Are there continental-wide relationships between community assembly processes and climate?

H4: We predict, as in H₃, that community overdispersion should increase with temperature and precipitation, which reflect overall productivity.

Mammal communities of Africa provide an ideal group to address these questions for several reasons. First, mammals are perhaps the most completely studied group of animals, and their distributions (Schipper et al., 2008), ecological traits (Kissling et al., 2014; Nowak, 1999; Smith et al., 2003), and phylogeny (Bininda-Emonds et al., 2007; Faurby and Svenning, 2015a) are relatively well-known. Second, both biotic and abiotic processes have been shown to be important for community assembly in mammals, and vary across environmental gradients (e.g., Cisneros et al., 2014; Dreiss et al., 2015; Kamilar et al., 2015; Stevens et al., 2012; Stevens and Gavilanez, 2015). Finally, Africa is particularly suited for addressing these questions because sub-Saharan Africa is the peak of world's current mammal diversity and was largely spared from late Quaternary extinctions (Faurby and Svenning, 2015b; Sandom et al., 2014). Thus, mammal communities of Africa offer the most 'natural' test case to address these questions.

2. Methods

2.1 Community data

We obtained data on the distributions of mammal species in sub-Saharan Africa, here defined as all of continental Africa below 15°N, from International Union for Conservation of Nature (IUCN) Red List assessments (IUCN, 2017). Analyses were restricted to sub-Saharan Africa because North Africa was heavily impacted by late Quaternary and recent extinctions (Faurby and Svenning, 2015b; Sandom et al., 2014). Additionally, North Africa falls within the Palearctic biogeographic realm and contains a distinct mammalian fauna compared to sub-Saharan Africa, which comprises the Afrotropical realm (Olson et al., 2001). For convenience, sub-Saharan Africa is referred to as ‘Africa’ in the rest of this work.

IUCN species distributions were checked against the literature and handbooks (e.g., Kingdon, 1971, 1974a, 1974b, 1977, 1979, 1982a, 1982b; Monadjem et al., 2010, 2013; Skinner and Chimimba, 2005) and four species were removed as a result. These include three invasive micromammal species, the Asian house shrew *Suncus murinus*, house mouse *Mus musculus*, and black rat *Rattus rattus*. The Mauritian little mastiff bat *Mormopterus acetabulosus* was also removed as this species is doubtfully known from continental Africa. It is possibly represented from a single specimen described in the 1800s from ‘near Port Natal’ (i.e., Durban, South Africa), but this is now thought to have been a vagrant from Mauritius where the species is native (Goodman et al., 2008).

The final dataset contained 1,005 mammal species, which were divided into three groups. Macromammals encompasses 269 species in nine orders, including Artiodactyla ($n=85$), Carnivora ($n=74$), Hyracoidea ($n=5$), Lagomorpha ($n=12$), Perissodactyla ($n=6$), Pholidota ($n=4$), Primates ($n=81$), Proboscidea ($n=1$), and Tubulidentata ($n=1$).

Macromammals are orders with non-volant species over 500g on average. Micromammals encompasses 542 species in four orders, including Afrosoricida ($n=24$), Eulipotyphla ($n=145$), Macroscelidea ($n=18$), and Rodentia ($n=355$). Micromammals are orders with non-volant species less than 500g on average. Bats includes 194 species in a single order, Chiroptera ($n=194$). These groups were devised based on similarities in body mass and dietary ecology, traits likely to influence community assembly. For example, large carnivorans and carnivorous rodents do not compete for the same prey items, whereas interspecific competition among large carnivorans is well-documented (e.g., Creel and Creel, 1996; Durant, 1998). However, we also decided to directly analyze community assembly for three macromammal orders: Artiodactyla, Carnivora, and Primates. These orders were chosen because they are specious and have many co-occurring species that are broadly similar in body size and dietary requirements. Therefore, intraordinal competition and abiotic filtering for similar traits should have shaped their community structure. For each group and order, species ranges were overlaid and a presence-absence matrix was generated using a 0.5° grid over Africa with the package *letsR* (Vilela and Villalobos, 2015). This generated roughly 6,475 cells (hereafter, ‘communities’) for each group and artiodactyls and carnivorans, and 6,250 communities for primates. Only communities with at least four species were used in subsequent analyses.

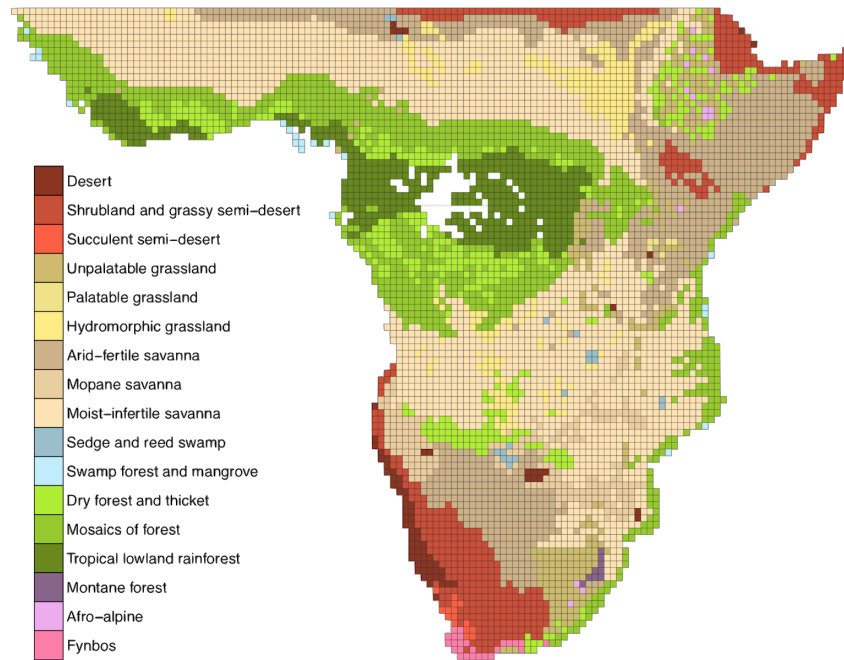


Figure 2.2. Biomes for sub-Saharan Africa based on White (1983).

2.2 Biome and climate data

We used a modified version of White’s (1983) physiognomic classification of African vegetation biomes (Figure 2.2) to compare how aspects of community assembly change across biomes. White’s (1983) classification was used because it is one of the most comprehensive biome maps made for the continent, was built over decades of fieldwork (versus interpolation from satellite imagery), and because it has similar spatial resolution to IUCN range maps. We use 17 physiognomically distinct vegetation units (Table 2.1) that also differ in regional climate, topography, and edaphic characteristics. White’s (1983) anthropic landscape category for land heavily modified by humans was not used because the interest of our work is in natural assembly (i.e., non-anthropogenic) processes. A biome classification was assigned to each community using the packages *dismo* (Hijmans et al., 2017a) and *raster* (Hijmans et al., 2017b). Net primary

productivity (NPP) data were collected for each biome from NASA and the Center for International Earth Science Information Network (Imhoff et al., 2004). NPP was measured in grams of carbon per year.

Table 2.1. White’s 17 physiognomically-defined vegetation biomes of Africa used in this work. These biomes differ in their net primary productivity (NPP), mean annual temperature (MAT), and mean annual precipitation (MAP), as well as other characteristics (e.g., topography and edaphics). Climate data were collected from WorldClim (Hijmans et al., 2005) and NPP data come NASA and the Center for International Earth Science Information Network (Imhoff et al., 2004).

Biome Group	White’s Biome	NPP	MAT	MAP
Afro-montane	Afro-alpine	5.28067E+11 g	11.2 °C	1131 mm
Savanna	Arid-fertile savanna	2.06624E+11 g	24.0 °C	465.6 mm
Desert and semi-desert	Desert	64448887870 g	19.4 °C	147.1 mm
Forests	Dry forest and thicket	6.21985E+11 g	23.1 °C	1232 mm
Fynbos	Fynbos	2.42289E+11 g	16.0 °C	474.1 mm
Grassland	Hydromorphic grassland	3.99125E+11 g	25.5 °C	889.0 mm
Savanna	Moist-infertile savanna	4.62907E+11 g	24.2 °C	971.7 mm
Afro-montane	Montane forest	5.17444E+11 g	16.8 °C	877.4 mm
Savanna	Mopane savanna	3.18653E+11 g	22.4 °C	543.9 mm
Forests	Mosaics of forest	6.18543E+11 g	24.5 °C	1417 mm
Grassland	Palatable grassland	3.35E+11 g	20.4 °C	699.6 mm
Swamps and mangroves	Sedge and reed swamp	3.79229E+11 g	22.9 °C	788.7 mm
Desert and semi-desert	Shrubland and grassy semi-desert	80803975659 g	22.1 °C	228.0 mm
Desert and semi-desert	Succulent semi-desert	85073467563 g	17.1 °C	182.4 mm
Swamps and mangroves	Swamp forest and mangrove	2.95979E+11 g	26.3 °C	2240 mm
Forest	Tropical lowland rainforest	8.84219E+11 g	24.6 °C	1894 mm
Grassland	Unpalatable grassland	5.07744E+11 g	17.0 °C	1027 mm

Climate data were downloaded from WorldClim (Hijmans et al., 2005) at 2.5m resolution for 19 climatic variables. Climate variables were extracted for each community using the packages *dismo* (Hijmans et al., 2017a) and *raster* (Hijmans et al., 2017b) with each community’s central latitude and longitude. All variables were screened for collinearity using a pairwise correlation matrix; when two variables had a Pearson correlation coefficient over 0.85, one of them was removed in order to avoid multicollinearity in the models. The final set of six climate variables used in subsequent analyses are shown in Table 2.2. These variables capture averages and seasonality of temperature and precipitation, as well as climate extremes that shape productivity (e.g.,

rainfall of the driest month). All temperature variables are measured in degrees Celsius (°C) and precipitation variables in millimeters (mm). The seasonality variables are measured differently for temperature and precipitation – temperature seasonality is measured as the standard deviation of temperature throughout the year multiplied by 100 and precipitation seasonality is measured as the coefficient of variation of rainfall throughout the year (Hijmans et al., 2005).

Table 2.2. Climate variables used in linear models to predict the phylogenetic and functional trait structure of African mammal communities. Temperature variables are measured in degrees Celsius (°C) and precipitation variables in millimeters (mm). Note that the seasonality variables are calculated differently for temperature and precipitation. Climate data were collected from WorldClim (Hijmans et al., 2005),

Variable Acronym	Variable Description	WorldClim Code
MAT	Mean Annual Temperature	BIO1
TS	Temperature Seasonality (standard deviation*100)	BIO4
TCM	Temperature of the Coldest Month	BIO6
MAP	Mean Annual Precipitation	BIO12
PS	Precipitation Seasonality (coefficient of variation)	BIO15
PDM	Precipitation of the Driest Month	BIO14

2.3 Functional trait and phylogenetic data

Functional trait data were collected for all 1,005 species from the primary literature and handbooks; data were cross-referenced with as many sources as possible. We used body mass and diet as functional traits of mammals, as these traits reflect fundamental aspects of species' ecologies and therefore influence community assembly processes. For example, previous work has shown that African ungulates with similar dietary ecologies partition resources by body size (Du Toit, 1990; Kleynhans et al., 2011). Body size differentiation between co-occurring species has also been demonstrated in African carnivorans (Radloff and Du Toit, 2004), along with ranging patterns that minimize encounters with potential competitors (Vanak et al., 2013). Likewise, there is ample evidence for intense dietary resource competition among

African carnivorans, which includes interspecific killing during fights over prey items (Creel and Creel, 1996; Palomares and Caro, 1999). Thus, the available evidence strongly suggests that body size and diet are fundamental to mammal community assembly in Africa, although we acknowledge that other traits (e.g., substrate use) are also important. Macromammal trait data were collected from Butynski et al. (2013), Kingdon (1971, 1977, 1979, 1982a, 1982b), Kingdon et al. (2013), Kingdon and Hoffmann (2013a, 2013b), and Skinner and Chimimba (2005). Micromammal trait data were collected from Happold (2013), Happold and Happold (2013), Kingdon (1974a, 1974b), Kingdon et al. (2013), Monadjem et al. (2013), and Skinner and Chimimba (2005). Bat trait data were collected from Happold and Happold (2013), Kingdon (1974a), Monadjem et al. (2010), and Skinner and Chimimba (2005).

Macromammal body mass was recorded as a continuous variable in kilograms (kg). Body mass had to be estimated for ~ 6% of macromammal species and was interpolated from nearest relatives or species with which a taxon was formerly considered conspecific. Micromammal body mass was recorded as a continuous variable in grams (g). Body mass was estimated for ~ 18% of micromammal species and was interpolated from the congener most similar in head-body length. There is a strong correlation between head-body length and body mass among micromammals in the dataset (e.g., in golden-moles $r=0.93$, sengis $r=0.94$, shrews, $r=0.93$, and rodents, $r=0.91$) and therefore this was considered the best method to fill in missing data. Bat body mass was measured in grams (g) and estimated for ~ 4% of species. Missing bat body mass data was interpolated from nearest relatives or species with which a taxon was formerly considered conspecific.

For all three groups, diet was recorded on an ordinal scale from 0-3 (0 = ‘not consumed’, 1 = rarely consumed, 2 = often consumed, 3 = primary food resource) for 11 food items (Table 2.3). This classification scheme was modeled after Kissling et al. (2014) but differs from their dataset as it was compiled from and checked by several primary sources and very little of the dietary data was interpolated (cf. Kissling et al., 2014). We used a principal coordinates analysis (PCoA) with Gower distances to compress the dietary data into a series of components that summarized the overall distribution of diets for each group. Gower distance was used because it is a robust way of generating distances with non-normal data (in our case, ordinal data) and has been widely used in analyses of functional trait structure (e.g., Mazel et al., 2014; Newbold et al., 2014; Safi et al., 2011). The package *vegan* (Oksanen et al., 2017) was used to generate the Gower matrix of pairwise distances and perform the PCoA.

Phylogenetic data for all groups comes from the phylogeny of Faurby and Svenning (2015a), which was compiled based on a novel heuristic-hierarchical Bayesian algorithm using genetic data. The Faurby and Svenning (2015a) phylogeny was used because it includes all species within the dataset and is the most recent and comprehensive estimate of species-level relationships for mammals. Although some robust order-level phylogenies have been recently published (e.g., primates, Perelman et al., 2011; bats, Teeling et al., 2005; artiodactyls, Hassanin et al., 2012), these trees have sparse species-level sampling and are focused more on broad relationships across each clade. Visual examination of the Faurby and Svenning (2015a) topology for different groups was consistent with these recently published order-level phylogenies.

Table 2.3. Dietary classifications for mammal species. An ordinal rank (0 = ‘not consumed’, 1 = ‘rarely consumed’, 2 = ‘often consumed’, 3 = ‘primary food resource’) was assigned for each diet category for each species based on published sources (see Materials and Methods).

Diet Category	Description
Mammal	Consumes mammalian prey
Bird	Consumes avian prey
Herptile	Consumes reptile or amphibian prey
Fish	Consumes fish prey
Invertebrate	Consumes invertebrate prey
Seed	Consumes seeds
Fruit	Consumes fleshy fruits
Nectar	Consumes nectar
Root	Consumes roots
Woody	Consumes leaves of woody plants (e.g., tree leaves)
Herbaceous	Consumes leaves of herbaceous plants (e.g., grasses)

2.4 Phylogenetic signal of species’ functional traits

To test the hypothesis that phylogenetic and functional trait structure will match one another if ecological traits are phylogenetically conserved, one needs to measure the degree to which the latter is true. This can be done using a trait’s phylogenetic signal, which is essentially a measure of the covariance between trait similarity and phylogenetic relatedness (Cadotte and Davies, 2016). We used Blomberg’s K to measure the phylogenetic signal in mammal species’ functional traits following Blomberg et al. (2003). Blomberg’s K is a variance ratio measure of how conserved a trait is across a phylogeny of species. A K value of one indicates that the trait matches a Brownian motion model of evolution, where trait variance among the tips of the tree is proportional to time. A K value greater than one indicates a high phylogenetic signal, where traits are strongly conserved across clades and most of the trait variation occurs between them. Conversely, a K value less than one indicates a low phylogenetic signal. This indicates that traits have convergently evolved across the tree and much of the trait variation is concentrated within clades.

Blomberg's K was calculated using the function *phylosig* in the package *phytools* (Revell et al., 2012) and 1,000 simulations of a randomization test were used to judge its significance. Because Blomberg's K is a traditional parametric test, all variables were log-transformed to ensure normality when measuring their phylogenetic signal.

2.5 Community structure metrics

The phylogenetic structure of communities was measured using the net-relatedness index (NRI) of Webb (2000) and Webb et al. (2002). NRI is calculated as the average phylogenetic distance among species in a community, where distance is measured as divergence time in millions of years. NRI was chosen as the metric for measuring the phylogenetic structure of communities because it has been shown to be the least sensitive to phylogenetic resolution and species richness, whereas other metrics like the nearest-taxon index (NTI) are very sensitive to small changes in community composition such as the addition or removal of a single species (Molina-Venegas and Roquet, 2014). NRI was standardized against a null model of 1,000 communities which were used to judge the statistical significance of each community's observed NRI value. A non-significant p-value indicates that a community's phylogenetic composition does not differ from what would be expected from a random draw of species from the regional species pool. Conversely, a significant p-value for NRI indicates a non-random structure to the phylogenetic composition of the community. Significant NRI values that are positive indicate phylogenetic clustering, while significant negative NRI values indicate phylogenetic overdispersion. NRI was calculated using the package *picante* (Kembel et al., 2010). NRI is a two-tailed test, so α of 0.025 and 0.975 were used to determine significantly clustered or overdispersed communities, respectively.

The functional trait structure of communities was calculated using the metrics Range and the standard deviation of successive neighbor distances divided by the overall trait range (SDNDR) following Kraft et al. (2008) and Kraft and Ackerly (2010) (Figure 2.3). Null model simulations have shown that these metrics are very powerful for detecting different community assembly processes (Kraft and Ackerly, 2010). Range is calculated as the overall trait range of a community and is used to detect abiotic filtering of traits. Abiotic filtering selects for particular ecological traits and therefore it is expected that communities with significantly smaller trait ranges than expected from a random draw of the regional pool have been shaped by this process. Conversely, SDNDR measures how regularly spaced species within a community are for a given trait relative to the overall trait range of the community. SDNDR thus reveals patterns of ‘even-spacing’, which is expected if competitive processes (niche partitioning, competitive exclusion) have most strongly influenced community assembly. Range and SDNDR were standardized against a null model of 100 communities to judge the significance of each community’s observed value. As these are one-tailed tests, α 0.05 was used to determine statistical significance. Range and SDNDR were calculated for body mass and the first two components from the dietary PCoAs for each group (diet PCoA1 and diet PCoA2).

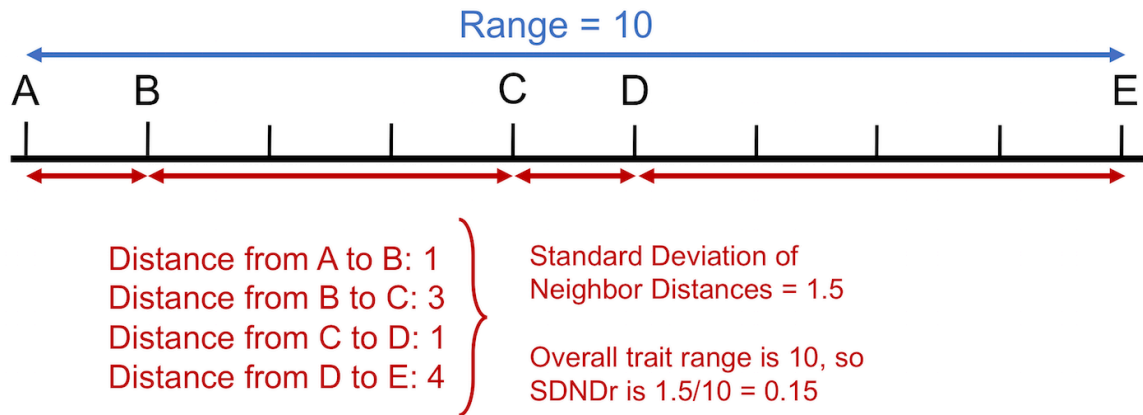


Figure 2.3. Schematic of Range and SDNDR (standard deviation of neighbor distances divided by overall trait range), functional trait metrics used in this study. Range is calculated as the overall trait range in a community. SDNDR is calculated as the standard deviation of neighbor distances along a trait axis divided by the overall trait range. Range is a metric sensitive to abiotic filtering, whereas SDNDR detects ‘even-spacing’, a common outcome of competition and niche partitioning.

2.6 Continent-wide climatic models

To test whether climatic gradients modulate community assembly, multi-predictor models with NRI, Range, and SDNDR as the response variables and all six climatic variables as predictors were constructed using Ordinary Least Squares (OLS) regression. However, preliminary analyses showed strong spatial autocorrelation in the residuals of these models (see spatial correlograms in SI Figures 1-6) and therefore spatially explicit models had to be implemented. Kissling and Carl (2008) found that spatial error models (SAR_{err}) were robust to analytical decisions (e.g., neighborhood distances) and produced consistent results while effectively controlling for the underlying spatial structure of the data. SAR_{err} models assume that the autoregressive process is found only in the error term of the model and is appropriate for situations where there is spatial autocorrelation in both the response and predictor variables, which was the case in this study. The model is specified similar to traditional OLS but includes the term $\lambda \mathbf{W}u$, which represents the spatial structure in the spatially dependent error term. The model is specified as

$$\mathbf{Y} = \mathbf{X}\beta + \lambda\mathbf{W}\mathbf{u} + \mathbf{e}$$

with λ as the spatial autoregression coefficient, \mathbf{W} as the spatial weights matrix, β as a vector representing the slopes associated with the predictor variables in the original predictor matrix \mathbf{X} , and \mathbf{e} as the spatially independent errors (Kissling and Carl, 2008). SAR_{err} models were constructed using the package *spdep* (Bivand, 2015; Bivand and Piras, 2015). Spatial correlograms of the SAR_{err} residuals showed that the spatial structure in the data was successfully controlled for by this model (SI Figures 1-6). In addition, likelihood ratio tests indicated that the SAR_{err} models were consistently better fits than their OLS counterparts (SI Tables 3, 6, 9, 12, 15, 18).

3. Results

3.1 Ordination of species' dietary data

Biplots of PCoA dimensions 1 and 2 are shown in Figure 2.4; in the following text the symbol + is used to denote a dietary variable loading positively and - is used to denote a dietary variable loading negatively on a PCoA axis. Overall, much of the dietary variation across groups is captured on the first two PCoA axes (SI Figures 7-12) and therefore these axes are an effective way of summarizing each species' diet relative to other species as a continuous variable.

The PCoA of macromammals effectively separated out different diets. For example, macromammal diet PCoA1 separated carnivores (+) from herbivores (-), with carnivorans loading most positively and artiodactyls and perissodactyls loading most negatively. Macromammal diet PCoA2 separated fruit and seed feeders and generalists (+), such as primates and duikers, from species with more specialized diets (-) that are

strict herbivores or carnivores. Micromammal diets were also well-discriminated by the PCoA, with rodents occupying all dimensions of the dietary niche space. Micromammal diet PCoA1 separated herbivores (+) from carnivores (-), while diet PCoA2 separated fruit and seed feeders (+) from strict carnivores and herbivores (-). Bat diets were mainly discriminated on diet PCoA1, which separated frugivores (+) from carnivores (-), with invertebrate feeders falling in-between these two groups. Exclusively frugivorous pteropodids loaded most positively and the large slit-faced bat *Nycteris grandis*, Africa's only carnivorous bat species, loaded most negatively.

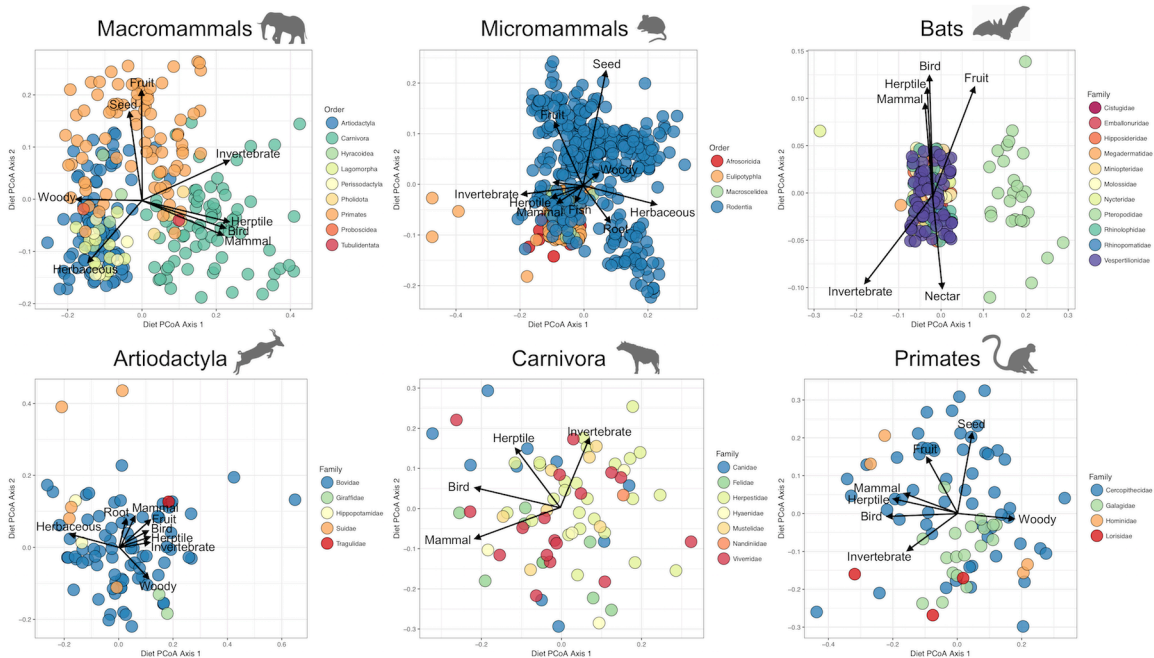


Figure 2.4. Biplots of dietary principal coordinates analysis (PCoA) axes one (diet PCoA1) and two (diet PCoA2) across mammal groups (top row) and orders (bottom row). Each PCoA effectively separated out species in dietary niche space. Note that points are ‘jittered’ on all plots so that the full distribution of species is easier to see.

PCoAs of the order-level data were also effective at separating out diets.

Artiodactyls have the lowest dietary diversity among the three orders as most species are strictly herbivorous. Artiodactyl diet PCoA1 separated frugivorous omnivores (+), almost

all duikers, from grazers (-). Artiodactyl diet PCoA2 separated root-feeding generalists (+) from browsers (-), with grazers falling in-between. Suids of the genus *Potamochoerus* load most positively on this axis and selective browsers such as gerenuk *Litocranius walleri* and dik-dik *Madoqua* spp. load most negatively. Carnivoran and primate diets were more clearly discriminated by their respective PCoAs. Carnivoran diet PCoA1 separated invertebrate feeders and generalists (+), like mongooses, from small-vertebrate feeders (-). Carnivoran diet PCoA2 separated small prey specialists (+) like foxes and mongooses from large prey specialists (-) such as lions *Panthera leo*. Primate diet PCoA1 separated folivores and seed feeders (+) from carnivores and omnivores (-), with frugivores falling in-between. Colobus monkeys (*Colobus* and *Procolobus* spp.) load most positively on this axis, while baboons *Papio* spp. load most negatively. Primate diet PCoA2 separated fruit and seed feeders (+) like drill-mangabeys *Cercocebus* spp. from invertebrate feeders (-) such as galagids and lorisisds.

3.2 Phylogenetic signal of species' functional traits

The phylogenetic signal of species' functional traits was much lower than expected under a Brownian motion model of evolution (for Brownian motion, $K = 1$), but across all of the groups and orders examined body mass had the highest K value of all traits (Table 2.4; Figure 2.5). Macromammal body mass was the most conserved across the three groups but still showed a relatively low phylogenetic signal ($K < 1$), indicating pervasive niche divergence between sister taxa and convergent evolution of similar body masses by distantly related taxa. The phylogenetic signal of species' diet (based on diet PCoA1 and diet PCoA2 axes) was very low. This should be expected after visualizing the group-level dietary PCoA biplots (Figure 2.4), which overall show no clear phylogenetic

patterning of dietary niche space.

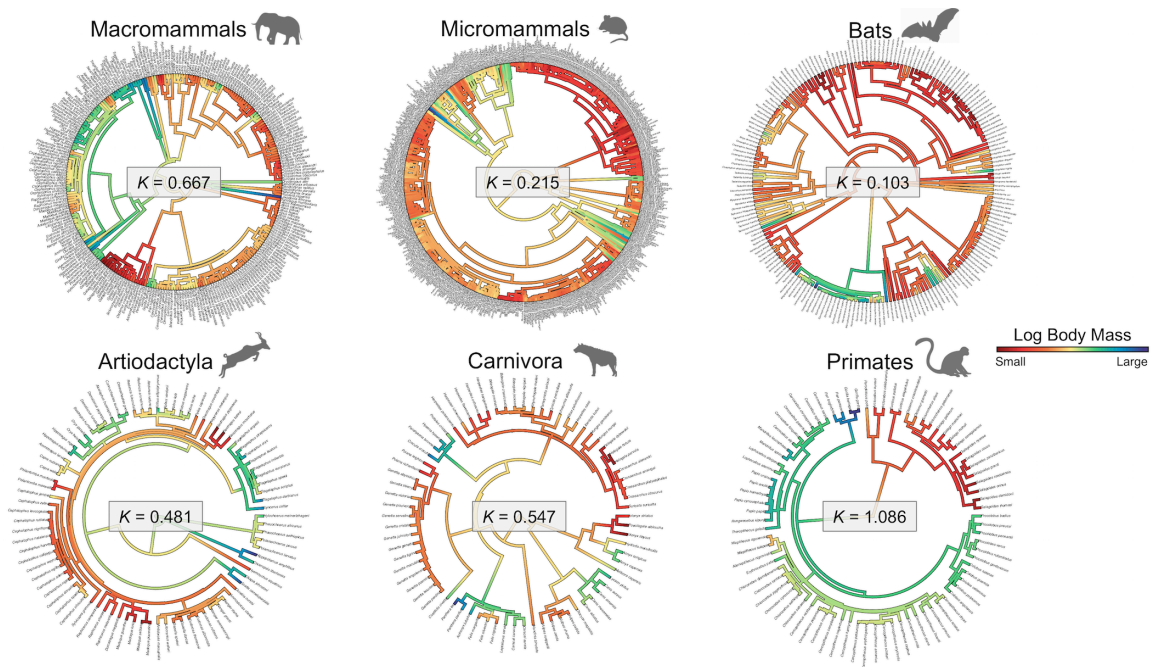


Figure 2.5. Phylogenetic signal in body mass across mammal groups (top row) and orders (bottom row). Overall, mammal body mass has a low phylogenetic signal (Blomberg's $K < 1$) except for primates ($K > 1$) where closely related species are more similar in their body masses than expected under a Brownian motion model of evolution, where $K = 1$. This implies strong niche conservatism in primate body mass but rampant homoplasy and niche divergence in body mass across all other groups and orders. Diet (not shown) had an even lower phylogenetic signal than body mass.

Order-level patterns of niche conservatism were similar to those at the group-level, except for primate body mass. Body mass in primates was the only trait to show a high phylogenetic signal ($K > 1$) indicating stabilizing selection for a particular body size across clades, with strepsirrhines being the smallest and hominids the largest and cercopithecids falling in-between. K values of artiodactyl and carnivoran body mass indicated great heterogeneity in body mass across clades. This is best exemplified by the carnivoran families Canidae and Felidae, which include both relatively large (e.g., wild dog *Lycaon pictus* and lion *Panthera leo*) and small (e.g., foxes *Vulpes* spp. and black-

footed cat *Felis nigripes*) species. The order-level phylogenetic signal of species' diets was low overall, but highest in artiodactyls. This perhaps reflects the overall limited dietary niche space of artiodactyls (see Figure 2.4) in which many species readily fall into a browser-grazer dichotomy.

Table 2.4. Phylogenetic signal in mammal functional traits across the three groups and three orders analyzed in this study. Phylogenetic signal was measured using Blomberg's K , which is a variance ratio measure of how conserved a trait is across a phylogeny of species. K values of one indicate that the trait matches a Brownian motion model of evolution, where trait variance among the tips of the tree is proportional to time. K values greater than one indicate high phylogenetic signal, where traits are strongly conserved across clades and most of the trait variation occurs between them. K values less than one indicate a low phylogenetic signal and that traits have convergently evolved across the tree and much of the trait variation is concentrated within clades. Overall, most traits analyzed here have very low K values with the exception of Primate body mass.

Group	Body Mass		Diet PCoA1		Diet PCoA2	
	K	p	K	p	K	p
Macromammals	0.667	0.001	0.157	0.001	0.169	0.001
Micromammals	0.215	0.001	0.133	0.001	0.149	0.001
Bats	0.103	0.001	0.276	0.001	0.296	0.314
Order						
Artiodactyla	0.481	0.001	0.348	0.001	0.158	0.001
Carnivora	0.547	0.001	0.115	0.002	0.076	0.156
Primates	1.086	0.001	0.104	0.002	0.169	0.001

3.3 Phylogenetic and functional trait structure of communities

Overall, there was a strong tendency across all groups towards phylogenetically random communities: over 90% of each group's communities were phylogenetically random (Table 2.5). The remaining communities tended to be phylogenetically clustered in macromammals (7.15%) and micromammals (2.59%) but were phylogenetically overdispersed in bats (3.20%). Results for overall order-level phylogenetic structure were similar (Table 2.5), with 94.98% of artiodactyl, 85.10% of carnivoran, and 98.30% of primate communities being phylogenetically random. The remaining order-level communities tended to be overdispersed, especially in carnivorans (14.90%).

Table 2.5. Summary of the phylogenetic structure of mammal communities across the three groups and three orders analyzed in this study. Groups are overwhelmingly phylogenetically random (> 90%), but the remaining communities tend to be phylogenetically clustered in macromammals and micromammals and overdispersed in bats. Across orders, many communities are also phylogenetically random, but some carnivoran communities are significantly overdispersed.

Group	Percent Clustered	Percent Random	Percent Overdispersed
Macromammals	7.15%	90.59%	2.26%
Micromammals	2.59%	97.41%	0%
Bats	0.91%	95.89%	3.20%
Order			
Artiodactyla	0.33%	94.98%	4.69%
Carnivora	0.00%	85.10%	14.90%
Primates	0.00%	98.30%	1.70%

Table 2.6. Summary of the functional trait structure of mammal communities across the three groups and three orders analyzed in this study. Percentages represent the proportion of communities with significant structure for a given trait (Body Mass, Diet PCoA1, Diet PCoA2) for each metric (Range, SDNDR).

Group	Range (Abiotic Filtering)			SDNDR (Biotic Interactions)		
	Body Mass	Diet PCoA1	Diet PCoA2	Body Mass	Diet PCoA1	Diet PCoA2
Macromammals	7.55%	0.03%	12.91%	3.62%	44.37%	6.63%
Micromammals	0.06%	2.12%	0.18%	0.11%	16.24%	13.03%
Bats	3.13%	16.93%	19.75%	2.20%	0.79%	5.91%
Order						
Artiodactyla	3.07%	1.53%	3.03%	0.28%	2.69%	0.21%
Carnivora	0.97%	41.54%	4.49%	8.86%	5.33%	3.22%
Primates	0.043%	0.02%	3.98%	13.82%	0.96%	3.72%

Community functional trait structure for groups varied by the metric and the trait analyzed with it (Table 2.6). Overall, diet appears to have a much stronger influence on mammal community assembly than does body mass. Macromammal communities were most strongly influenced by competitive interactions related to diet (SDNDR of diet PCoA1 is significant for 44.37% of communities). Micromammal communities were also influenced by dietary competition (16.24% and 13.03% of communities for SDNDR of diet PCoA1 and PCoA2, respectively). In contrast to these two groups, bat communities were most strongly influenced by abiotic filtering of diets (16.93% and 19.75% of diet PCoA1 and PCoA2 for Range). Order-level analyses of functional trait structure indicate

that most orders have communities that are more functionally random than was seen for the groups. Exceptions to this pattern include abiotic filtering of carnivoran diets (41.54% of communities had significant Range for diet PCoA1) and competition for primate body mass (13.82% of communities had significant SDNDR).

3.4 Community assembly across biomes

The phylogenetic structure of communities for mammal groups was mostly random across biomes (Table 2.7), but we highlight biomes that had the highest proportion of non-random communities. In macromammals, biomes that deviated from randomness include arid-fertile savannas (20.81% of communities), mopane savannas (18.22%), and sedge and reed swamps (36.84%), which had communities that were significantly phylogenetically clustered; the only biome to show moderate phylogenetic overdispersion was tropical lowland rainforest (13.06%). Afro-alpine micromammal communities were mostly phylogenetically clustered (53.33%), as were some in unpalatable grasslands (16.54%); no micromammal community was overdispersed across all biomes. Bat communities that deviated from randomness were both clustered, as in sedge and reed swamp (15.79%), and overdispersed, as in Afro-alpine (33.33%), shrubland and grassy semi-desert (10.60%), and unpalatable grassland (10.15%).

Table 2.7. Phylogenetic structure for groups by biomes. Groups are predominantly phylogenetically random across all biomes, with few exceptions. Abbreviations are: %C, percent clustered; %R, percent random; %O, percent overdispersed.

Biome	Macromammals			Micromammals			Bats		
	% C	% R	% O	% C	% R	% O	% C	% R	% O
Afro-alpine	0.00	100.00	0.00	53.33	46.67	0.00	0.00	66.67	33.33
Arid-fertile savanna	20.81	77.80	1.39	0.99	99.01	0.00	1.29	94.15	4.56
Desert	1.32	98.68	0.00	5.26	94.74	0.00	1.32	96.05	2.63
Dry forest and thicket	9.80	83.33	6.86	9.56	90.44	0.00	1.96	90.44	7.60
Fynbos	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00	0.00
Hydromorphic grassland	5.49	94.51	0.00	2.35	97.65	0.00	1.57	97.65	0.78
Moist-infertile savanna	5.18	94.57	0.25	1.81	98.19	0.00	0.60	97.99	1.41
Montane forest	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00	0.00
Mopane savanna	18.22	81.78	0.00	0.00	100.00	0.00	4.67	95.33	0.00
Mosaics of forest	0.22	97.28	2.50	0.22	99.78	0.00	0.55	99.34	0.11
Palatable grassland	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00	0.00
Sedge and reed swamp	36.84	63.16	0.00	0.00	100.00	0.00	15.79	84.21	0.00
Shrubland and grassy semi-desert	5.19	94.61	0.21	2.29	97.71	0.00	0.00	89.40	10.60
Succulent semi-desert	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00	0.00
Swamp forest and mangrove	0.00	100.00	0.00	0.00	100.00	0.00	0.00	94.44	5.56
Tropical lowland rainforest	0.00	86.94	13.06	0.00	100.00	0.00	0.00	99.14	0.86
Unpalatable grassland	0.75	96.24	3.01	16.54	83.46	0.00	0.00	89.85	10.15

For orders, community phylogenetic structure also tended to be phylogenetically random but there was much more variation (Table 2.8). For artiodactyls, deviation from randomness tended to be towards phylogenetic overdispersion. Artiodactyl communities in Afro-alpine (33.33%) and montane forest (22.22%) tended to be phylogenetically overdispersed, as were dry forest and thicket (7.35%) and mosaics of forest (9.06%), but to a lesser extent. No carnivoran communities were overdispersed across biomes, but several biomes showed phylogenetic overdispersion. Carnivoran communities that were overdispersed occurred in Afro-alpine (46.67%), arid-fertile savanna (28.37%), Fynbos (32%), hydromorphic grassland (21.18%), moist-infertile savanna (16.44%), palatable grassland (83.33%), sedge and reed swamp (15.79%), shrubland and grassy semi-desert (22.04%), succulent semi-desert (33.33%), and unpalatable grassland (29.32%) biomes. In contrast, virtually all primate communities had a random phylogenetic structure across biomes, with the exception of swamp and mangrove forest (16.67%), which was

phylogenetically overdispersed. No primate communities were phylogenetically clustered.

Table 2.8. Phylogenetic structure for orders by biomes. As with groups, many communities are phylogenetically random across biomes but both artiodactyls and carnivorans have many communities that are phylogenetically overdispersed in some biomes. Abbreviations are: %C, percent clustered; %R, percent random; %O, percent overdispersed.

Biome	Artiodactyla			Carnivora			Primates		
	% C	% R	% O	% C	% R	% O	% C	% R	% O
Afro-alpine	0.00	66.67	33.33	0.00	53.33	46.67	0.00	100.00	0.00
Arid-fertile savanna	0.42	95.59	3.99	0.00	71.63	28.37	0.00	100.00	0.00
Desert	0.00	100.00	0.00	0.00	93.42	6.58	0.00	100.00	0.00
Dry forest and thicket	0.00	92.65	7.35	0.00	94.61	5.39	0.00	95.81	4.19
Fynbos	0.00	100.00	0.00	0.00	68.00	32.00	0.00	100.00	0.00
Hydromorphic grassland	0.00	98.00	2.00	0.00	78.82	21.18	0.00	99.22	0.78
Moist-infertile savanna	0.00	98.32	1.68	0.00	83.56	16.44	0.00	99.09	0.91
Montane forest	0.00	77.78	22.22	0.00	100.00	0.00	0.00	100.00	0.00
Mopane savanna	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00	0.00
Mosaics of forest	0.00	90.94	9.06	0.00	98.25	1.75	0.00	97.49	2.51
Palatable grassland	0.00	100.00	0.00	0.00	16.67	83.33	0.00	100.00	0.00
Sedge and reed swamp	0.00	100.00	0.00	0.00	84.21	15.79	0.00	100.00	0.00
Shrubland and grassy semi-desert	3.67	95.87	0.46	0.00	77.96	22.04	0.00	100.00	0.00
Succulent semi-desert	0.00	100.00	0.00	0.00	66.67	33.33	0.00	100.00	0.00
Swamp forest and mangrove	0.00	88.89	11.11	0.00	100.00	0.00	0.00	83.33	16.67
Tropical lowland rainforest	0.00	88.87	11.13	0.00	100.00	0.00	0.00	93.58	6.42
Unpalatable grassland	0.00	87.97	12.03	0.00	70.68	29.32	0.00	99.13	0.87

Community functional trait structure was more varied for both groups and orders, and many communities deviated from random structure (Figure 2.6). For macromammals, abiotic filtering (inferred from the percentage of communities with significant Range) of body mass was weak overall except for in Afro-alpine communities (33.3%). Diet PCoA1 showed virtually no abiotic filtering across all biomes, but several communities in arid-fertile savanna (28.7%) and shrubland and grassy semi-desert (19.8%) had significant abiotic filtering for diet PCoA2. Roughly ~ 20% of macromammal communities in montane forest (22.2%) and sedge and reed swamp (21.1%) had body mass structures indicating competition (based on the percentage of communities with significant SDNDR). Diet was more strongly influenced by

competition, with eight biomes having > 50% of their communities structured by dietary competition for PCoA1, especially forests (mosaics of forest, 72.7%; tropical lowland rainforest, 85%). Communities structured by competition for PCoA2 also tended to be forests: dry forest and thicket (15%), mosaics of forest (14%), swamp forest and mangrove (16.7%), and tropical lowland rainforest (38.8%).

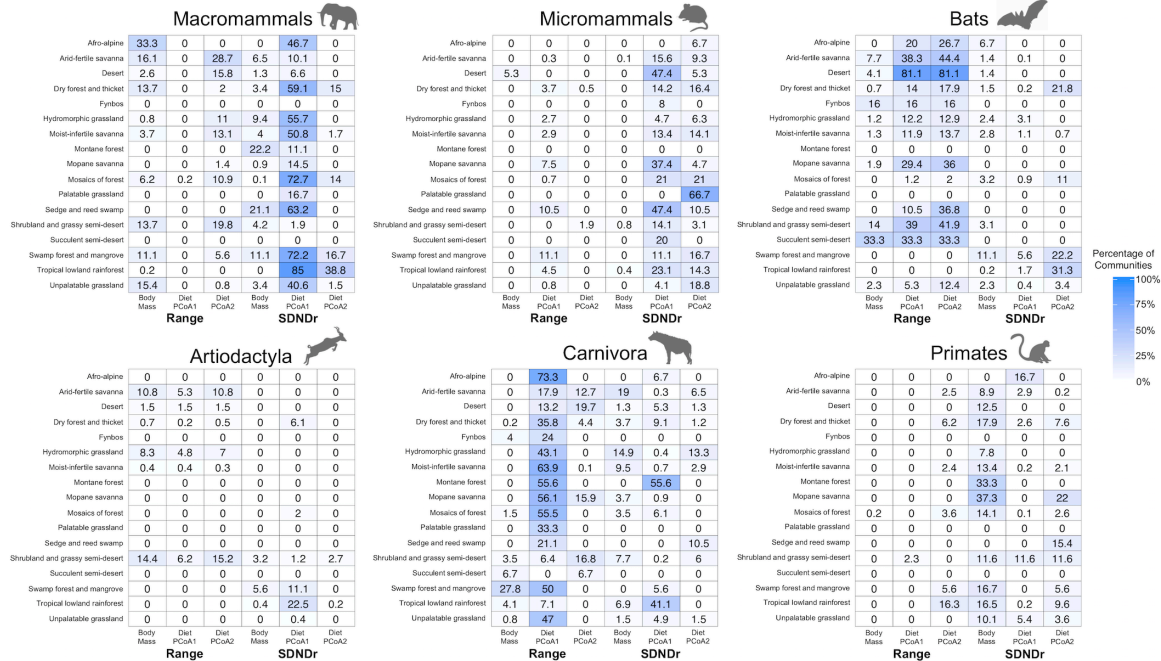


Figure 2.6. Heatmaps of the percentage of communities with significant Range and SDNdr for body mass and dietary (diet PCoA1, diet PCoA2) traits across biomes. Significant Range implies abiotic filtering of traits, whereas significant SDNdr implies a stronger influence of competition. Darker colors indicate a greater proportion of communities with significant functional trait structure. Overall, dietary variables have a stronger influence on community assembly than does body mass.

Abiotic filtering for all traits was weak across micromammal communities, although 11.1% of swamp forest and mangrove and 10.5% of sedge and reed swamp communities showed significant Range for diet PCoA1 (Figure 2.6). Competition was more influential on micromammal community functional trait structure, especially for diet PCoA1 as was the case for macromammals. Deserts (47.4%), sedge and reed swamp

(47.4%), and mopane savanna (37.4%) were most strongly influenced by diet PCoA1 competition, whereas diet PCoA2 competition was strongest in palatable grasslands (66.7%).

Bat communities were more strongly influenced by abiotic filtering than competition (Figure 2.6). Abiotic filtering for body mass was found in succulent semi-desert (33.3%), fynbos (16%), and shrubland and grassy semi-desert (14%) bat communities. Abiotic filtering for diet PCoA1 was found in deserts (81.1%), shrubland and grassy semi-desert (39%), arid-fertile savanna (38.3%), succulent semi-desert (33.3%), and mopane savanna (29.4%), among others. Diet PCoA2 was similar to diet PCoA1, in that bat communities in deserts (81.1%), arid-fertile savannas (44.4%), shrubland and grassy semi-desert (41.9%), mopane savanna (36%), and succulent semi-desert (33.3%) showed significant abiotic filtering, along with those in sedge and reed swamps (36.8%). Competition in bat communities was weak, with only 11.1% of communities in swamp forest and mangroves showing significant body mass competition, and 31.3% of tropical lowland rainforests, 22.2% of swamp forest and mangroves, 21.8% of dry forest and thickets, and 11% of mosaics of forest communities showing significant competition for diet PCoA2.

For order-level community functional trait structure, artiodactyl communities were weakly influenced by assembly processes overall (Figure 2.6), but abiotic filtering was stronger than competition. For body mass, communities in shrubland and grassy semi-desert (14.4%) and arid-fertile savannas (10.8%) were structured by abiotic filtering, as was the case for these biomes for diet PCoA1 (15.2% and 10.8%, respectively). Competition was only influential in artiodactyl communities found in tropical lowland rainforests (22.5%) and swamp forest and mangroves (11.1%).

Carnivoran communities were structured both by competition and abiotic filtering (Figure 2.6), although the latter dominated, especially for diet PCoA1. Only carnivoran communities in swamp forest and mangroves (27.8%) were significantly structured by abiotic filtering of body mass, whereas six biomes had > 50% of their communities structured by abiotic filtering for diet PCoA1. Abiotic filtering for diet PCoA1 was strongest in Afro-alpine (73.3%) communities. Abiotic filtering for diet PCoA2 was strongest in deserts (19.7%), shrubland and grassy semi-desert (16.8%), mopane savanna (15.9%), and arid-fertile savanna (12.7%). Communities with body mass distributions structured by competition were found in arid fertile savannas (19%) and hydromorphic grasslands (14.9%), while competition for diet PCoA1 was found in montane forests (55.6%) and tropical lowland forests (41.1%). Competition only weakly influenced community structure of diet PCoA2 in hydromorphic grasslands (13.3%) and sedge and reed swamps (10.5%).

Primate communities were most strongly influenced by competition (Figure 2.6), but tropical lowland rainforests (16.3%) showed abiotic filtering for diet PCoA2. Competition most strongly influenced body mass structure for primates, with mopane savanna (37.3%), montane forests (33.3%), dry forest and thicket (17.9%), swamp forest and mangroves (16.7%), and tropical lowland rainforests (16.5%) showing competition-structured body mass distributions. Afro-alpine (16.7%) communities were structured by diet PCoA1 competition, while mopane savanna (22%) and sedge and reed swamps (15.4%) were shaped by diet PCoA2 competition.

3.5 Continent-wide climatic controls on community assembly

Figure 2.7 shows the regression coefficients from SAR_{err} models predicting NRI,

Range, and SDNDR from six climate variables (mean annual temperature (MAT), temperature seasonality (TS), temperature of the coldest month (TCM), mean annual precipitation (MAP), precipitation seasonality (PS), precipitation of the driest month (PDM)). Results varied greatly across the groups and orders but overall NRI was more poorly predicted than functional trait structure metrics. In the following text the symbol + is used to denote a positive relationship between variables and - is used to denote a negative relationship between variables. I only focus on the most influential predictors, but full model results can be found in SI Tables 1-54.

Macromammal NRI was influenced by TS (+), TCM (-), and PS (-), all of which had roughly the same influence. For macromammal Range the most important predictors were MAT (+) for body mass, PS (+) for diet PCoA1, and TCM (-) and MAT (+) for diet PCoA2. For macromammal SDNDR the most important predictors were PS (+) for body mass, PDM (+) for diet PCoA1, and TCM (-) and MAT (+) for diet PCoA2.

Micromammal NRI was most strongly influenced by MAP (-). Micromammal Range was best predicted by MAT (+) and TCM (-) for body mass and diet PCoA1, but diet PCoA2 had no significant predictors. Micromammal SDNDR was influenced most strongly by TCM (-) for body mass, MAT (+) and TCM (-) for diet PCoA1, and PDM (+) and PS (+) for diet PCoA2. Bat NRI was only significantly influenced by MAP (+). Bat Range was most strongly influenced by TS (-) for body mass and TCM (+) for both diet PCoA1 and diet PCoA2. Bat SDNDR was weakly predicted by TS (+) for body mass and MAP (-) for diet PCoA1, but was more strongly influenced by MAT (+) for diet PCoA2.

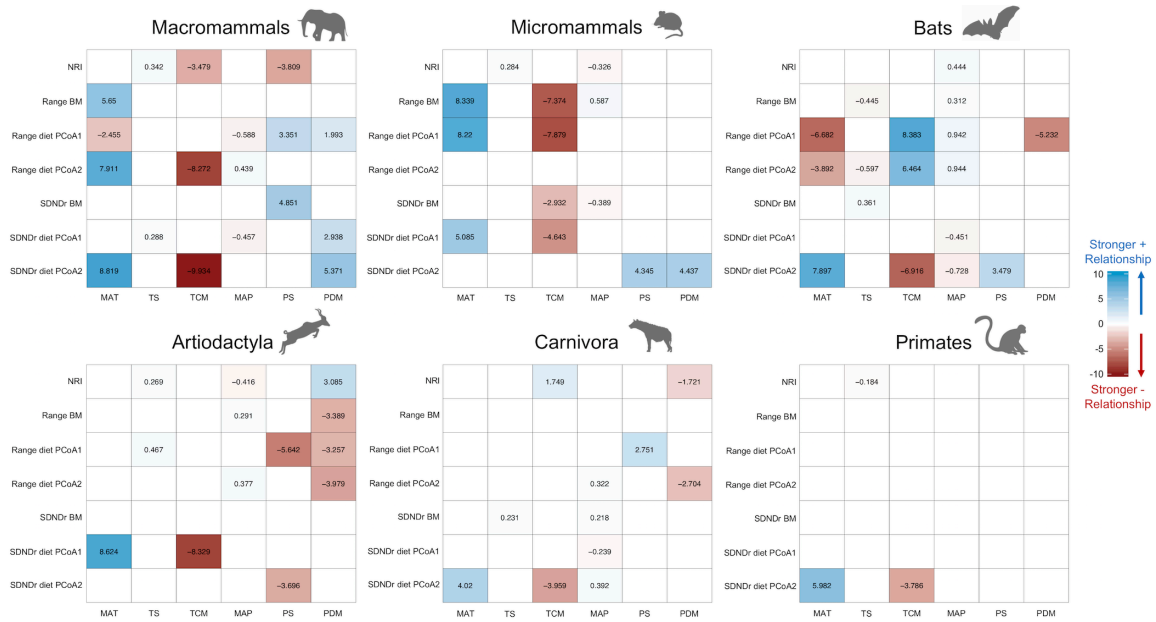


Figure 2.7. Heatmaps of regression coefficients from SAR_{err} models using six climate variables to predict the phylogenetic and functional trait structure of communities. For each group or order, each row represents the coefficients from a single linear model with predictor variables (climate variables) shown on the x-axis and response variables (phylogenetic or functional trait structure metrics) shown on the y-axis. Predictors are colored by the direction and strength of their relationship with the response variable: blue indicates a positive relationship and red indicates a negative relationship; blank boxes indicate a non-significant predictor. Abbreviations are: BM, body mass; MAT, mean annual temperature; TS, temperature seasonality; TCM, temperature of the coldest month; MAP, mean annual precipitation; PS, precipitation seasonality; PDM, precipitation of the driest month.

Order-level models were weaker predictors of community structure, but artiodactyl communities were the best predicted overall (Figure 2.7). Artiodactyl NRI was influenced by PDM (+), while Range was influenced by PDM (-) for body mass, PS (-) for diet PCoA1, and PDM (-) for diet PCoA2. Artiodactyl body mass SDNdr had no significant predictors, but SDNdr for diet PCoA1 was more or less equally influenced by MAT (+) and TCM (-), while diet PCoA2 was influenced by PS (-). Carnivoran NRI was influenced by TCM (+) and PDM (-). Carnivoran Range had no significant predictors for body mass, but was influenced by PS (+) for diet PCoA1 and PDM (-) for diet PCoA2. Primate community structure was poorly predicted by climate variables. Primate NRI was

weakly influenced by TS (-) and primate diet PCoA2 SDNDr was influenced by MAT (+) and TCM (-); all other models were non-significant.

4. Discussion

4.1 Phylogenetic signal of ecological traits and consilience of community metrics

The first question we asked was “if ecological traits are phylogenetically conserved, do phylogenetic and functional trait structure metrics track one another?”; we predicted that if functional traits had a high phylogenetic signal, then analyses of phylogenetic and functional trait structure should track one another (H_1). This question cannot be adequately answered by our study because virtually all of the traits analyzed here had a very low phylogenetic signal (Table 2.4; Figure 2.5). This is a significant result in itself because it suggests that the bedrock assumption of phylogenetic community ecology – that important ecological traits are phylogenetically conserved and therefore relatedness can be used as a proxy of ecological similarity (Webb, 2000; Webb et al., 2002) – does not hold, at least in African mammals. Several studies have used phylogenetic relatedness as a proxy for ecological similarity without ever testing this assumption (e.g., Cooper et al., 2008; Kamilar et al., 2015; Kissling et al., 2012) and thus the conclusions drawn in these studies are potentially spurious. It is important for future studies to either demonstrate phylogenetic niche conservatism of important ecological traits or, preferably, analyze the phylogenetic signal of traits along with the phylogenetic and functional trait structure of communities. Analyzing both the phylogenetic and functional trait structure of communities with knowledge of ecological trait conservatism provides a robust way of probing what drives community structure along these different dimensions.

The low phylogenetic signal of body mass and diet in almost all groups and orders analyzed here leads to very different inferences regarding the importance of abiotic filtering versus competition in structuring communities. For example, many carnivoran communities were phylogenetically overdispersed (Table 2.8), which would be interpreted as reflecting competition and niche partitioning for resources among closely related and ecologically similar species. In contrast, functional trait analyses of carnivoran communities found significant clustering of diet PCoA1 in many biomes (Figure 2.6), suggesting species with similar diets co-occur more often than expected by chance. The only way that these two results are reconcilable is by accepting that either the traits analyzed here are unimportant in community assembly or that the traits are not phylogenetically conserved. With respect to the first scenario, it is true that any study of community functional trait structure must carefully select traits based on the biology and ecology of the clade of interest (Petchey and Gaston, 2006). Selection of traits irrelevant to community assembly (i.e., those that do not determine dispersal limitation or potential for competition) may lead to incongruence between phylogenetic and functional trait analyses of community structure. It would be difficult to argue, however, that the traits analyzed here (body mass and diet) are unimportant in mammalian community assembly, although other traits such as habitat preference and activity pattern are also certainly important. Thus, one is left with the second scenario, which is confirmed by the direct analysis of trait phylogenetic signal. Recognition of weak niche conservatism of body mass and diet in African mammals clarifies the incongruence between the phylogenetic and functional trait structure of communities found in this study. It does not, however, reveal the drivers of community phylogenetic structure. Although many communities

were phylogenetically random, several were not, which begs the question – what determines the phylogenetic structure of communities?

Over half (53.3%) of Afro-alpine micromammal communities were phylogenetically clustered, which is to be expected based on previous studies that have shown high clade endemism in tropical mountain systems, especially in Africa (Schipper et al., 2008; Rosauer and Jetz, 2015). Afro-alpine micromammal communities are overwhelmingly comprised of endemic rodent and shrew lineages, such as the rodent genera *Desmomys* and *Stenocephalemys* and the *Crocidura glassi* species-complex in the Ethiopian Highlands (Yalden and Largen, 1992), which contains the greatest proportion of the Afro-alpine biome (Happold and Lock, 2013; White, 1983). Likewise, the equatorial Eastern Arc Mountains are well-known for their high diversity of endemic or near-endemic lineages, including several micromammals (Burgess et al., 2007), as well as those from the Albertine Rift (e.g. *Ruwenzorisorex* and *Delanymys*) (Plumptre et al., 2007). It is possible, perhaps likely, that the phylogenetic clustering of micromammal communities in Afro-alpine habitats simply reflects the colonization of this biome by a handful of lineages that subsequently radiated within it. Thus, the phylogenetic structure of communities would be more indicative of historical biogeography than community assembly processes when important ecological traits are not conserved.

Support for the historical biogeography hypothesis is also found among carnivoran communities that, as mentioned above, tended to be phylogenetically overdispersed when they deviated from randomness (no carnivoran community was phylogenetically clustered). This is not surprising when considering carnivoran biogeography – almost all carnivoran families, regardless of how diverse they are, have species adapted to the full range of African environments. For example, among

Herpestidae (26 African species) the meerkat *Suricata suricatta* and Kaokoveld slender mongoose *Herpestes flavescens* are restricted to hyper-arid regions near the Kalahari while other taxa are exclusive to rainforests, such as the genera *Crossarchus* and *Xenogale* (Kingdon, 2015). This degree of habitat breadth can be found in even the most species-poor families, such as Hyaenidae (4 species). Spotted hyenas *Crocuta crocuta* are the most ubiquitous large carnivoran in Africa and are found in virtually every African environment except extreme desert and dense rainforests (East and Hofer, 2013). It is the great habitat breadth and geographic extent of almost all carnivoran families, regardless of how specious they are, that leads to the emergence of similar phylogenetic structure in biomes that are otherwise very different. For example, both Afro-alpine and palatable grassland biomes had a significant proportion of carnivoran communities overdispersed (46.67% and 83.33%, respectively). These biomes have similar phylogenetic structure in that they contain large (*Panthera* spp.) and small felids (*Caracal*, *Leptailurus*), large hyaenids (*Crocuta*), large (*Canis* and *Lycaon*, respectively) and small canids (*Canis* spp.), genets (*Genetta* spp.), civets (*Civettictis*) and herpestids (*Herpestes* spp.). Thus, despite differences in climates and environments, these biomes sample virtually the entire range of African carnivoran phylogeny and therefore have overdispersed phylogenetic structures.

Other studies have reached similar conclusions regarding the drivers of community phylogenetic structure at large spatial scales. A global analysis of ruminant communities by Cantalapiedra et al. (2013) found that historical biogeography strongly influenced phylogenetic community structure. For example, phylogenetically clustered Neotropical ruminant assemblages reflect the single colonization of this realm by a subset of a more widely dispersed Palearctic clade during Pliocene faunal exchange in the Americas.

Likewise, phylogenetically clustered ruminant assemblages occur in the Sahara Desert, the Arabian Desert, and the southwestern Arabian savannas, all of which are relatively young biomes (later Neogene) colonized by two tribes of arid-adapted bovids (Antilopini and Hippotragini). Older biomes, such as southeast Asian rainforests, were phylogenetically overdispersed because their long history has permitted colonization by several ruminant lineages in addition to their retention of very basal clades (e.g., Tragulidae).

Kissling et al. (2012) showed that the global phylogenetic structure of palm assemblages is strongly linked to the history of isolation and dispersal of different lineages throughout the Cenozoic, as well as Cenozoic climate and biome change. Thus, the phylogenetic structure of communities, whether they be plants or animals, primarily reflects deep-time events in the history of clades. If traits are conserved, then the phylogenetic structure of communities may also reflect ‘re-shuffling’ of species and their traits during community assembly, but that is not the case for African mammals. Most African mammal communities are phylogenetically random and those that deviate from this pattern seem to have deep-time causes.

4.2 Community assembly processes across mammal groups and orders

The second question we asked was “does the relative influence of community assembly processes differ across mammal groups and, if it does, how so?” We predicted that the relative influence of competition and abiotic filtering would differ across mammal groups and orders (H_2). Macromammal communities were predicted to be overdispersed, while micromammal and bat communities were predicted to be largely clustered or randomly structured. This was based on the notion that small mammals are

more dispersal limited than large mammals (Bowman et al., 2002) and therefore competition should have a stronger role in shaping large mammal communities, whereas smaller mammals are subject to stronger abiotic filtering. Carnivoran communities were expected to be overdispersed, while primates and artiodactyls were expected to be clustered or random, reflecting either abiotic filtering or a mix of assembly processes. These hypotheses were formulated based on evidence for intense competition within the carnivore guild (Creel and Creel, 1996; Durant, 1998) and the fact that primates and ungulates are mostly primary consumers and are therefore tightly linked to specific environments. We focus only on assembly processes inferred from the functional trait structure of communities because of weak niche conservatism (Table 2.4; Figure 2.5).

Macromammal communities were most strongly influenced by dietary competition as 51% had significant SDNDR for diet PCoA1 and diet PCoA2. This indicates that the 'dietary niche space' of these communities is more evenly spaced than would be expected from a random draw of species from the regional pool, which supports the hypothesis that dispersal limitation is weak on large mammals (here, > 500g) and that competition is the primary modulator of macromammal community composition. This result is further supported by previous studies that have suggested that dietary competition might be the strongest influence in structuring mammal communities because food is a limited resource in virtually all environments (e.g., Roughgarden, 1986). A small number of communities, however, did show weak evidence for abiotic filtering of body mass (7.55% of communities had significant Range) and diet PCoA2 (12.91% of communities had significant Range), suggesting that this process can also be important.

Micromammal communities, as with macromammals, were strongly influenced by dietary competition, but to a lesser degree (only 30.17% of communities had significant diet SDNDR). Thus, the hypothesis that micromammal communities are shaped primarily by dispersal limitation is not supported. Although studies with which to compare this result are scant for Africa, several long-term studies of the taxonomically and functionally diverse rodent communities of the American southwest are available (Fox and Brown, 1993; Heske et al., 1994; Kelt and Brown, 1999; Brown et al., 2000). Important to note is that these studies demonstrate how the effects of competition at local scales (e.g., abundance shifts, microhabitat differentiation) scale up to affect local distributions and, in turn, the presence or absence of species in communities. The signature of interspecific competition is therefore reflected in non-random community structures at large geographic scales (Brown et al., 2000), a cornerstone assumption of the analyses used in the present work. In the American southwest, coexisting rodent species are more distant in their functional traits than expected from a random draw of the regional species pool, especially when considering dietary guilds (Fox and Brown, 1993; Brown et al., 2000). Similar results were found for Australian (Fox, 1987), North American (Fox and Kirkland, 1992), and South American (Kelt et al., 1995) small mammal communities, suggesting dietary competition is particularly intense amongst micromammals.

Bat communities were most strongly influenced by abiotic filtering of diets (Range was significant for ~ 37% of communities for diet PCoA1 and diet PCoA2 combined). Compared to macromammals and micromammals, bats have the most specialized diets (e.g., compare their multivariate dispersion to other groups and orders in Figure 2.4). This is especially true for the echolocating (i.e., non-pteropodid) species

which have evolved complex motor and sensory systems that have interlinking morphological, behavioral, and physiological adaptations for detecting insect prey at night (Schnitzler and Kalko, 2001; Schnitzler et al., 2003). Furthermore, competition among insectivorous bats is likely mitigated by the sheer abundance and diversity of insect prey in the tropics (Ballesteros-Mejia et al., 2017). As in this study, Heller and Volleth (1995) found that wing morphology (which is tightly linked to diet (e.g., Monadjem et al., 2010; Patterson et al., 2003)) was a more important variable in driving bat community structure than body mass in their comparisons of New World and Old World insectivorous bat communities. Bats on both continents had radiated into very specific foraging niches, irrespective of body size variation, and were evolutionarily constrained in their foraging niches (Heller and Volleth, 1995).

Aside from the echolocating bats, the remaining African species are comprised of frugivorous and nectivorous pteropodids. These bats are non-echolocating, except for cave-dwelling *Rousettes* spp. and *Lissonycteris angolensis* that have convergently evolved echolocation via tongue-clicking (true echolocators use laryngeal signals). The distribution of pteropodids is largely determined by the seasonal availability of fruits and flowers and some taxa undergo seasonal migrations to track these resources. For example, the five- to ten- million individual population of straw-colored fruit bat *Eidolon helvum* in Kasanka National Park, Zambia, undertakes annual migrations over 2500 km following seasonal pulses of fruit production (Richter and Cumming, 2006, 2008). Others have evolved strong symbiotic relationships with plant species such as baobabs (*Adansonia digitata*), which are pollinated almost exclusively by pteropodids, mostly epauletted bats *Epomophorus* spp. (Monjadem et al., 2010). Indeed, several hundred plant species in the Old World tropics rely on bat pollination (Fujita and Tuttle, 1991), while ~

95% of forest regrowth in tropical Africa is attributed to seed dispersal by frugivorous bats (Monjadem et al., 2010). The tight integration between pteropodids and fruit- and nectar-productive habitats, then, explains why this portion of Africa's bat fauna is subject to strong abiotic filtering of diets. Collectively, the results for echolocating bats and pteropodids support the hypothesis that bat communities are more strongly influenced by abiotic filters related to diet than by competitive interactions.

Artiodactyl communities were mostly functionally random. Only ~ 3% of communities had significant Range for body mass or diet PCoA1, and 2.69% had significant SDNDR for diet PCoA1. Thus, the hypothesis that artiodactyl communities are primarily shaped by abiotic filtering is not supported, although it is important to note that although artiodactyls comprise most of the African herbivore guild, they are not the only members. Perissodactyls (rhinoceroses and zebras) and proboscideans (elephants) were not considered here but have well-known competitive or facilitative interactions with sympatric artiodactyl species. For example, Fritz et al. (2002) showed that the abundance of savanna elephants *Loxodonta africana* negatively influences medium-sized mixed-feeders and browsers, most of which are bovids. On the other hand, plains zebra *Equus quagga* initiate the annual Serengeti migration and facilitate the movement of blue wildebeest *Connochaetes taurinus* and Thomson's gazelles *Eudorcas thomsoni* across the western portion of the ecosystem during the grazing succession (Bell, 1970, 1971). Therefore, any analysis of artiodactyl communities without other ungulate taxa that have competitive, facilitative, mutualistic, or commensalistic interactions is likely incomplete. Furthermore, the influence of domestic species (i.e., cattle, goats, and sheep) was not considered although it is well-known that they influence the composition of wild artiodactyl communities, especially in pastoralists lands of eastern Africa (Du Toit and

Cumming, 1999; Odadi et al., 2011). Finally, a third potential explanation for the functional randomness of artiodactyl communities is that they have lost several critical components during Quaternary extinctions. Although Quaternary extinctions have historically been considered to have been minor in Africa (Barnosky et al., 2004), recent fossil evidence has documented a large number of extinct artiodactyls, many of which persisted to the Pleistocene-Holocene boundary or beyond. These include extinct aepycerotin (*Aepyceros* sp. nov.), alcelaphin (*Damaliscus hypsodon*, *Megalotragus priscus*, *Rusingoryx atopocranium*), antilopine (*Antidorcas australis*, *A. bondi*), bovine (*Syncerus antiquus*), and hippotragin (*Hippotragus leucophaeus*) bovids, as well as the suid genera *Kolpochoerus* and *Metridiochoerus* (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Faith et al., 2012; Faith, 2014). Although no formal analysis of functional changes in Quaternary African artiodactyl communities has been published, the available evidence for eastern Africa suggests that the functional composition of late Pleistocene communities differed markedly from those in the region today. In addition to facilitative extinction, local extirpation of ungulate species in eastern Africa during the late Pleistocene (e.g., beisa oryx *Oryx beisa*, Grevy's zebra *Equus grevyi*) contributed to relatively recent changes to community structure (Marean and Gifford-Gonzalez, 1991), which, among the other reasons noted above, may contribute to the functional randomness of modern artiodactyl communities in Africa.

Carnivoran communities were strongly influenced by abiotic filtering of diet (~46% of communities had significant Range for diet PCoA1 and diet PCoA2). The prediction that carnivoran communities are mostly shaped by competition is unsupported, although it is unlikely they are subject to abiotic filtering as commonly understood. Abiotic filtering of carnivoran diets is likely not a direct effect of the environment, but

rather a bottom-up effect of climate determining local vegetation that, in turn, determines prey availability for many carnivoran species. For example, Sandom et al. (2013) found that predator and prey species richness patterns were tightly linked across most of continental Africa, especially among large predators and their prey. Large carnivorans like lions *Panthera leo*, cheetah *Acinonyx jubatus*, and spotted hyenas *Crocuta crocuta* are strongly dependent on large ungulate prey in open to mixed cover environments, mainly in eastern and southern African savannas (Hayward, 2006; Hayward and Kerley, 2008). These species cannot persist in closed environments because forest ungulates are smaller, cryptic, and often solitary, making them much more difficult to locate compared to large-bodied and gregarious savanna ungulates (Bro-Jørgensen, 2008; Jarman, 1974). Other examples include otters (*Aonyx* spp., *Hydrictis maculicollis*) being tied to permanent water sources for aquatic prey and genets (*Genetta* spp.) being tied to forests for fruit and large invertebrate prey. Thus the ‘abiotic filter’ inferred for carnivoran diets is only indirectly abiotic – rather, it is related to the prey that occurs in specific environments, which are ultimately determined by abiotic factors.

Primate communities were mainly influenced by body mass competition (~ 14% of communities had significant SDNDR for body mass), which is surprising given that diet was most important for other groups and orders. This is likely related to the fact that nearly all primates are dietary generalists, and many are omnivorous, whereas other mammal clades have much lower dietary diversity and are dominated by specialists (Janson and Chapman, 1996; Price et al., 2012). In Africa, work on forest guenons (*Cercopithecus* spp.) has shown that resource switching facilitates multi-species associations and limits food competition (Chapman and Chapman, 1990; Gautier-Hion, 1988; Lambert, 2004). Lambert (2004) attributed the dietary flexibility of guenons to

their generalized digestive systems, but resource switching has also been documented for several colobine species. For example, leaves comprise 89% of the annual diet of populations of *Colobus guereza* in Kibale, Uganda, while those from Kakamega, Kenya, have diets made up of 81% fruit when this resource is abundant (Fashing and Oates, 2013). Baboons (*Papio* spp.) are perhaps the most extreme generalists among African primates; populations of olive baboon *Papio anubis*, for example, depend on a variety of food items including stems, leaves, ripe and unripe fruit, eggs, insects, small vertebrates (e.g., frogs, lizards, birds), and even large vertebrates (e.g., monkeys and small antelope) (Palombit, 2013).

In light of the above examples, the finding that competition for food resources is less intense in primates than in other mammals is not surprising. Body mass, on the other hand, is phylogenetically conserved across African primates (Table 2.4) and is correlated with several variables that might influence community assembly and species coexistence, including group size and population density (Janson and Goldsmith, 1995), predation susceptibility (Isbell, 1994), activity pattern (Fleagle, 2013), and life history rates (Harvey and Clutton-Brock, 1985). Body mass may also influence competition for non-food resources, such as sleeping sites (Bearder et al., 2003). Body mass is therefore a good 'proxy variable' for other important ecological and behavioral attributes of primate species that determine their potential for coexistence or competition. This is consistent with prior studies of primate community structure in Africa. For example, Ganzhorn (1996) found that body mass ratios between co-occurring species increased with species richness in African haplorhine communities, suggesting increased niche partitioning of body mass correlates (see above) as communities become more specious.

4.3 Community assembly across biomes and climates

The third and fourth questions we asked were “within mammal groups, how does the relative influence of community assembly processes differ across biomes?” and “are there continental-wide relationships between community assembly processes and climate?” As these questions are related, we discuss them together here. These questions were addressed by analyzing community functional trait structure at the biome-level (see Section 3.4 in Results) and continent-wide analyses of climatic correlates of community structure (see Section 3.5 in Results). These analyses are closely related, as differences in climate and, in turn, vegetation, delimit biomes across the African continent (White, 1983; Happold and Lock, 2013). It was predicted (H_3 and H_4) that the relative influence of competition versus abiotic filtering within a given group or order varies along a gradient based on the biome’s overall productivity: biomes with high net primary productivity (NPP) are expected to be overdispersed, reflecting strong competition for resources, whereas those with low NPP are expected to be clustered, reflecting filtering of species with specialized ecological and physiological adaptations (Graham et al., 2009; Dreiss et al., 2015). Correlations between functional trait structure and NPP are discussed below and the strongest relationships are shown in Figure 2.8, although all are provided in SI Figures 13-18. For reference, we provide boxplots of climate variables across biomes in SI Figures 19-24. It is important to note that although significant Range values are elsewhere interpreted as reflecting a non-random trait distribution due to abiotic filtering, all Range values (both significant and non-significant) were analyzed in the linear models. Therefore, in these models, increasing Range cannot be interpreted as reflecting stronger abiotic filtering. Instead, Range reflects the overall trait range of a

community (see Figure 2.3) and thus provides a simple proxy of the ecological diversity of a community. This is an important distinction for the following discussion.

Macromammal communities strongly support the prediction that competition dominates in high productivity environments. Mean biome NPP has a strong positive correlation ($r=0.73$) with SDNDR of diet PCoA1 (Figure 2.8), meaning that co-occurring species in high productivity biomes (e.g., tropical lowland rainforests, mosaics of forest) have either excluded functionally similar competitors or have differentiated their niches to alleviate competition. Macromammal communities in low productivity biomes (e.g., succulent semi-desert, shrubland and grassy semi-desert) are mostly random, suggesting that competitive interactions are weak or that a mixture of assembly processes operate evenly (Figure 2.6). Similarly, mean annual temperature (MAT) was the strongest climatic predictor across all traits and metrics, and body mass Range, diet PCoA2 Range, and diet PCoA2 SDNDR had strong positive relationships with MAT (Figure 2.7). This indicates that although the body mass and dietary diversity of macromammal communities (inferred from overall trait range) is positively related to MAT and, in turn NPP, only dietary competition significantly increases in high productivity environments. Body mass SDNDR is unrelated to NPP ($r=-0.07$) and is not correlated with MAT or mean annual precipitation (MAP) implying that macromammal communities are randomly structured in their body mass distributions regardless of overall productivity. Body mass SDNDR is positively related to precipitation seasonality (PS), however, suggesting that body mass competition is important in highly seasonal environments, most of which are savannas or grasslands in Africa.

Overall, macromammal communities are most strongly structured by dietary competition that increases with productivity, as predicted in H₃ and H₄. The biome with

the most intense dietary competition is tropical lowland forest, which also has the highest NPP of all biomes; mosaics of forest and dry forest and thicket also have relatively high NPP and strong dietary competition (Figure 2.7). Thus, our results suggest that forested and semi-forested biomes provide the greatest venue for competition among large-bodied mammals, which we propose is linked to the variety, abundance, and temporal stability of food resources they provide. For example, forests have exceptionally high plant diversity compared to other biomes of Africa and are abundant in fruit-bearing species (e.g., *Ficus* spp.) that provide important food resources for many mammals (White, 1983; Happold and Lock, 2013). By virtue of their stratified canopy structure, forests also allow mammal species to differentiate their locomotor and, as a consequence, feeding behaviors by foraging at different levels of the canopy. This phenomenon has been well-documented for primates (Thomas, 1991; Kamilar and Ledogar, 2011), but likely applies to other mammal clades that include predominantly terrestrial, terrestrial-arboreal, and arboreal species (e.g., Viverridae). Forests are also relatively aseasonal – e.g. the, one- to two-month dry season in the Congo (Happold and Lock, 2013) – meaning that food resources for a variety of mammal species are available more or less year-round.

Dietary competition had a strong positive relationship to NPP ($r=0.49$) in micromammal communities (Figure 2.8), as was the case for macromammals. Likewise, MAT was the strongest climatic predictor of body mass Range, diet PCoA1 Range, and diet PCoA1 SDNDR (Figure 2.7), all of which were positive relationships. Collectively, these results suggest that the overall ecological diversity of micromammal communities increases in high productivity environments, but only dietary competition is an important assembly process, as was found for macromammals. SDNDR for diet PCoA2 was positively related to PS and precipitation of the driest month (PDM), implying that

dietary competition can also be strong in environments with seasonal rainfall but receive relatively high precipitation (Figure 2.7). Our results for micromammal communities are consistent with previous studies linking community assembly to climatic and productivity gradients. For example, Dreiss et al. (2015) found that lowland rainforest rodent communities in the Manu Biosphere Reserve of southeastern Peru were mainly structured by interspecific competition in comparison to high elevation montane vegetation biomes. They proposed that the vertical and structural complexity of forests likely facilitates niche differentiation between competing species, as we have suggested above for African macromammals.

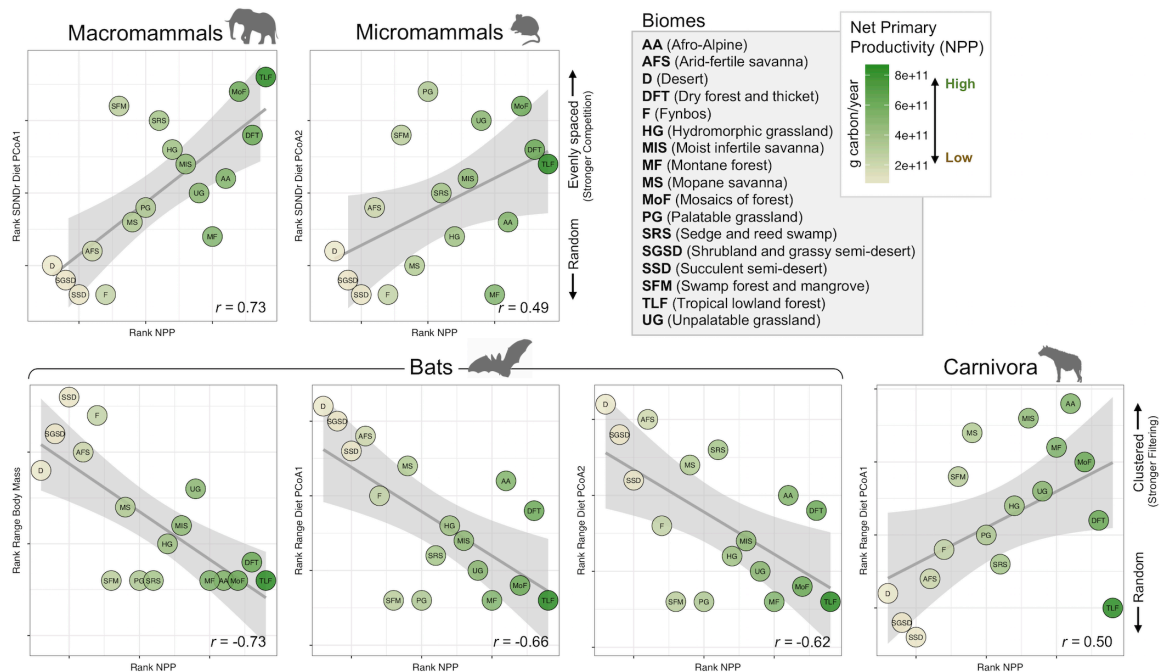


Figure 2.8. Rank correlations between mean net primary productivity (NPP) and community functional trait structure of groups and orders across biomes. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric. Dietary competition (SDNDR) increases with NPP in macromammals and micromammals, whereas low NPP environments impose a strong filter on body mass and diet in bats. Carnivoran diets become more clustered as NPP increases. Biome classifications from White (1983) and NPP data from NASA and the Center for International Earth Science Information Network (Imhoff et al., 2004).

The strength of abiotic filtering of African bat communities is very clearly influenced by NPP (Figure 2.8). Body mass Range was most strongly related ($r=-0.73$) to NPP, but diet was also heavily influenced by this variable (diet PCoA1 $r=-0.66$; diet PCoA2 $r=-0.62$). The strongest predictor of Range for diet PCoA1 and diet PCoA2 was TCM, to which they were positively related, meaning that environments with warmer minimum temperatures have a greater ecological diversity of bats than those with lower minimum temperatures (Figure 2.7); this is consistent with the results for NPP. Likewise, deserts, shrubland and grassy semi-desert, and succulent semi-desert all showed strong abiotic filtering of bat communities, while those from tropical lowland rainforests, swamp forests and mangroves, and montane forests had no filtering (Figure 2.6).

Our results for bat communities contrasts with those from previous studies. For example, Cisneros et al. (2014) found that phylogenetic dispersion, assumed to reflect competition, in South American bat assemblages is highest in low productivity montane environments. This contradicts our findings that low productivity environments select for similar ecological traits (which these authors infer from phylogenetic proximity). The study of Cisneros et al. (2014) implies intense competition among bats when resources and productivity is low. Their results, however, are largely based on results of phylogenetic community structure and they did not test for ecological niche conservatism among taxa examined, which we found to be weak for African bats. Indeed, Cisneros et al. (2014) found that bat functional trait diversity does not vary much across elevation and productivity gradients, suggesting different drivers of community phylogenetic and functional trait structure, as implied here for African bats. It is then clear that more research is needed to determine how bat community assembly, which has received far less attention compared to larger mammal species, varies across continents and biomes.

Artiodactyl community structure was unrelated to NPP (SI Figure 16), which is perhaps not surprising given that most artiodactyl communities were functionally random. Diet PCoA1 SDNDR, however, had a strong positive relationship to MAT and a strong negative relationship to TCM (Figure 2.7), implying that dietary competition is relatively important in artiodactyl communities in warmer climates with relatively cool periods of the year, such as savannas and grasslands (see SI Figure 19 and SI Figure 21). In agreement with this finding, niche partitioning, the outcome of competition – either by niche divergence or competitive exclusion – has been well-documented among savanna artiodactyl communities. Sinclair (2000) reviewed examples of how co-occurring bovid species have differentiated themselves in terms of habitat and dietary requirements. For example, Gwynne and Bell (1968) and Bell (1970, 1971) showed that sympatric bovids in Serengeti National Park differentiated along soil catenas – Thomson’s gazelles *Eudorcas thomsonii* preferring ridge tops, topi *Damaliscus lunatus* and wildebeest *Connochaetes taurinus* preferring medium-height grasses at mid-catena, and buffalo *Syncerus caffer* preferring the valley bottom where grasses are tall, and soils are silty and deep. This degree of niche partitioning among sympatric bovids is not seen in other environments, such as forests that are dominated by ecologically-similar cephalophins.

Carnivoran diet PCoA1 Range was positively related to NPP ($r=0.50$) (Figure 2.8), suggesting an increased diversity of carnivoran diets in high productivity environments, as was found for macromammals and micromammals (Figure 2.7). Indeed, carnivorans in forest environments are known to consume a wide variety of food resources, ranging from the piscivorous aquatic genet *Genetta piscivora* and Congo clawless otter *Aonyx congicus*, to specialized insectivores and frugivores (*Genetta* spp.), to hyper-carnivorous leopards *Panthera pardus*. As with macromammals, we propose

that the vast dietary diversity of forest carnivoran communities reflects the variety, abundance, and temporal stability of food resources found in these biomes (particularly for smaller-bodied, omnivorous carnivorans). On the other hand, we found that abiotic filtering of carnivoran diets was strongest in Afro-alpine environments (Figure 2.6; Figure 2.8). Afro-alpine environments likely filter carnivoran diets by virtue of the limited prey resources they contain, as species richness declines with altitude. For example, Peters et al. (2016) showed that richness was negatively related to altitude across a diversity of 25 plants and animal taxa on Mount Kilimanjaro. They found that richness declines were mostly driven by cooler temperatures, which are unfavorable for many ectotherm animals (e.g., insects and amphibians), as well as small-bodied endotherms (e.g., birds). This significantly reduces the prey availability for smaller mammalian carnivorans and provides a potential explanation for why Afro-alpine carnivoran communities may be functionally clustered.

Primate communities were weakly influenced by NPP and climate variables overall (SI Figure 18; Figure 2.7). Only SDNDR of diet PCoA2 had significant climatic predictors and was positively related to MAT and negatively related to TCM (Figure 2.7), as was the case for macromammals, bats, and carnivorans, implying increasing dietary competition in overall warmer environments with cooler minimum temperatures, namely tropical forests, where primate foods are especially abundant.

5. Conclusions

Understanding the processes that govern community assembly is a central goal of ecological research. Our analyses of African mammal communities strongly suggest that the structure of functional traits within a community can be used to infer the processes

that have shaped it, regardless of whether communities be ecological (macromammal, micromammal, bat) or phylogenetic (Artiodactyla, Carnivora, Primates) in nature. Important functional traits for each of these groups and clades, however, show relatively weak phylogenetic signals, which cautions against the use of phylogenetic community ecology without first testing for niche conservatism, as was done in this study. We propose that the phylogenetic structure of African mammal communities reflects deep-time processes (e.g., historical biogeography) versus comparatively recent community assembly.

We found that macromammal and micromammal communities are primarily shaped by dietary competition, whereas abiotic filtering of body mass and diets is most important for bat communities. Among orders, we found that artiodactyl communities are mostly functionally random, carnivoran communities are shaped by abiotic filtering of diets, and primate communities are shaped by body mass competition, albeit weak. The relative strength of assembly processes is strongly related to climatic gradients across most groups and orders, particularly variables related to overall net primary productivity (e.g., mean annual temperature). A consistent pattern across most groups and orders is that dietary competition is particularly elevated in high productivity forest biomes, especially tropical lowland forest. Overall, our study strongly supports the role of climates, productivity, and biome structure in driving community assembly across mammals in Africa.

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CHAPTER 4: STRONG INFLUENCE OF PALEOCLIMATE ON THE STRUCTURE OF MODERN AFRICAN MAMMAL COMMUNITIES

Title: Strong influence of paleoclimate on the structure of modern African mammal communities

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Abstract

Ecological research often assumes that species are adapted to their current climatic environments. However, climate fluctuations over geologic time scales have influenced species dispersal and extinction, which in turn may affect community structure. Modern community structure is likely to be the product of both paleoclimate and modern climate, with the relative degrees of influence of past and present climates unknown. Here we assessed the influence of climate at different time periods on the phylogenetic and functional trait structure of 203 African mammal communities. We found that the climate of the mid-Holocene (~ 6,000 years ago) and Last Glacial Maximum (~ 22,000 years ago) were frequently better predictors of community structure than modern climate for mammals overall, carnivorans, and ungulates. Primate communities were more strongly influenced by modern climate than paleoclimate. Overall, community structure of African mammals appears to be related to the ecological flexibility of the groups considered here and the regions of continental Africa that they occupy. Our results indicate that the future redistribution, expansion, and contraction of particular biomes due to human activity, such as climate and land-use change, will differentially affect mammal groups that vary in their sensitivity to environmental change.

Keywords: Community assembly, paleoclimate, functional Traits, phylogenetic Structure

1. Introduction

Understanding the factors that shape biological communities, and the relative strength of those factors, is a central goal of ecology. Among potential factors, it is widely accepted that climate plays a major role in shaping communities, and thus the interaction between climate and community structure patterns is a principal focus of ecological research (Kraft and Ackerly, 2010; Cardillo, 2011; Graham et al., 2012; Soudzilovskaia et al., 2013; Kamilar et al., 2015). Much of this research operates under the assumptions that 1) species are fundamentally in equilibrium with their current environment (Franklin, 2010), and 2) species are adapted to current climatic conditions (Araújo and Peterson, 2012). These two related assumptions, however, are not always met, and can affect both applied and theoretical conclusions. For example, most species distribution models project future species distributions based on the climatic conditions where a species is currently found (Elith and Leathwick, 2009; Franklin, 2010), implicitly or explicitly assuming that species are in equilibrium with current climatic conditions (Araújo and Peterson, 2012) and accordingly will track climate change in real time. It is possible, however, that species distributions are more strongly shaped by factors other than today's climate, such as paleoclimate, and that models built only on modern climate will have limited predictive power. Likewise, an organism or community's functional traits may be adapted to past climatic conditions and have been retained despite climate change. When an anticipated relationship between functional traits and modern climate is not found, many studies invoke "phylogenetic inertia" or some other non-adaptive mechanism to explain their findings (Blomberg and Garland, 2002; Losos, 2008; Kamilar and Cooper, 2013), even when paleoclimatic influences remain unexplored and may offer

insight into observed patterns. Few studies have assessed the paleoclimatic influence on functional diversity, as recently noted by Svenning et al. (2015).

Analyses of the phylogenetic and functional trait structure of communities have been used as a proxy to understand the relative roles of assembly processes that structure communities, primarily competition and habitat filtering (Webb et al., 2002; Cavendar-Bares et al., 2009; Kraft and Ackerly, 2010; Graham et al., 2012). These metrics are sensitive to the “clustering” or “overdispersion” of related taxa or traits within a community and are based on ecological theory (Webb et al., 2002; Cardillo, 2011; Kamilar et al., 2015). For example, the outcome of competition within a community is often niche partitioning or niche differentiation between competitors, resulting in an “even spacing” pattern of close relatives or traits (Webb et al., 2002; Stubbs and Wilson, 2004; Kraft et al., 2008; Kraft and Ackerly, 2010). Conversely, habitat filtering is based on the concept that environmental gradients across space may serve as a filter because only species with specialized physiological or ecological traits can successfully inhabit particular, often stressful, environments (Cornwell et al., 2006). The resulting pattern is one where closely related taxa or similar traits are “clustered”. Thus, it can be expected that competition is a strong factor in community assembly in environments where numerous taxa can successfully persist, while habitat filtering is more likely to be strong in environments where only a few taxa with specialized adaptations can successfully persist.

Here we analyze the relative influence of modern climate and paleoclimate on the phylogenetic and functional trait structure of terrestrial African mammal communities. Mammals are an excellent faunal group for such a study, as their modern distributions are relatively well known and data on species traits are more readily available than for other

animal clades. Mammals vary considerably in their functional traits, such as substrate use, dispersal ability, body size, and diet, which may in turn affect underlying community assembly processes (Qian, 2009). Africa is also home to a great diversity of species in 17 of the world's 20 orders of terrestrial mammals (Ceballos and Ehrlich, 2006; Buckley et al., 2010; Kingdon, 2013), and is virtually the only continent relatively unscathed by the late Quaternary extinction events (Barnosky et al., 2004; Faurby and Svenning, 2015a). Nevertheless, late Quaternary paleoclimate change has been noted as a particularly important time period in the evolution and biogeography of African mammals (Wallace 1903, Lydekker, 1908; Lönnberg, 1929; Wayland, 1940; Kingdon, 1971, 1990; Vrba, 1992, 1995; Faith et al., 2012, 2013; Faith, 2014; Rowan et al., 2015), especially recurrent expansions and contractions of major vegetation biomes as climates changed (Kingdon, 1990; Anthony et al., 2007; Cowling et al., 2008; Tosi, 2008; Lorenzen et al., 2012; Levinsky et al., 2013).

We quantified the phylogenetic and functional trait structure of 203 African mammal communities and predicted these community structure metrics using both modern and paleoclimatic datasets of the Last Glacial Maximum (LGM; ~ 22,000 years ago) and mid-Holocene (~ 6,000 years ago) with linear models and multimodel inference. Using these analyses, we address the question “what are the relative influences of modern and paleoclimate on the phylogenetic and trait structure of African mammal communities?” We predict that if mammal taxa strongly track climatic and environmental change, then modern climate should be the best predictor of community structure. Alternatively, if taxa are more ecologically flexible and/or if paleoenvironmental history is important, then community structure may be better predicted by paleoclimate.

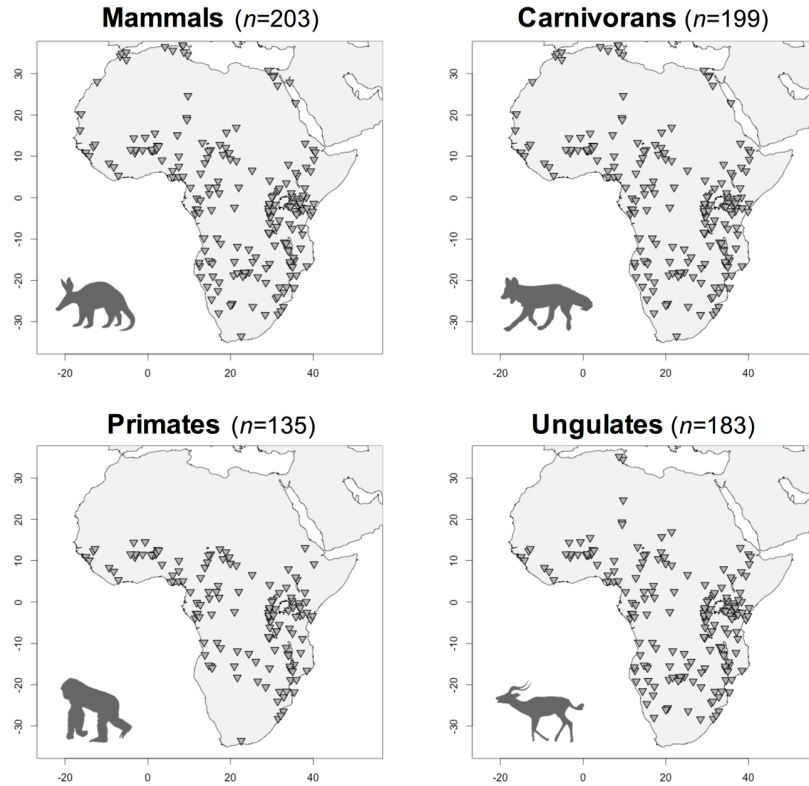


Figure 3.1. Map of mammal, carnivoran, primate, and ungulate communities used in this study.

2. Methods

2.1 Community and trait data

We compiled species lists of terrestrial mammal communities for 203 communities from national parks, game reserves, and protected areas, spanning the entire African continent (Figure 3.1; Table SI 1). Data came from published field surveys and park lists, existing databases, and primary literature; we avoided using range maps because they often overestimate species occurrences (Hurlbert and White, 2005; Hurlbert and Jetz, 2007). Only terrestrial mammals weighing >500 g were included, as data for micromammals (e.g., trapping of rodent species) and bats are generally less available and less reliable. The overall mammal dataset included representatives from nine mammalian

orders (Table SI 2). We then subdivided three groups from the overall mammal data: carnivorans (order Carnivora), primates (order Primates), and ungulates (orders Artiodactyla and Perissodactyla). We use the gradistic term “ungulate” to include all African species of Artiodactyla and Perissodactyla, as the species in these orders broadly overlap in body size and dietary ecology (Kingdon, 2015) and thus likely influence one another more so than other groups during community assembly processes. All communities included a minimum of four species. Our final database consisted of 203 mammal, 199 carnivoran, 135 primate, and 183 ungulate communities.

We used body mass and diet as functional traits, as these traits are important characteristics of a species’ niche, and therefore are likely strongly linked to processes determining community structure (e.g., habitat filtering, interspecific competition). For example, body mass is highly correlated with many physiological, life history and ecological traits in carnivorans, primates, and ungulates (Harvey and Clutton-Brock, 1985; Gittleman, 1986; du Toit and Owen-Smith, 1989). Trait data for mammal species were collected from Kingdon et al. (2013) for body mass and Kissling et al. (2014) for dietary data. The Kissling et al. (2014) dietary dataset consists of categorical dietary variables (e.g., “invertebrate”, “mammal”, “fruit”, or “seed”) that are ranked by importance for each species. These data were crosschecked and supplemented with sources from other databases and field guides (Estes, 1991; Skinner and Chimimba, 2005; Jones et al., 2009) for consistency.

Body mass was recorded as a continuous variable in grams, based on the average female body mass per species. Diet was also measured as a continuous variable, obtained from the ordination of the Kissling et al. (2014) dietary data matrix. These data were used in a correlation matrix-based principal components analysis (PCA) using the *prcomp*

function in R (Figure SI 1). We used the first two principal components in all analyses (55.5% total variance explained), as these were the only components with eigenvalues greater than 1.0. The component loadings were used to determine the dietary signal (e.g., carnivory, frugivory, herbivory) that each axis captured. Therefore, each mammal's score from the ordination represented its diet relative to all of the other mammals in the analysis. In addition, we also calculated dietary axes using principal coordinates analysis (PCoA) with Gower distances. However, the dietary axes generated using PCoA were strongly related to those generated from the PCA (e.g., PCoA axis 1~PCA axis 1 $r^2=0.98$) and therefore we only used the PCA dietary axes for analyses. Raw trait data are presented in Table SI 2.

2.2 Climate data

A central geospatial coordinate (latitude, longitude) was collected for each community.

Rasters of climate data for three periods (modern, mid-Holocene, LGM) were downloaded from ecoClimate (Lima-Ribeiro et al., 2015) for seven different general circulation models (GCMs) from the Couple Model Inter-comparison Project (CMIP5) and Paleoclimate Modeling Intercomparison Project (PMIP3) working groups. These GCMs are widely used in ecological studies involving paleoclimate (e.g., Collevatti et al., 2013; Gavin et al., 2014; Feng et al., 2015; Ordonez and Svenning, 2016a, 2016b) From each of these GCMs, six bioclim variables were extracted using the central point of each community: BIO1, annual mean temperature (MAT), BIO4, temperature seasonality (TS), BIO6, minimum temperature of the coldest month (MT), BIO12, mean annual precipitation (MAP), BIO14, precipitation of the driest month (PDM), and BIO15,

precipitation seasonality (PS) (Table SI 1). We used these variables because they were not highly correlated with one another and are important for structuring African mammal communities (Kamilar et al., 2015). For the results presented in the main text of the paper, we averaged bioclim variables across all GCMs to create an “average” model for each time period. However, we include results from the 7 individual GCMs in the supplemental information.

For each of the 7 GCMs and the average model, the six climate variables were log transformed and used in a correlation matrix-based PCA using the *prcomp* function in R. Individual PCAs were used for each of the three climate datasets for each of the GCMs and the average model (Figure SI 2-4). We used the first two principal components in all analyses, as these encompassed ~ 80% of the variation within the data and had eigenvalues greater than 1.0. The component loadings were used to determine the climatic signals along each axis.

2.3 Community structure metrics

We used two metrics to characterize the phylogenetic structure of communities, the nearest taxon index (NTI) and the net relatedness index (NRI), following Webb et al. (2002) (Table SI 3). NTI is calculated as the phylogenetic distance between the two most closely related co-occurring taxa in a community relative to the entire species pool (i.e. all species in all communities). NRI is calculated as the average phylogenetic distance among species in a community related to the species pool. These methods have been applied extensively to plant (Kraft et al., 2007; Kraft and Ackerly, 2010) and animal (Kamilar and Guidi, 2010; Cardillo, 2011; Graham et al., 2012; Cantalapiedra et al., 2013; Kamilar et al., 2015) communities. We used the PHYLOCOM software package

(Webb et al., 2008) to calculate NTI and NRI using a null model of 4,999 randomizations to standardize these metrics. Pausas and Verdu (2010) and Miller et al. (2015) provide overviews of the null model approach for analyzing community phylogenetic structure. The mammalian phylogeny of Bininda-Emonds et al. (2007) was used for all phylogenetic analyses, as this phylogeny contains all species in our dataset and has been widely used in previous research (Cardillo, 2011; Cooper et al., 2012; Pointer et al., 2012; Kamilar et al., 2015). However, we also calculated NRI and NTI from the newly available Faurby and Svenning (2015b) species-level phylogeny of all extant mammals. The NRI and NTI values calculated from the Faurby and Svenning (2015b) phylogeny were in almost all cases highly correlated with those using the Bininda-Emonds et al. (2007) phylogeny (mammals NRI, $r^2=0.97$; carnivorans NRI, $r^2=0.88$; primates NRI, $r^2=0.98$; ungulates NRI, $r^2=0.97$; mammals NTI, $r^2=0.81$; carnivorans NTI, $r^2=0.68$; primates NTI, $r^2=0.94$; ungulates NTI, $r^2=0.84$). The single exception was carnivoran NTI ($r^2=0.68$) and therefore we re-ran our linear models only for carnivoran NTI using the new Faurby and Svenning (2015b) phylogeny.

We used four metrics outlined by Kraft et al. (2008) and Kraft and Ackerly (2010) to characterize the functional trait structure of communities: Range, Variance, the standard deviation of nearest neighbor distance divided by the overall trait range (SDNNr), and the standard deviation of neighbor distance divided by the overall trait range (SDNDr). Two of these metrics (Range, Variance) are sensitive to habitat filtering, while the other two metrics (SDNNr, SDNDr) detect even spacing—a common pattern resulting from interspecific competition and niche partitioning (Kraft and Ackerly, 2010). Range is calculated as the difference between maximum and minimum trait value for a community and Variance measures how widely species' trait values deviate from the

community mean. SDNNr measures how distant the two most similar pair of species are to other species in the community, while SDNDr measures how regularly spaced taxa in a community are across a given trait range. More details on these metrics are provided in Kraft et al. (2008) and Kraft and Ackerly (2010). As with the phylogenetic structure metrics, we used a null model approach to generate random communities of equal richness by extracting taxa from the entire meta-community pool weighted by their frequency of occurrence in the pool. We used 4,999 randomizations to standardize these metrics.

2.4 Models

We used linear regression models to analyze the relationship between phylogenetic and functional trait metrics and modern and paleoclimate variables. Each model contained up to six climate predictors, as represented by the first two principal components from the PCAs of the three climate datasets (modern, mid-Holocene, and LGM). In addition, each model included latitude and longitude of communities as predictors. Including latitude and longitude as predictors allowed us to account for potential spatial autocorrelation in the models (e.g., Borcard et al., 1992; Legendre et al., 2005; Kamilar et al., 2009). Moran's I values generated across all models show very little spatial autocorrelation (Table SI 9).

We used the corrected Akaike Information Criterion (AICc) to determine the best models of community structure. In addition, we calculated the sum of AICc weights for each climate principal component (i.e. predictor) to determine which climate variables were the best predictor of community structure metrics. We produced these values from the *dredge* function in the package MuMIn (Barton, 2014). We averaged the models

within the top 95% of model weights following Burnham and Anderson (2002); the sum of AICc weights for variables were calculated from all possible models. In addition, as some of our climate PC axes were correlated (e.g., Mod1, Hol1, LGM1), we also examined whether models containing only paleoclimate (e.g., trait~LGM1+LGM2) were stronger than those containing only modern climate (e.g., trait~Mod1+Mod2).

We ran a total of 56 models for each GCM and the average model (448 models total): for phylogenetic structure, a model was run for each group (mammals, carnivorans, primates, ungulates) and for each phylogenetic structure metric (NRI, NTI), resulting in eight total phylogenetic models per GCM and the average model; for functional traits, models were run for each group for four metrics (Range, Variance, SDNNr, SDNDr) of three traits (body mass, diet PC1, diet PC2), which resulted in a total of 48 functional trait models per GCM.

3. Results

3.1 PCA Loadings

PC1 of the dietary PCA (diet PC1) represented animal matter versus plant matter in the diet. PC2 (diet PC2) represented fruit consumption and distinguishes invertebrate from vertebrate animal matter in the diet (Figure SI 1).

For the climate PCAs, modern PC1 (Mod1) represented temperature seasonality (BIO4, TS) and mean annual precipitation (BIO12, MAP). Modern PC2 (Mod2) represented mean annual temperature (BIO1, MAT) and precipitation intensity (BIO14, PDM) (Figure SI 2). Mid-Holocene PC1 (Hol1) represented variables related to temperature seasonality or intensity (BIO4, TS; BIO6, MT), while mid-Holocene PC2 (Hol2) represented precipitation seasonality and intensity (BIO14, PDM; BIO15, PS)

(Figure SI 3). LGM PC1 (LGM1) represented temperature seasonality (BIO4, TS) and mean annual precipitation (BIO12, MAP) and LGM PC2 (LGM2) represented mean annual temperature (BIO1, MAT) and precipitation intensity (BIO14, PDM) (Figure SI 4).

3.2 Phylogenetic structure metrics

Mammal community phylogenetic structure was most strongly predicted by paleoclimate, with LGM1 and Mod1 being the most important variables for NRI, while Hol2 and LGM2 strongly predicted NTI (Figure 3.2; Table SI 5). Carnivoran phylogenetic structure was poorly predicted by climate variables overall, although mid-Holocene climate was the strongest predictor of both NRI and NTI (Figure 3.2; Table SI 6). Primate phylogenetic community structure was influenced by both modern and paleoclimate, as NRI was most strongly tied to Hol2, while NTI was strongly influenced by Mod1, although Mod2, Hol1, and Hol2 are also important variables (Figure 3.2; Table SI 7). For ungulates, LGM2 was the most important variable for NRI, and Hol2 was the most important predictor of NTI (Figure 3.2; Table SI 8).

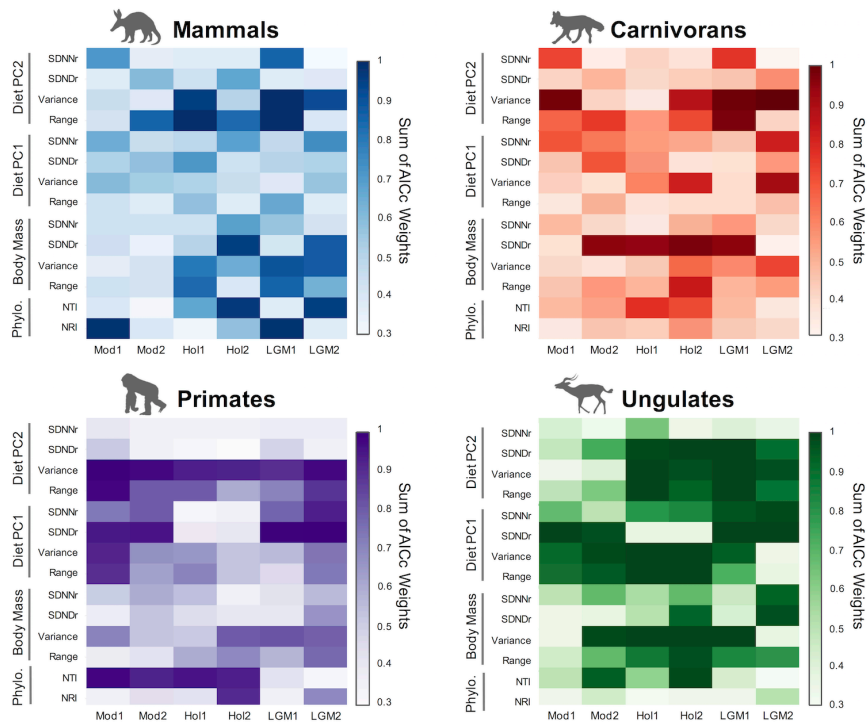


Figure 3.2. Heatmap of sum of Akaike Information Criterion (AICc) weights for each climate predictor across all phylogenetic and functional trait metrics. Climate data represent the first two principal component axes for an ordination of six climate variables per time period (see Methods). Phylogenetic structure metrics are net relatedness index (NRI) and nearest taxon index (NTI). Functional trait metrics include Range, Variance, the standard deviation of nearest neighbor distance divided by the overall trait range (SDNNr), and the standard deviation of neighbor distance divided by the overall trait range (SDNDr).

3.3 Functional trait structure metrics

Functional trait structure of mammal communities was strongly influenced by paleoclimate variables, especially LGM climate (Figure 3.2; Table SI 4-8). LGM climate most strongly influenced mammal body mass and diet PC2, while diet PC1 was not strongly influenced by any climate variable, although mid-Holocene and LGM climate variables were the most important. Carnivoran functional trait structure was also best predicted by paleoclimate overall, with mid-Holocene and LGM variables being the most important for body mass and diet PC2, while diet PC1 was influenced by both modern and

LGM climate. The functional trait structure of primate communities, unlike the other groups, was similarly influenced by both modern and paleoclimate, with Mod1 and LGM2 being especially strong. Conversely, ungulate communities showed the strongest influence of paleoclimate as mid-Holocene and LGM climate were the top variables for all metrics and traits, but also had many more influential climate variables overall.

4. Discussion

We quantified several aspects of the phylogenetic and functional trait structure of modern African mammal communities and found that mid-Holocene and LGM climate were often equivalent if not better predictors of community structure than modern climate (Table 3.1). The finding that African mammal community structure overall has been strongly influenced by paleoclimate implies that many species are ecologically flexible, and/or that dispersal limitation has been strong enough to have prevented climate tracking over the last several thousand years.

Table 3.1. Mean of sum of Akaike Information Criterion (AICc) weights for climate predictors across all phylogenetic and functional trait metrics.

	Mod1	Mod2	Hol1	Hol2	LGM1	LGM2
Mammals	0.52	0.46	0.62	0.61	0.67	0.60
Carnivorans	0.53	0.54	0.53	0.63	0.60	0.57
Primates	0.68	0.63	0.55	0.56	0.57	0.69
Ungulates	0.54	0.68	0.75	0.81	0.75	0.69

The relative strength of modern climate and paleoclimate varied between mammalian groups (Table 3.1). Most notably, primate community structure was strongly influenced by modern climate, whereas mammals, carnivorans, and ungulates were more strongly influenced by paleoclimate. A potential explanation for this pattern may lie in differences in ecological flexibility between mammal groups and the biomes of Africa

they occupy. Primates are largely biome specific (Hernandez-Fernandez and Vrba, 2005a) with most of the African primate radiation is dependent on forest blocks in equatorial West and Central Africa (Eeley and Foley, 1999; Andrews and O'Brien, 2010; Gouveia et al., 2014). LGM and mid-Holocene climate change are known to have significantly altered the distribution of forests across Africa, with forests contracting into small refugia during the arid LGM and subsequently expanding during the mid-Holocene as wetter conditions prevailed (Jolly et al., 1998; Elenga et al., 2000; Anhuf et al., 2006; Cowling et al., 2008). Molecular evidence suggests that shifts in forest vegetation during glacial and interglacial climate change strongly influenced African primates, including vicariance and dispersal in guenons (Tosi, 2008; Kamilar et al., 2009) and gorillas (Anthony et al., 2007), and demographic patterns in chimpanzees (Hvilsom et al., 2014) and mandrills (Ting et al., 2012). In addition, bioclimatic envelope models of African mammals and birds provide evidence for three major forest refugia in Central and West Africa (Levinsky et al., 2013), which would have represented the only viable habitats for most of Africa's primates during glacial periods. The combination of molecular and biogeographic evidence suggests that the highly forest-dependent primate radiation is a sensitive group to climatic and environmental change. Primate communities experienced local extinction and range contraction during glacial periods, whereas warm and wet interglacial periods provided opportunities for dispersal via the expanding forest biome. The 'tracking' of forests explains why biome-dependent primate communities are most closely tied to modern climate, whereas the comparatively ecologically resilient ungulate communities are more strongly predicted by paleoclimate.

Ungulate communities were the most strongly influenced by paleoclimate among all mammalian groups in our study (Table 3.1). The connection between modern ungulate

communities and paleoclimate may be related to the ecological flexibility of ungulate species and the relative stability of savanna habitats compared to forests during the late Quaternary (Jolly et al., 1998; Elenga et al., 2000; Anhuf et al., 2006; Cowling et al., 2008). Ungulates are medium to large-sized mammals and ecological flexibility increases with body size in African mammals in general (Hernandez-Fernandez and Vrba, 2005b) and African ungulates specifically (du Toit and Owen-Smith, 1989). In addition, ungulates rely on leaves and/or grasses as a primary food source and these types of foods are widely distributed across several biomes ranging from semi-desert to forest ecotones (White, 1983). Conversely, fruits play an important role in most primate diets and therefore primates are more closely tied to a single biome (forests) where fruit production is more plentiful (White, 1983). Thus ungulate communities, as compared to primates, are more 'ecologically resilient' and could have persisted in a greater diversity of biomes both across space and through time during Quaternary climate change. This ecological resilience of mammal communities has also been shown by Rodriguez (2004, 2006) using fossil assemblages. Additionally, in contrast to forests, the savannas of southern and eastern Africa were relatively stable throughout the Quaternary, experiencing only moderate encroachment from deserts along its perimeters during glacials (White, 1983; Anhuf et al., 2006) and expansion of forests during interglacials (Jolly et al., 1998). The stability of savanna environments extends deeper in time than the Quaternary, as fossil mammals and paleoenvironmental proxies from paleontological sites dating from the late Miocene onwards document a persistence of savanna mosaics over at least the last six to seven million years in southern and eastern Africa (Sikes, 1994; Reed, 1997, 2008; de Ruiter et al., 2008; Cerling et al., 2011; Rowan and Reed, 2015). Today, these savannas are home to the vast majority of the continent's ungulate diversity (du Toit and

Cumming, 1999; Andrews and O'Brien, 2010), and thus ungulate communities here experienced less habitat change than other areas of the continent. Furthermore, equatorial forests today and in the past have had less seasonal temperatures and rainfall regimes compared to savannas, suggesting that ungulates may be more tolerant of climate and habitat shifts over longer time scales than primate species that are adapted to relatively stable forests environments.

That carnivoran communities are also best predicted by paleoclimate is likely related to the patterning of mammal predator and prey species richness at macroscales. As with ungulates, carnivoran species richness is concentrated in the savannas of eastern and southern Africa (Andrews and O'Brien, 2010). Mammal predator-prey species richness in Africa is only tightly linked in open habitats (e.g., savannas); forests are skewed towards higher predator-prey ratios (Sandom et al., 2013). This discrepancy likely arises as the result of different environmental histories of savannas and forests in Africa (Sandom et al., 2013), but also from the fact that many predators of mammal species in forests are non-mammalian, such as snakes and raptors, which are major predators of primates (Isbell, 2006, 2009; Wheeler et al., 2011). Furthermore, carnivoran species are largely secondary and tertiary consumers and are not as dependent on local vegetation for subsistence as primates and ungulates. It is also clear that carnivoran communities have been greatly influenced by human activity today (Ripple et al., 2014) and, at least, since the early Pleistocene during which the genus *Homo* evolved derived dietary strategies that placed hominins in direct conflict with Africa's diverse carnivore guild (Lewis and Werdelin, 2010; Werdelin and Lewis, 2005, 2013).

Despite the importance of mid-Holocene and LGM climate in our analyses, it is likely that we have underestimated the role of paleoclimate. Some of the climate

variables in our analyses were highly correlated (e.g. Mod1, Hol1, LGM1) and this could result in inflated type II error rates (Freckleton, 2011). Yet, this issue should not impact our main findings since high levels of collinearity result in increased type II error rates for individual predictors, especially when correlated predictors contain different levels of unbiased error (Quinn and Keough, 2002; Freckleton, 2011). In our case, paleoclimate variables certainly contain more error because they are reconstructed values, as opposed to modern climate data based on direct measurements or interpolation from weather stations (Hijmans et al., 2005). Therefore, the paleoclimate variables should be associated with increased type II error, yet were often found to be better predictors of community structure than modern climate variables. In addition, models containing only paleoclimate variables (e.g., trait~LGM1 or trait~LGM1+LGM2) generally had lower AICc values and higher model weights than those containing only modern climate (e.g., trait~Mod1 or trait~Mod1+Mod2) (Table SI 9). Thus, even given potential multi-collinearity issues, paleoclimate was often a stronger predictor of community structure metrics than modern climate.

In sum, we found a strong role of paleoclimate on modern community patterns and found that modern climate alone was not sufficient to explain the total influence of climatic factors on community structure in African mammals. Our results have implications for predicting the future of tropical biodiversity, as the tropics are the heart of the world's mammalian diversity (Ceballos and Ehlrich, 2006; Buckley et al., 2010) but are threatened by human activity. Anthropogenic climate change represents a major threat to the world's remaining mammalian diversity as novel climates are projected to appear mainly in the tropics, with annual temperatures projected over the next century to be up to 7°C warmer than today (Williams et al., 2007; Corlett, 2012). Both temperature

and precipitation changes will result in a redistribution of major vegetation biomes across Africa (Scheiter and Higgins, 2008; Midgley and Bond, 2015; Muciriff et al., 2015). Climatically induced biome changes are being exacerbated by extensive land cultivation (e.g., agriculture, logging) (Schmitz et al., 2014) by an ever-expanding human population in Africa, which is expected to contribute to most of global population growth over the next century (Gerland et al., 2014). Our results indicate that the future redistribution, expansion, and contraction of particular biomes due to human activity will differentially affect mammal communities that vary in their sensitivity to environmental change.

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CHAPTER 5: DISCUSSION

Discussion

This chapter briefly discusses and summarizes the results of the three dissertation papers in the context of the late Cenozoic fossil record of eastern Africa, which has produced the vast majority of data bearing on Plio-Pleistocene human evolution. For decades, major patterns of hominin and faunal evolution have been causally linked to records of paleo-climatic change and this has since emerged as the major paradigm in hominin paleoecological studies (e.g., deMenocal 1995, 2004; Levin, 2015; Potts, 1998; Vrba, 1985, 1988, 1999). The central tenets of this paradigm, however, remain largely untested and/or poorly developed in terms of theory and are mainly based on coarse temporal correlations between taxonomic or behavioral milestones in the hominin fossil record and proxy data for climatic and environmental change (Marean et al., 2015). Plio-Pleistocene hominin paleoecology is at a major crossroads: our field now has a substantial body of spatiotemporally high-resolution, state-of-the-art paleobiological and paleoenvironmental data bearing on the ecology of hominins and their constituent faunal communities and – at the same time – a comparatively outdated theoretical framework within which we interpret them (Kingston, 2007). Indeed, the major prevailing theories of how climatic or environmental change might have shaped early human and faunal evolution are now decades old. These include the widely-cited variability selection model of Potts (1998), the resource-use and turnover pulse hypotheses of Vrba (1987), and the aridity and grassland expansion models of deMenocal (1995, 2004) and others (e.g., Bobe and Behrensmeyer, 2004).

The overarching goal of this dissertation was to critically evaluate or re-evaluate some of the central tenets of the ‘climate-evolution’ paradigm as they relate to the Plio-

Pleistocene fossil record of human and faunal evolution, using biogeographic and macroecological analyses of present-day African mammal communities as a test case. It is not our aim to critique or trivialize the many important contributions of previous studies, but instead to provide novel tests of prevailing models and hypotheses as a way forward. Three dissertation papers tested: 1) the degree to which differences in ecological niche breadth (measured as biotic, climatic, and dietary niche breadth) have shaped divergent patterns of macroevolutionary turnover across mammal clades over the last seven million years (Myr); 2) the relative importance of biotic interactions (e.g., niche partitioning, competitive exclusion) versus abiotic filtering (e.g., habitat filtering, dispersal limitation) in community assembly; 3) the relative influence of paleo- versus modern climate in shaping the present-day structure of communities. The results of these three studies call into question many foundational assumptions of the ‘climate-evolution’ paradigm that prevails in hominin paleoecology today. It is proposed that significant progress can be made if paleoanthropological and paleoecological research shifts towards: 1) careful consideration of the spatial and temporal scales at which hominins and other large-bodied mammals interact with their environments through space and time and 2) a renewed effort to develop an up-to-date conceptual framework with proximate, causal explanations for climatic and environmental forcing, as well as biotic interactions, in human and faunal evolution grounded in modern-day theory and methods from community ecology and biogeography.

1.1 Niche breadth differences play little role in driving macroevolution

Studies of origination and extinction patterns in the late Cenozoic fossil records of hominins and their contemporaneous fauna in eastern Africa have often been associated

with changes in climates or environments. Many of these studies are rooted in the foundation laid by the mammalian paleontologist Elisabeth Vrba who commendably developed a detailed, testable theory for how differences in ecological niche breadth may underlie the varied diversification histories of mammal clades throughout the Plio-Pleistocene. Vrba (1980, 1987, 1992, 1995, 1999) progressively formalized this theory under her resource-use hypothesis (RUH), in which ecologically specialized clades are predicted to have higher incidences of range fragmentation and contraction, and therefore speciation and extinction, than generalist clades in the face of climate or environmental change.

The results of Chapter 1 fail to support Vrba's RUH. Putting methodological considerations of data and statistical analysis aside (see Chapter 1 discussion), it was found that differences in biotic, climatic, and dietary niche breadth, whether alone or in combination, did not predict origination and extinction rates in a comprehensive sample of large-bodied genera and tribes of African mammals that have relatively complete fossil records. Failure to support Vrba's RUH may stem from the multiple factors acting on macroevolution and the study of its outcome – these being scale-dependency, the correlates of niche breadth, and the choice of biological and ecological traits, among others. Some potential explanations are discussed below.

First, turnover can be driven by multiple factors and, as a consequence, the explicit formalization of process models for macroevolution in the fossil record must consider the significant changes that occur across both spatial and temporal scales (Benton, 2009; Hannisdal and Liow, 2018). Biotic interactions, such as predation and competition, mainly act across short geographic and temporal scales, whereas long-term extrinsic drivers, such as climatic or tectonic change, predominate at larger scales

(Benton, 2009; Jackson and Blois, 2015) as shown in Figure 4.1. These scale-dependent processes are known as the ‘Red Queen’ (van Valen, 1973) and the ‘Court Jester’ (Barnosky, 2001), respectively. It is possible that the importance of niche breadth in determining speciation and/or extinction is also scale-dependent and that niche breadth influences at one scale may counteract those at the other, effectively canceling out the importance of this variable. Alternatively, it is possible that niche breadth is altogether unimportant across all scales, at least for large-bodied mammals.

Second, it could be that the correlates of niche breadth, and not niche breadth itself, are more important in determining macroevolutionary turnover – for example, Harnik et al. (2012) found that range size is the most important variable for determining extinction vulnerability, whereas habitat specialization, although related to range size, plays a comparatively minor role. Regardless of habitat niche breadth, broad geographic ranges confer extinction resistance as any potential climatic or environmental catastrophe is unlikely to affect the entirety of the species’ range, thus increasing its probability of survival (Saupe et al., 2015). Similarly, Finnegan et al. (2015) found that geographic range size and taxonomic membership were the most consistent predictors of extinction risk in a global sample of fossil marine animals from the Neogene and Quaternary. Taxonomic membership is a strong extinction correlate as many life history variables that directly relate to population dynamics (e.g., age at first reproduction, gestation length, interbirth interval length) are phylogenetically conserved (Cardillo et al., 2008).

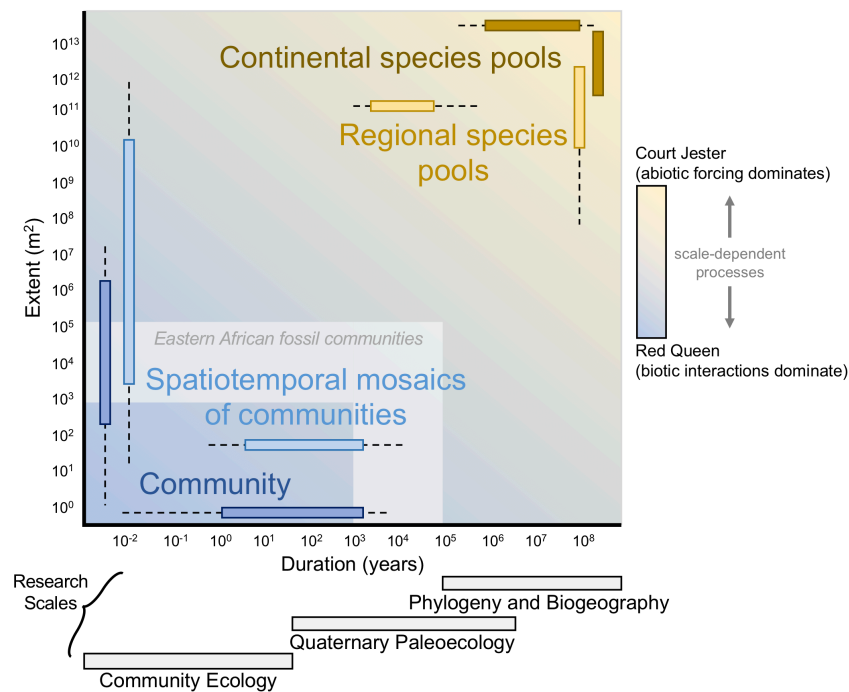


Figure 4.1. Climate’s influence on mammal communities is strong scale-dependent. At small temporal and spatial scales, biotic interactions (Red Queen) are proposed to be a more important process than abiotic forcing (Court Jester). The spatiotemporal resolution of the eastern African fossil record (gray box) suggests that biotic interactions are a more important process in determining assemblage structure and that climate-based explanations have limited explanatory power. Modified from Jackson and Blois (2015).

Third, it is possible that niche position (i.e., average niche requirements) and not niche breadth is the most important ecological character influencing macroevolutionary rates. This scenario emphasizes that paleo-climatic and environmental changes in single direction (e.g., cold to warm or arid to wet) will favor a handful of clades over most others (Ricklefs, 2006). An example of this from the Plio-Pleistocene eastern African fossil record would be the synchronous radiation of grassland-adapted herbivores coincident with the expansion of C₄ ecosystems through time (e.g., Bobe, 2006), as was the case on other continents (Edwards et al., 2010). Thus, clade diversification histories – and, by extension, present-day diversity patterns – may be mainly shaped by unique

historical influences favoring the success of one clade over another (Ricklefs, 2004). Origination dates of taxa are also an important consideration, as it is well-documented that species richness is positively related to clade age, even when speciation and extinction rates are more or less equal (Rabosky, 2009). Clades that have originated earlier have had more opportunities for speciation and adaptive radiation as climates and environments change in their favor (Orr and Smith, 1998).

Overall, it is clear that there are a number of processes operating across different spatial, temporal, and phylogenetic scales that may influence the macroevolutionary turnover of clades through geologic time. It is therefore perhaps inappropriate to develop explanatory models based on a single biological or ecological aspect – such as niche breadth – and implore it alone to explain the evolutionary history of a clade. Though evolutionary and ecological theory aims to establish universal explanations that transcend the specific nature of taxonomic groups, it may be that the drivers of macroevolution are at least in part dependent on the taxon of interest. For example, the influence of climatic and environmental drivers on small-bodied ectothermic vertebrates and large-bodied endothermic vertebrates, such as mammals, certainly differ considerably based on aspects of body size and physiology alone (e.g., Sunday et al., 2012). Even among mammals, there are likely to be differences among clades. Though we found no evidence for niche breadth differences, variation in other traits such as body size and trophic level are likely to be important factors for consideration in future research (Liow, 2008; Price et al., 2012).

1.2 Competitive interactions dominate community assembly in large mammals

As with macroevolutionary turnover, climates and environments are seen as the primary determinant of changes in mammalian paleocommunity composition through time. Temporal shifts in the structure of fossil assemblages are often attributed to climatic or environmental forcing, whether it be gradual (e.g., Badgley et al., 2008) or pulsed (e.g., Azanza et al., 2000). Likewise, uniformitarian approaches to paleoenvironmental reconstruction, in which taxonomic and/or ecological aspects of a fossil mammal assemblage are used to infer vegetation and climatic features of the ancient habitat, are predicated on the assumption that these are in fact tightly linked (Andrews et al., 1979; Hernandez-Fernandez and Vrba, 2006; Reed, 1997, 1998). Such studies rarely consider the effects of biotic interactions, implicitly or explicitly assuming that abiotic factors are the dominant control on mammal community assembly and therefore the taxonomic and/or ecological structure of communities.

The results of Chapter 2 indicate that biotic interactions – specifically competitive interactions – play the strongest role in shaping present-day large mammal communities in Africa. The strength of competition, however, varied across climatic and productivity gradients, with competitive interactions being strongest in high-productivity environments where food resources are both diverse and abundant. Abiotic filtering, on the other hand, was found to be relatively unimportant, suggesting little direct role of climate on community assembly. This is perhaps unsurprising, as large-bodied mammals, by virtue of their size, are less dispersal limited than smaller-bodied organisms (Bowman et al., 2002) and have broader thermal tolerances than ectotherms (Bennett et al., 2018) and even non-mammalian endotherms (Khaliq et al., 2014). Borrowing from Ernst Mayr's (1961) 'proximate' versus 'ultimate' dichotomy, we can hypothesize that

competitive outcomes between co-occurring species are the proximate cause of community structure, but by modulating the strength of those interactions, climate can be considered an ultimate cause. Accepting this multidimensional view of climate's role may in part reconcile the finding that competition mainly structures large mammal communities today with the fact that paleocommunity structure seems to track climate and environmental change through time. Such apparent scale-effects are likely common in the fossil record given its coarse resolution in both space and time (Benton, 2009).

1.3 Historical legacy, time lags, and community-climate disequilibrium

Studies of how ecological communities respond to climate change are central to identifying the drivers of biodiversity patterns (Gaston, 2000; Ricklefs, 2004) and feed directly into predictive models of global change over the next century (Maguire et al., 2015; Walther, 2010). In Chapter 3, it was found that climates of the Last Glacial Maximum (~ 22,000 years ago) and mid-Holocene (~ 6,000 years ago) have a greater influence on the structure of present-day African mammal communities than modern climate. This finding adds to a growing number of studies spanning virtually all groups of organisms suggesting that contemporary biodiversity patterns may be mainly structured by paleoclimatic legacies (Svenning et al., 2015). For example, Sandel and et al. (2011) showed that the velocity of late Quaternary climate change shapes global patterns of endemism in amphibians, mammals, and birds today. Similarly, Ordonez and Svenning (2015, 2016) found that functional diversity gradients in European plants species were codetermined by late Quaternary climate change and the extent of past glaciations. In a similar vein, the results of Chapter 3 were interpreted as reflecting climatically-induced late Quaternary shifts in biome distribution across Africa, such as the cyclical expansions

and contractions of equatorial forests. Together, these studies emphasize the need for neoecological research to draw on knowledge of past climate-community changes from the fossil record (Fritz et al., 2013) as well as to begin to incorporate paleoclimatic data directly into studies of present-day communities (Svenning et al., 2015).

Another important conclusion drawn from Chapter 3 is that time lags between climate and community change may be common in large-bodied mammals. Time lags in community responses to climate change can range between the extremes of ‘no-lag’, in which communities track shifting climates in real time and are in an equilibrium state, to long-term lags wherein communities go through transient disequilibrium states (Blonder et al., 2017). The no-lag hypothesis assumes that as climates change, certain species will remain present in the community either because they have well-matched niches or because they have wide niche breadths or environmental tolerances, while other species with poorly matched niches will undergo local extinction (Blonder et al., 2017). As these mismatched species disappear from the community, other taxa with well-matched niches will immigrate in from the regional species pool (Blonder et al., 2017). On the other hand, long-term lags between climate change and community reorganization may emerge when dispersal limitation is high or when the regional species pool does not contain taxa well-matched to the new climate (Svenning and Sandel, 2013; Blonder et al., 2015).

Although we know of no study where time lags have been measured for large mammal communities, our analyses suggest that they can be at least 10^3 - 10^4 years in duration based on the age of the mid-Holocene and Last Glacial Maximum, respectively. This finding has significant implications for species distribution models (SDMs) and related methods (e.g., ecophysiological models) that are founded on equilibrium assumptions but are critical to forecasting species responses to future climate change

(Franklin, 2010; Blonder et al., 2017). We believe that it is unlikely that climate disequilibrium in African mammal communities is driven by dispersal limitation, given that our findings in Chapter 2 suggest this process is relatively unimportant in large mammals. Likewise, regional species pools for African mammals are relatively rich in terms of phylogenetic and functional sampling (Rowan et al., 2016), so it is improbable that a deficit in appropriate biological and/or ecological traits can explain disequilibrium. Instead, we propose that the fact present-day communities are mainly structured by paleoclimate speaks to some degree of community resilience, implying that climate plays a relatively unimportant – or at least distal – role in shaping the community structure of large-bodied mammals.

The ‘community resilience’ hypothesis for large mammals finds support from studies of the fossil record. For example, Rodriguez (2004) showed that the functional structure of fossil communities from the Pleistocene of Spain (Sierra de Atapuerca) was relatively stable despite marked climate changes between ~ 750,000-200,000 years ago. He found that the faunas of Atapuerca, though spanning half a million years and multiple glacial and interglacial phases, were more similar to one another in terms of ecology than present-day communities from a single Eurasian biome (e.g., temperate deciduous forest, steppe). Rodriguez (2004) proposed that structural continuity of mammal communities through time reflected historical and biogeographic factors that shaped the regional species pool, therefore limiting the number of possible ecological structures for any given community drawn from it. A similar argument was made by Saupe et al. (2015), who proposed that species ranges themselves are driven by “unique historical, dispersal, and biotic constraints” that determined the species’ filling of geographic space during a

particular time period and therefore may be in disequilibrium with its contemporary environments.

1.4 Conclusions and future directions

The overall conclusion of this dissertation is that the influence of climate and climate change on the evolution and ecology of large-bodied mammals, both today and in the fossil record, has been overestimated in previous research. Though not unimportant altogether, climate's direct role is strongly scale-dependent and of relatively minor importance for understanding on-the-ground processes governing mammal distributions and community structure. At the level of ecological communities, climate's biggest role may be in modulating the strength, direction, and frequency of biotic interactions between species in a community (Blois et al., 2013), but it is the interactions themselves that shape the evolution and ecology of species. Climatic factors become more important as geographic and temporal scales increase, and undoubtedly plays a key role in shaping continental species pools and global diversity gradients in deep time (Jackson and Blois, 2015).

Given the scale-dependency of climate's influence, it is important to consider the spatial and temporal resolution of mammal assemblages in the Plio-Pleistocene eastern African fossil record (Figure 4.1). Although estimates of outcrop area are rare for many Plio-Pleistocene sites, most must fall between the extremes of the Denen Dora Member of the Hadar Formation of Hadar (12 km²) and the Tulu Bor Member of the Koobi Fora Formation (450 km²) (Rowan and Du, 2018). Thus, most fossil sites likely span 10⁴-10⁵ m² of space, which for mobile large-bodied mammals probably means little in terms of climatically-mediated dispersal boundaries. With respect to time, we can again use the

Denen Dora and Tulu Bor members as good examples of minima and maxima: the former is well-constrained between two volcanic tephras dated to 3.24-3.20 million years ago and spans ~ 40,000 years (Campisano and Feibel, 2008), while the latter ranges from 3.44-2.64 million years ago (McDougall et al., 2012), amounting to ~ 800,000 years. Thus, we can approximately bound most eastern African fossil site durations between ~ 10^3 - 10^5 years of time. Based on the finding that time lags between climate and mammal community change can be at least 10^3 - 10^4 years long (Rowan et al., 2016) and that fossil assemblages underwent little change through marked glacial-interglacial cycles in the Pleistocene of Spain (Rodriguez, 2004), it is unlikely climate plays a major role in shaping mammal communities at these temporal scales. Indeed, this hypothesis finds support in the many studies of the eastern African fossil record that have failed to find a relationship between community turnover and climate change through time (e.g., Bibi and Kiessling, 2015; Frost, 2007; Kimbel, 1995; Werdelin and Lewis, 2005; White, 1995).

In light of these findings, it is proposed that non-climatic influences – namely, biotic interactions – largely shape mammal communities at the spatiotemporal scales afforded by the Plio-Pleistocene eastern African fossil record (Figure 4.1). Future research into the evolution and ecology of hominins and other mammals should shift away from studies aimed at correlating climate with species turnover and community change that dominate hominin paleoecology today (Marean et al., 2015). Putting aside the fact that inferring causality from paleontological time series is full of potential pitfalls (Hannisdal and Liow, 2018), correlative approaches ignore the scale-dependency of Court Jester versus Red Queen influences (Benton, 2009) and therefore confuse ultimate (climate) and proximate (biotic interactions) causation for community change (Figure

4.1). It would be rewarding to refocus eastern African paleoecological research towards understanding the proximate causes of mammalian community change through time. Network analyses, which permit mechanistic (versus inferential) understandings of community evolution, lend themselves well to such an endeavor and are now emerging as powerful tools for paleoecological studies (e.g., Yeakel et al., 2013, 2014; Pires et al., 2015).

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APPENDIX A

SUPPLEMENTARY MATERIALS FOR CHAPTER 3

Supplementary Materials for:

Climate and primary productivity modulate the relative influence of competition and abiotic filtering across African mammal communities

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1. SI Text

This supplemental information provides detailed output on the linear models used to predict the phylogenetic and functional trait structure of African mammal communities from a series of climatic predictors. I provide model outputs and comparisons between Ordinary Least Squares (OLS) and spatial error models (SAR_{err}) models for phylogenetic structure metrics. In each of these cases, the SAR_{err} model was a significantly better fit based on AIC and likelihood ratio tests (SI Tables 2-3, 5-6, 8-9, 11-12, 14-15, 17-18). Likewise, spatial correlograms demonstrated that the SAR_{err} models effectively controlled for spatial autocorrelation in the community and climate data (SI Figures 1-6). Therefore, only SAR_{err} results are presented in the main text. I only present SAR_{err} results here for functional trait structure metrics because adding OLS and likelihood ratio tests metrics for each metric across each group and order would bring the total number of SI tables to over 100. However, all functional trait SAR_{err} models were checked against their OLS counterpart

2. SI Tables

2.1 SI Tables for group-level phylogenetic structure

SI Table 1. Macromammal OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	4.846	1.142	4.242	0.000
TS (Temp. Seasonality)	-0.049	0.065	-0.764	0.445
TCM (Temp. Coldest Month)	-9.333	0.821	-11.374	0.000
MAP (Mean Annual Precip.)	-0.759	0.059	-12.957	0.000
PS (Precip. Seasonality)	-15.656	0.912	-17.171	0.000
PDM (Precip. Driest Month)	0.858	0.656	1.307	0.191
Overall model: $R^2=0.359$, $F=590.96$, $p < 0.001$				

SI Table 2. Macromammal SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.996	1.575	1.267	0.205
TS (Temp. Seasonality)	0.342	0.134	2.561	0.010
TCM (Temp. Coldest Month)	-3.479	1.407	-2.471	0.013
MAP (Mean Annual Precip.)	-0.249	0.134	-1.861	0.063
PS (Precip. Seasonality)	-3.809	1.728	-2.204	0.027
PDM (Precip. Driest Month)	1.513	1.215	1.245	0.213
Overall model: $R^2=0.899$, $AIC=5127.4$ (AIC for $lm=16798$), $p < 0.001$				

SI Table 3. Likelihood fits for the OLS versus SAR_{err} model for explaining macromammal net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-8390.764
Log-likelihood SAR _{err}	-2554.680
Likelihood ratio=11672, $p < 0.001$	

SI Table 4. Micromammal OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	8.500	1.019	8.345	0.000
TS (Temp. Seasonality)	-0.453	0.057	-7.886	0.000
TCM (Temp. Coldest Month)	-8.506	0.731	-11.629	0.000
MAP (Mean Annual Precip.)	-0.389	0.052	-7.430	0.000
PS (Precip. Seasonality)	-4.805	0.812	-5.918	0.000
PDM (Precip. Driest Month)	0.470	0.585	0.804	0.421
Overall model: $R^2=0.091$, $F=106.082$, $p < 0.001$				

SI Table 5. Micromammal SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.690	1.346	-0.513	0.608
TS (Temp. Seasonality)	0.284	0.115	2.467	0.014
TCM (Temp. Coldest Month)	0.740	1.206	0.614	0.539
MAP (Mean Annual Precip.)	-0.326	0.115	-2.832	0.005
PS (Precip. Seasonality)	-0.112	1.481	-0.075	0.939
PDM (Precip. Driest Month)	0.663	1.045	0.6346	0.526
Overall model: $R^2=0.869$, $AIC=3073.9$ (AIC for $lm=15315$), $p < 0.001$				

SI Table 6. Likelihood fits for the OLS versus SAR_{err} model for explaining micromammal net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-7649.726
Log-likelihood SAR _{err}	-1527.958
Likelihood ratio= 12244, $p < 0.001$	

SI Table 7. Bat OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	4.552	1.001	4.547	0.000
TS (Temp. Seasonality)	0.304	0.057	5.370	0.000
TCM (Temp. Coldest Month)	-6.367	0.719	-8.857	0.000
MAP (Mean Annual Precip.)	0.794	0.053	15.113	0.000
PS (Precip. Seasonality)	-7.294	0.794	-9.182	0.000
PDM (Precip. Driest Month)	-2.669	0.575	-4.642	0.000
Overall model: $R^2=0.120$, $F=143.255$, $p < 0.001$				

SI Table 8. Bat SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.778	1.370	1.298	0.194

TS (Temp. Seasonality)	0.196	0.119	1.652	0.099
TCM (Temp. Coldest Month)	-1.668	1.212	-1.376	0.169
MAP (Mean Annual Precip.)	0.444	0.119	3.729	0.000
PS (Precip. Seasonality)	-1.529	1.491	-1.025	0.305
PDM (Precip. Driest Month)	0.381	1.098	0.347	0.729
Overall model: $R^2=0.859$, $AIC=3435.3$ (AIC for $lm=14890$), $p < \mathbf{0.001}$				

SI Table 9. Likelihood fits for the OLS versus SAR_{err} model for explaining bat net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-7436.760
Log-likelihood SAR _{err}	-1708.642
Likelihood ratio=11456, $p < \mathbf{0.001}$	

2.2 SI Tables for order-level phylogenetic structure

SI Table 10. Artiodactyl OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	0.755	0.889	0.850	0.396
TS (Temp. Seasonality)	0.439	0.050	8.831	0.000
TCM (Temp. Coldest Month)	-1.906	0.636	-2.995	0.003
MAP (Mean Annual Precip.)	-1.033	0.046	-22.448	0.000
PS (Precip. Seasonality)	2.151	0.732	2.939	0.003
PDM (Precip. Driest Month)	0.113	0.546	0.206	0.837
Overall model: $R^2=0.312$, $F=447.330$, $p < \mathbf{0.001}$				

SI Table 11. Artiodactyl SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-2.347	1.518	-1.547	0.123
TS (Temp. Seasonality)	0.269	0.128	2.096	0.036
TCM (Temp. Coldest Month)	1.039	1.347	0.774	0.439
MAP (Mean Annual Precip.)	-0.416	0.127	-3.278	0.001
PS (Precip. Seasonality)	1.306	1.615	0.809	0.419
PDM (Precip. Driest Month)	3.085	1.222	2.525	0.016
Overall model: $R^2=0.822$, $AIC=4525.5$ (AIC for $lm=12499$), $p < \mathbf{0.001}$				

SI Table 12. Likelihood fits for the OLS versus SAR_{err} model for explaining artiodactyl net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-6241.570
Log-likelihood SAR _{err}	-2253.774
Likelihood ratio=7975.6, $p < \mathbf{0.001}$	

SI Table 13. Carnivoran OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	-4.549	0.629	-7.231	0.000
TS (Temp. Seasonality)	0.574	0.036	16.158	0.000
TCM (Temp. Coldest Month)	6.168	0.452	13.649	0.000
MAP (Mean Annual Precip.)	0.974	0.032	30.186	0.000
PS (Precip. Seasonality)	4.6215	0.502	9.246	0.000

PDM (Precip. Driest Month)	-0.818	0.361	-2.266	0.024
Overall model: $R^2=0.291$, $F=432.444$, $p < \mathbf{0.001}$				

SI Table 14. Carnivoran SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.574	0.790	-0.727	0.467
TS (Temp. Seasonality)	0.059	0.069	0.846	0.398
TCM (Temp. Coldest Month)	1.749	0.700	2.498	0.012
MAP (Mean Annual Precip.)	0.112	0.069	1.607	0.108
PS (Precip. Seasonality)	-1.041	0.866	-1.202	0.229
PDM (Precip. Driest Month)	-1.721	0.629	-2.737	0.006
Overall model: $R^2=0.907$, $AIC=-3558.9$ (AIC for $lm=9263.6$), $p < \mathbf{0.001}$				

SI Table 15. Likelihood fits for the OLS versus SAR_{err} model for explaining carnivoran net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-4623.789
Log-likelihood SAR _{err}	1788.464
Likelihood ratio=12825, $p < \mathbf{0.001}$	

SI Table 16. Primate OLS model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	t-value	p-value
MAT (Mean Annual Temp.)	10.272	0.714	14.393	0.000
TS (Temp. Seasonality)	-0.427	0.041	-10.329	0.000
TCM (Temp. Coldest Month)	-4.063	0.514	-7.912	0.000
MAP (Mean Annual Precip.)	-0.142	0.041	-3.428	0.001
PS (Precip. Seasonality)	6.740	0.507	13.284	0.000
PDM (Precip. Driest Month)	2.004	0.524	3.824	0.000
Overall model: $R^2=0.128$, $F=117.539$, $p < \mathbf{0.001}$				

SI Table 17. Primate SAR_{err} model explaining phylogenetic structure, measured by net-relatedness index (NRI), across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.822	0.927	0.886	0.376
TS (Temp. Seasonality)	-0.184	0.075	-2.457	0.014
TCM (Temp. Coldest Month)	0.052	0.815	0.063	0.949
MAP (Mean Annual Precip.)	0.044	0.072	0.613	0.540
PS (Precip. Seasonality)	-0.979	0.819	-1.195	0.232
PDM (Precip. Driest Month)	0.117	0.815	0.144	0.886
Overall model: $R^2=0.826$, $AIC=-1215.8$ (AIC for $lm=6473.3$), $p < \mathbf{0.001}$				

SI Table 18. Likelihood fits for the OLS versus SAR_{err} model for explaining primate net-relatedness index (NRI) across Africa. Higher log-likelihood values indicate a better fit.

Log-likelihood OLS	-3228.657
Log-likelihood SAR _{err}	616.899
Likelihood ratio=7691.1, $p < \mathbf{0.001}$	

2.3 SI Tables for group-level Range functional structure

SI Table 19. Macromammal SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	5.650	2.231	2.533	0.011
TS (Temp. Seasonality)	-0.243	0.179	-1.359	0.174
TCM (Temp. Coldest Month)	-2.644	1.942	-1.361	0.173
MAP (Mean Annual Precip.)	0.332	0.179	1.854	0.064
PS (Precip. Seasonality)	1.820	2.348	0.775	0.438
PDM (Precip. Driest Month)	-1.765	1.661	-1.062	0.288
Overall model: $R^2=0.717$, AIC=10636 (AIC for lm=17783), $p < 0.001$				

SI Table 20. Macromammal SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-2.455	0.942	-2.607	0.009
TS (Temp. Seasonality)	0.101	0.074	1.357	0.175
TCM (Temp. Coldest Month)	1.599	0.816	1.959	0.050
MAP (Mean Annual Precip.)	-0.588	0.074	-7.914	0.000
PS (Precip. Seasonality)	3.351	0.982	3.412	0.001
PDM (Precip. Driest Month)	1.993	0.691	2.886	0.004
Overall model: $R^2=0.776$, AIC=15.168 (AIC for lm=5836), $p < 0.001$				

SI Table 21. Macromammal SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	7.911	1.978	4.000	0.000
TS (Temp. Seasonality)	0.111	0.167	0.661	0.508
TCM (Temp. Coldest Month)	-8.272	1.743	-4.747	0.000
MAP (Mean Annual Precip.)	0.439	0.169	2.603	0.009
PS (Precip. Seasonality)	1.012	2.138	0.473	0.636
PDM (Precip. Driest Month)	2.126	1.541	1.380	0.167
Overall model: $R^2=0.843$, AIC=8363.1 (AIC for lm=17508), $p < 0.001$				

SI Table 22. Micromammal SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	8.339	1.607	5.190	0.000
TS (Temp. Seasonality)	-0.173	0.137	-1.266	0.206
TCM (Temp. Coldest Month)	-7.374	1.419	-5.198	0.000
MAP (Mean Annual Precip.)	0.587	0.137	4.285	0.000
PS (Precip. Seasonality)	-2.179	1.736	-1.255	0.209
PDM (Precip. Driest Month)	0.760	1.253	0.607	0.544
Overall model: $R^2=0.837$, AIC=5721.4 (AIC for lm=15100), $p < 0.001$				

SI Table 23. Micromammal SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	8.220	2.608	3.152	0.002
TS (Temp. Seasonality)	-0.338	0.226	-1.497	0.134
TCM (Temp. Coldest Month)	-7.879	2.310	-3.411	0.001
MAP (Mean Annual Precip.)	0.177	0.226	0.758	0.448

PS (Precip. Seasonality)	-0.978	2.839	-0.345	0.730
PDM (Precip. Driest Month)	2.513	2.058	1.221	0.222
Overall model: $R^2=0.876$, AIC=11641 (AIC for lm=22518), $p < 0.001$				

SI Table 24. Micromammal SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.269	1.236	1.027	0.304
TS (Temp. Seasonality)	-0.003	0.104	-0.031	0.975
TCM (Temp. Coldest Month)	-1.051	1.089	-0.965	0.335
MAP (Mean Annual Precip.)	0.104	0.104	0.996	0.319
PS (Precip. Seasonality)	-1.370	1.330	-1.030	0.303
PDM (Precip. Driest Month)	-0.990	0.957	-1.034	0.301
Overall model: $R^2=0.805$, AIC=2512.7 (AIC for lm=11620), $p < 0.001$				

SI Table 25. Bat SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.426	1.656	0.861	0.389
TS (Temp. Seasonality)	-0.445	0.138	-3.238	0.001
TCM (Temp. Coldest Month)	0.108	1.454	0.074	0.941
MAP (Mean Annual Precip.)	0.312	0.138	2.258	0.024
PS (Precip. Seasonality)	0.376	1.771	0.213	0.832
PDM (Precip. Driest Month)	-1.585	1.286	-1.233	0.218
Overall model: $R^2=0.824$, AIC=6256.6 (AIC for lm=14015), $p < 0.001$				

SI Table 26. Bat SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-6.682	2.336	-2.860	0.004
TS (Temp. Seasonality)	0.042	0.199	0.210	0.834
TCM (Temp. Coldest Month)	8.383	2.002	4.187	0.000
MAP (Mean Annual Precip.)	0.942	0.173	5.450	0.000
PS (Precip. Seasonality)	-3.021	1.739	-1.737	0.082
PDM (Precip. Driest Month)	-5.232	2.069	-2.529	0.011
Overall model: $R^2=0.797$, AIC=4120.6 (AIC for lm=6795.1), $p < 0.001$				

SI Table 27. Bat SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-3.892	1.942	-2.004	0.045
TS (Temp. Seasonality)	-0.597	0.160	-3.720	0.000
TCM (Temp. Coldest Month)	6.464	1.594	4.052	0.000
MAP (Mean Annual Precip.)	0.944	0.139	6.762	0.000
PS (Precip. Seasonality)	0.691	1.339	0.516	0.606
PDM (Precip. Driest Month)	-3.025	1.674	-1.807	0.071
Overall model: $R^2=0.891$, AIC=3624.1 (AIC for lm=7158.9), $p < 0.001$				

2.4 SI Tables for group-level SDNDR functional structure

SI Table 28. Macromammal SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa. 218

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.554	2.006	0.775	0.439
TS (Temp. Seasonality)	-0.087	0.162	-0.538	0.590
TCM (Temp. Coldest Month)	0.237	1.751	0.136	0.892
MAP (Mean Annual Precip.)	0.237	0.163	1.452	0.146
PS (Precip. Seasonality)	4.851	2.123	2.285	0.022
PDM (Precip. Driest Month)	0.506	1.507	0.336	0.737
Overall model: $R^2=0.738$, AIC=9137.7 (AIC for lm=16714), $p < 0.001$				

SI Table 29. Macromammal SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.183	1.245	0.148	0.883
TS (Temp. Seasonality)	0.288	0.107	2.699	0.007
TCM (Temp. Coldest Month)	-1.227	1.099	-1.116	0.264
MAP (Mean Annual Precip.)	-0.457	0.107	-4.263	0.000
PS (Precip. Seasonality)	2.619	1.352	1.938	0.053
PDM (Precip. Driest Month)	2.938	0.977	3.001	0.003
Overall model: $R^2=0.900$, AIC=2413.2 (AIC for lm=12112), $p < 0.001$				

SI Table 30. Macromammal SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	8.819	2.232	3.951	0.000
TS (Temp. Seasonality)	0.049	0.193	0.253	0.800
TCM (Temp. Coldest Month)	-9.934	1.973	-5.034	0.000
MAP (Mean Annual Precip.)	0.108	0.194	0.559	0.576
PS (Precip. Seasonality)	0.303	2.430	0.125	0.901
PDM (Precip. Driest Month)	5.371	1.759	3.052	0.002
Overall model: $R^2=0.906$, AIC=9706.2 (AIC for lm=20011), $p < 0.001$				

SI Table 31. Micromammal SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.364	1.698	-0.214	0.830
TS (Temp. Seasonality)	-0.052	0.143	-0.372	0.710
TCM (Temp. Coldest Month)	-2.932	1.494	-1.963	0.049
MAP (Mean Annual Precip.)	-0.389	0.144	-2.709	0.007
PS (Precip. Seasonality)	-0.048	1.829	-0.026	0.979
PDM (Precip. Driest Month)	0.554	1.315	0.421	0.674
Overall model: $R^2=0.812$, AIC=6535.6 (AIC for lm=16013), $p < 0.001$				

SI Table 32. Micromammal SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	5.085	2.394	2.124	0.034
TS (Temp. Seasonality)	-0.163	0.207	-0.789	0.429
TCM (Temp. Coldest Month)	-4.643	2.119	-2.190	0.029
MAP (Mean Annual Precip.)	0.202	0.207	0.974	0.330
PS (Precip. Seasonality)	-1.585	2.603	-0.609	0.543
PDM (Precip. Driest Month)	1.046	1.886	0.555	0.579

Overall model: $R^2=0.854$, AIC=10592 (AIC for lm=21756), $p < 0.001$

SI Table 33. Micromammal SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	2.243	1.951	1.149	0.250
TS (Temp. Seasonality)	0.023	0.169	0.135	0.892
TCM (Temp. Coldest Month)	-2.084	1.728	-1.206	0.228
MAP (Mean Annual Precip.)	-0.234	0.169	-1.377	0.168
PS (Precip. Seasonality)	4.345	2.125	2.044	0.041
PDM (Precip. Driest Month)	4.437	1.542	2.876	0.004
Overall model: $R^2=0.888$, AIC=7956.8 (AIC for lm=18605), $p < 0.001$				

SI Table 34. Bat SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-1.637	1.964	-0.833	0.405
TS (Temp. Seasonality)	0.361	0.160	2.254	0.024
TCM (Temp. Coldest Month)	0.153	1.718	0.089	0.929
MAP (Mean Annual Precip.)	-0.165	0.161	-1.024	0.306
PS (Precip. Seasonality)	-0.151	2.082	-0.072	0.942
PDM (Precip. Driest Month)	0.774	1.503	0.515	0.606
Overall model: $R^2=0.760$, AIC=8605.5 (AIC for lm=15934), $p < 0.001$				

SI Table 35. Bat SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.957	1.792	1.092	0.275
TS (Temp. Seasonality)	0.175	0.153	1.146	0.252
TCM (Temp. Coldest Month)	-1.988	1.535	-1.295	0.195
MAP (Mean Annual Precip.)	-0.451	0.133	-3.402	0.001
PS (Precip. Seasonality)	1.259	1.333	0.945	0.345
PDM (Precip. Driest Month)	2.115	1.586	1.334	0.182
Overall model: $R^2=0.758$, AIC=2685 (AIC for lm=5646.6), $p < 0.001$				

SI Table 36. Bat SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	7.897	2.119	3.726	0.000
TS (Temp. Seasonality)	0.226	0.175	1.289	0.197
TCM (Temp. Coldest Month)	-6.916	1.740	-3.974	0.000
MAP (Mean Annual Precip.)	-0.728	0.152	-4.777	0.000
PS (Precip. Seasonality)	3.479	1.461	2.382	0.017
PDM (Precip. Driest Month)	3.204	1.827	1.754	0.079
Overall model: $R^2=0.789$, AIC=4100.1 (AIC for lm=6861.3), $p < 0.001$				

2.5 SI Tables for order-level Range functional structure

SI Table 37. Artiodactyl SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-1.320	1.455	-1.075	0.282

TS (Temp. Seasonality)	-0.159	0.123	-1.296	0.195
TCM (Temp. Coldest Month)	1.900	1.282	1.483	0.138
MAP (Mean Annual Precip.)	0.291	0.123	2.365	0.018
PS (Precip. Seasonality)	-1.463	1.558	-0.939	0.348
PDM (Precip. Driest Month)	-3.389	1.173	-2.890	0.004
Overall model: $R^2=0.859$, AIC=4022.9 (AIC for lm=12078), $p < 0.001$				

SI Table 38. Artiodactyl SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.963	2.041	-0.472	0.637
TS (Temp. Seasonality)	0.467	0.165	2.832	0.005
TCM (Temp. Coldest Month)	0.113	1.782	0.063	0.949
MAP (Mean Annual Precip.)	0.144	0.166	0.867	0.386
PS (Precip. Seasonality)	-5.642	2.153	-2.621	0.009
PDM (Precip. Driest Month)	-3.257	1.609	-2.024	0.043
Overall model: $R^2=0.773$, AIC=8538.8 (AIC for lm=15523), $p < 0.001$				

SI Table 39. Artiodactyl SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-1.406	1.457	-0.966	0.334
TS (Temp. Seasonality)	-0.160	0.123	-1.305	0.192
TCM (Temp. Coldest Month)	1.936	1.283	1.509	0.131
MAP (Mean Annual Precip.)	0.377	0.123	3.069	0.002
PS (Precip. Seasonality)	-2.089	1.559	-1.339	0.180
PDM (Precip. Driest Month)	-3.979	1.173	-3.393	0.001
Overall model: $R^2=0.858$, AIC=4051.3 (AIC for lm=12087), $p < 0.001$				

SI Table 40. Carnivoran SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.720	1.382	1.245	0.213
TS (Temp. Seasonality)	0.075	0.115	0.6460	0.518
TCM (Temp. Coldest Month)	-1.473	1.215	-1.213	0.225
MAP (Mean Annual Precip.)	-0.142	0.116	-1.224	0.221
PS (Precip. Seasonality)	-0.198	1.485	-0.133	0.894
PDM (Precip. Driest Month)	2.053	1.066	1.926	0.054
Overall model: $R^2=0.804$, AIC=4002.7 (AIC for lm=12599), $p < 0.001$				

SI Table 41. Carnivoran SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.650	1.260	1.309	0.190
TS (Temp. Seasonality)	0.041	0.109	0.376	0.706
TCM (Temp. Coldest Month)	-1.198	1.114	-1.075	0.282
MAP (Mean Annual Precip.)	-0.017	0.109	-0.153	0.878
PS (Precip. Seasonality)	2.751	1.371	2.007	0.045
PDM (Precip. Driest Month)	0.569	0.992	0.573	0.566
Overall model: $R^2=0.873$, AIC=2498.8 (AIC for lm=12383), $p < 0.001$				

SI Table 42. Carnivoran SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.764	1.391	-0.549	0.583
TS (Temp. Seasonality)	-0.137	0.117	-1.171	0.242
TCM (Temp. Coldest Month)	1.835	1.224	1.499	0.134
MAP (Mean Annual Precip.)	0.322	0.118	2.727	0.006
PS (Precip. Seasonality)	-2.880	1.499	-1.920	0.055
PDM (Precip. Driest Month)	-2.704	1.079	-2.505	0.012
Overall model: $R^2=0.847$, AIC=3985.8 (AIC for lm=13217), $p < 0.001$				

SI Table 43. Primate SAR_{err} model explaining functional trait structure of body mass, measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.829	1.085	1.685	0.092
TS (Temp. Seasonality)	0.000	0.086	0.000	0.999
TCM (Temp. Coldest Month)	-1.538	0.944	-1.629	0.103
MAP (Mean Annual Precip.)	-0.089	0.083	-1.077	0.281
PS (Precip. Seasonality)	1.484	0.949	1.564	0.118
PDM (Precip. Driest Month)	1.221	0.931	1.312	0.189
Overall model: $R^2=0.669$, AIC=515.33 (AIC for lm=5303.2), $p < 0.001$				

SI Table 44. Primate SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.354	1.314	0.269	0.788
TS (Temp. Seasonality)	-0.070	0.105	-0.671	0.503
TCM (Temp. Coldest Month)	0.037	1.146	0.032	0.974
MAP (Mean Annual Precip.)	0.0295	0.101	0.293	0.769
PS (Precip. Seasonality)	-1.581	1.153	-1.372	0.170
PDM (Precip. Driest Month)	-0.064	1.134	-0.057	0.955
Overall model: $R^2=0.689$, AIC=2293.6 (AIC for lm=6950), $p < 0.001$				

SI Table 45. Primate SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by Range, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.321	1.455	0.221	0.825
TS (Temp. Seasonality)	0.099	0.117	0.844	0.399
TCM (Temp. Coldest Month)	-1.194	1.277	-0.936	0.349
MAP (Mean Annual Precip.)	-0.203	0.112	-1.808	0.071
PS (Precip. Seasonality)	-1.325	1.285	-1.031	0.302
PDM (Precip. Driest Month)	1.989	1.275	1.559	0.119
Overall model: $R^2=0.829$, AIC=3132.3 (AIC for lm=10674), $p < 0.001$				

2.6 SI Tables for order-level SDNDR functional structure

SI Table 46. Artiodactyl SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.252	1.361	0.185	0.853
TS (Temp. Seasonality)	0.022	0.114	0.271	0.786

TCM (Temp. Coldest Month)	0.259	1.201	0.213	0.831
MAP (Mean Annual Precip.)	0.169	0.114	1.487	0.137
PS (Precip. Seasonality)	-2.401	1.450	-1.655	0.098
PDM (Precip. Driest Month)	0.700	1.096	0.639	0.523
Overall model: $R^2=0.808$, AIC=3302.5 (AIC for lm=11621), $p < 0.001$				

SI Table 47. Artiodactyl SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	8.624	2.193	3.932	0.000
TS (Temp. Seasonality)	0.363	0.190	1.912	0.056
TCM (Temp. Coldest Month)	-8.329	1.951	-4.269	0.000
MAP (Mean Annual Precip.)	0.093	0.187	0.497	0.619
PS (Precip. Seasonality)	-4.599	2.351	-1.956	0.050
PDM (Precip. Driest Month)	-2.738	1.784	-1.535	0.125
Overall model: $R^2=0.902$, AIC=8600.5 (AIC for lm=18454), $p < 0.001$				

SI Table 48. Artiodactyl SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	0.775	1.371	0.565	0.572
TS (Temp. Seasonality)	0.004	0.114	0.038	0.969
TCM (Temp. Coldest Month)	-0.138	1.207	-0.114	0.909
MAP (Mean Annual Precip.)	0.172	0.115	1.497	0.134
PS (Precip. Seasonality)	-3.696	1.460	-2.531	0.011
PDM (Precip. Driest Month)	-0.592	1.106	-0.535	0.593
Overall model: $R^2=0.799$, AIC=3401.4 (AIC for lm=11561), $p < 0.001$				

SI Table 49. Carnivoran SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	1.250	1.181	1.058	0.289
TS (Temp. Seasonality)	0.231	0.099	2.328	0.019
TCM (Temp. Coldest Month)	-1.711	1.039	-1.646	0.099
MAP (Mean Annual Precip.)	0.218	0.099	2.179	0.029
PS (Precip. Seasonality)	-1.443	1.272	-1.135	0.257
PDM (Precip. Driest Month)	-1.332	0.914	-1.457	0.145
Overall model: $R^2=0.817$, AIC=1960.7 (AIC for lm=11095), $p < 0.001$				

SI Table 50. Carnivoran SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-1.033	1.013	-1.019	0.308
TS (Temp. Seasonality)	0.144	0.082	1.752	0.079
TCM (Temp. Coldest Month)	0.155	0.885	0.176	0.861
MAP (Mean Annual Precip.)	-0.239	0.083	-2.898	0.004
PS (Precip. Seasonality)	-0.311	1.074	-0.289	0.772
PDM (Precip. Driest Month)	1.451	0.763	1.901	0.057
Overall model: $R^2=0.778$, AIC=450.26 (AIC for lm=7992.5), $p < 0.001$				

SI Table 51. Carnivoran SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	4.020	1.452	2.769	0.006
TS (Temp. Seasonality)	0.057	0.126	0.453	0.650
TCM (Temp. Coldest Month)	-3.959	1.284	-3.083	0.002
MAP (Mean Annual Precip.)	0.392	0.126	3.098	0.002
PS (Precip. Seasonality)	0.216	1.583	0.137	0.891
PDM (Precip. Driest Month)	-0.238	1.147	-0.207	0.836
Overall model: $R^2=0.898$, AIC=4247.5 (AIC for lm=16407), $p < 0.001$				

SI Table 52. Primate SAR_{err} model explaining functional trait structure of body mass, measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.293	1.428	-0.205	0.838
TS (Temp. Seasonality)	-0.014	0.115	-0.120	0.904
TCM (Temp. Coldest Month)	1.137	1.252	0.908	0.364
MAP (Mean Annual Precip.)	0.204	0.110	1.856	0.063
PS (Precip. Seasonality)	-1.225	1.260	-0.972	0.331
PDM (Precip. Driest Month)	-0.364	1.249	-0.292	0.770
Overall model: $R^2=0.835$, AIC=2972.6 (AIC for lm=10113), $p < 0.001$				

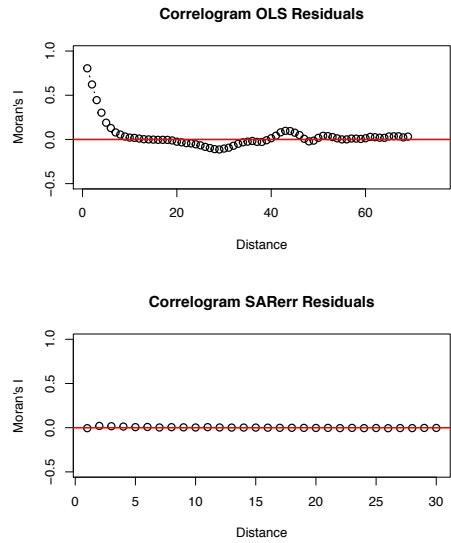
SI Table 53. Primate SAR_{err} model explaining functional trait structure of the first axis of the dietary principal coordinates analysis (diet PCoA1), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	-0.550	1.804	-0.305	0.760
TS (Temp. Seasonality)	0.093	0.145	0.644	0.519
TCM (Temp. Coldest Month)	1.479	1.584	0.934	0.350
MAP (Mean Annual Precip.)	0.269	0.139	1.939	0.052
PS (Precip. Seasonality)	-1.661	1.591	-1.044	0.296
PDM (Precip. Driest Month)	1.329	1.579	0.842	0.399
Overall model: $R^2=0.815$, AIC=5182.4 (AIC for lm=11992), $p < 0.001$				

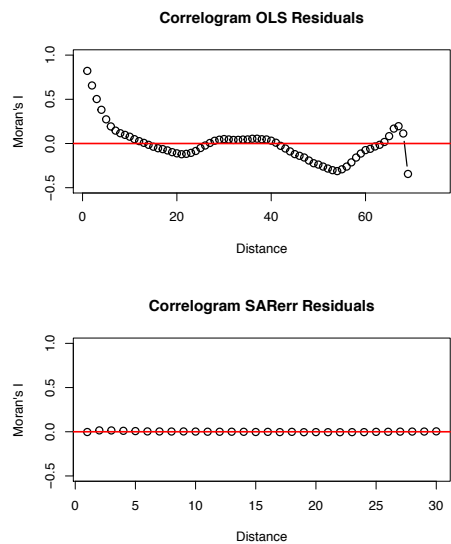
SI Table 54. Primate SAR_{err} model explaining functional trait structure of the second axis of the dietary principal coordinates analysis (diet PCoA2), measured by SDNDR, across Africa.

	Estimate	Std. Error	z-value	p-value
MAT (Mean Annual Temp.)	5.982	1.638	3.653	0.000
TS (Temp. Seasonality)	-0.205	0.132	-1.554	0.120
TCM (Temp. Coldest Month)	-3.786	1.436	-2.638	0.008
MAP (Mean Annual Precip.)	0.252	0.126	1.996	0.046
PS (Precip. Seasonality)	-0.067	1.445	-0.046	0.963
PDM (Precip. Driest Month)	-0.161	1.432	-0.113	0.910
Overall model: $R^2=0.802$, AIC=4272.1 (AIC for lm=11177), $p < 0.001$				

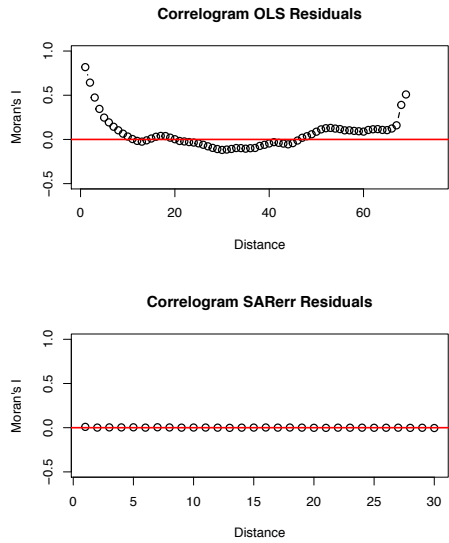
3. SI Figures



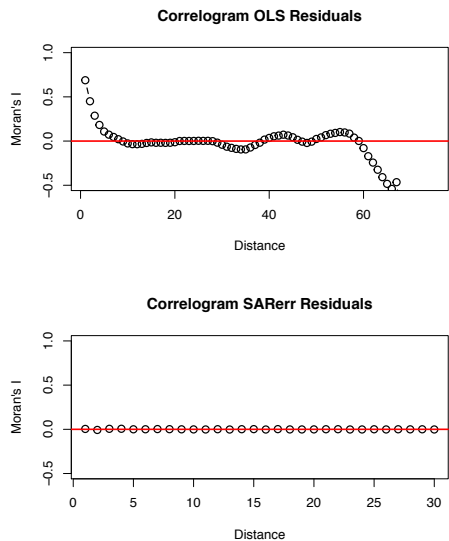
SI Figure 1. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting macromammal phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



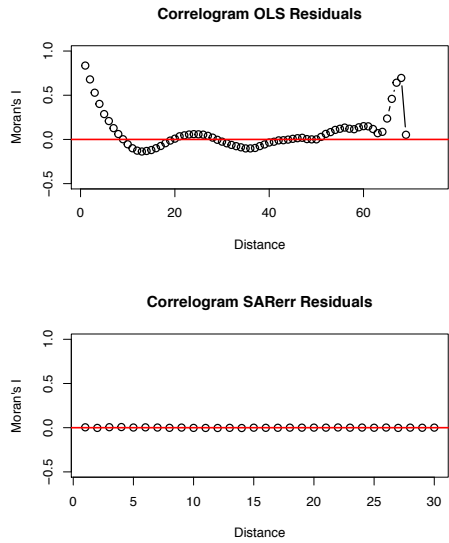
SI Figure 2. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting micromammal phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



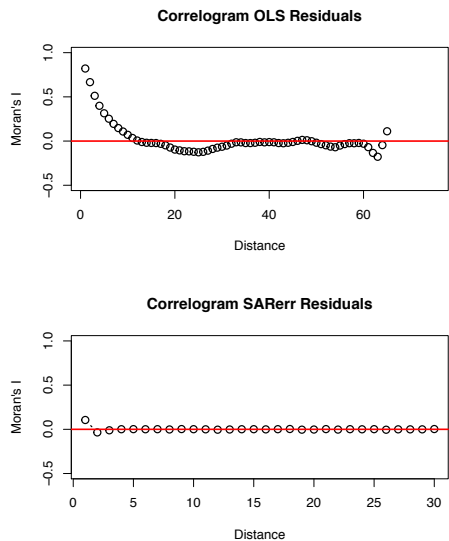
SI Figure 3. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting bat phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



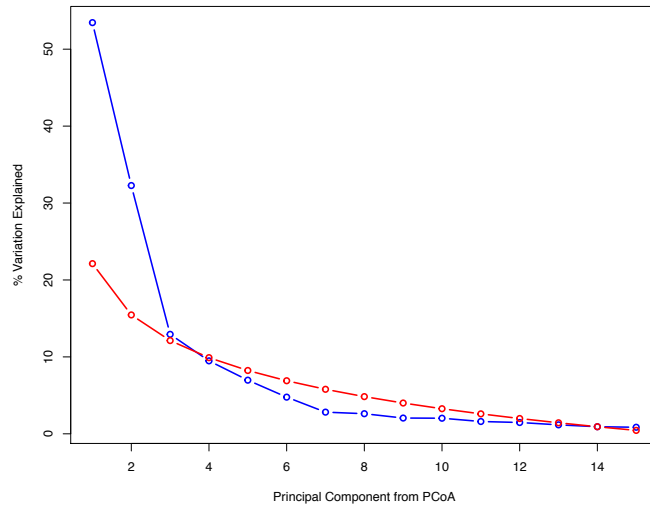
SI Figure 4. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting artiodactyl phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



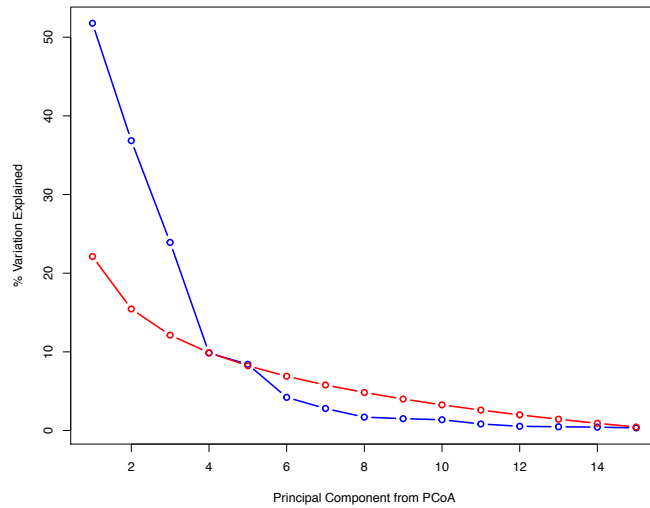
SI Figure 5. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting carnivoran phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



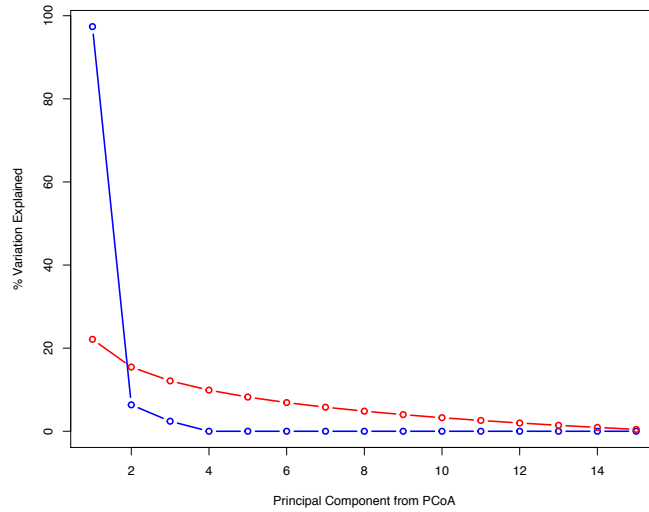
SI Figure 6. Spatial correlograms of model residuals from ordinary least squares (OLS) and spatial error models (SAR_{err}) models predicting primate phylogenetic structure from six climate variables. Moran's I values of zero indicate no spatial autocorrelation, whereas a value of positive one indicates strong positive spatial autocorrelation and a value of negative one indicates strong negative spatial autocorrelation.



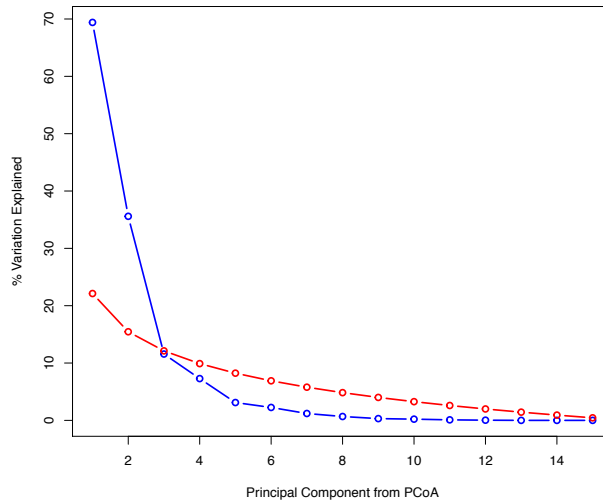
SI Figure 7. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of macromammals. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across macromammals.



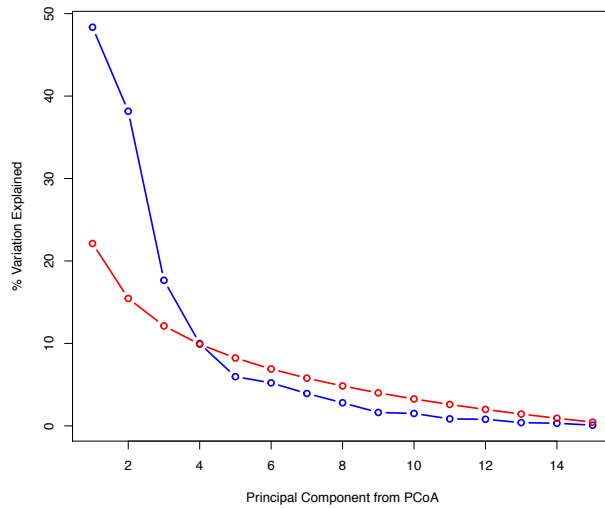
SI Figure 8. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of micromammals. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across micromammals.



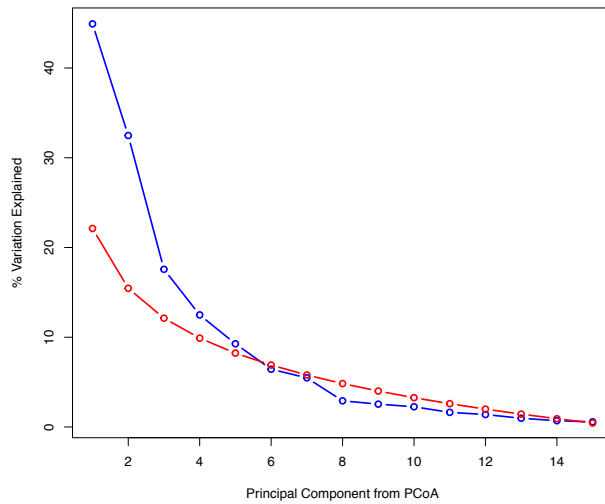
SI Figure 9. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of bats. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across bats.



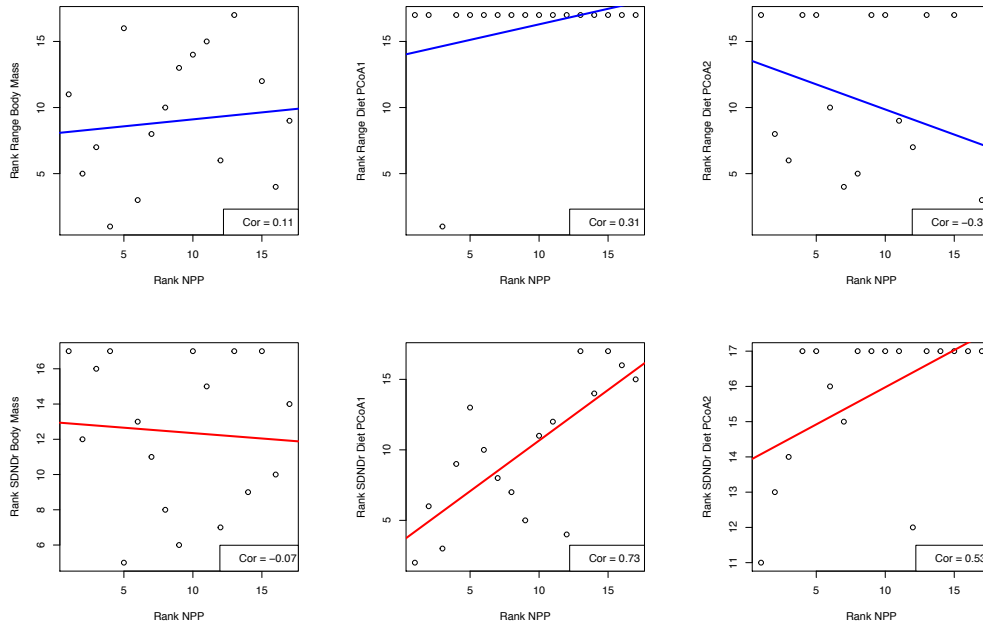
SI Figure 10. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of artiodactyls. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across artiodactyls.



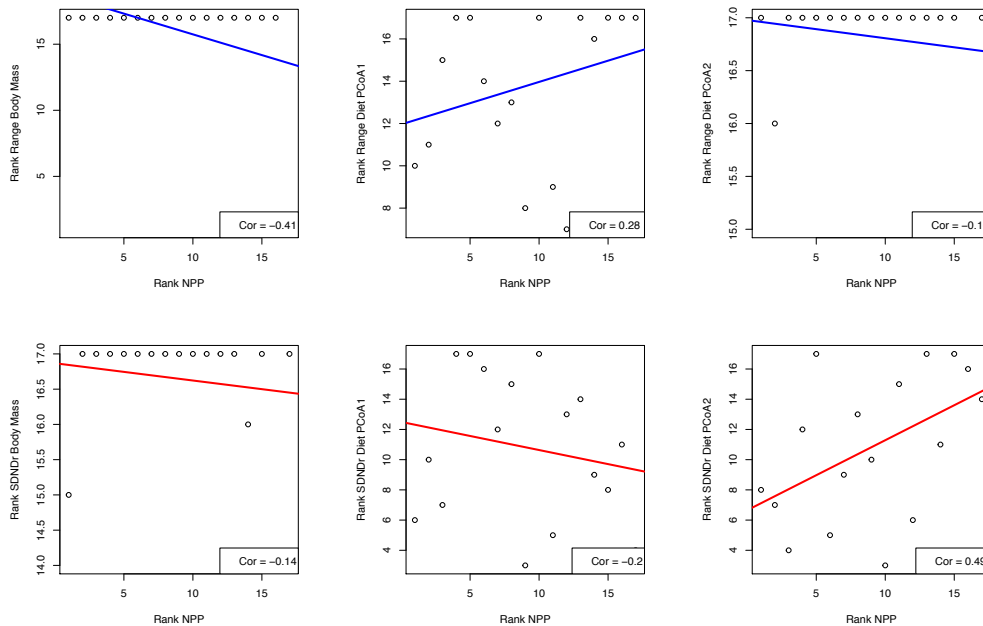
SI Figure 11. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of carnivorans. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across carnivorans.



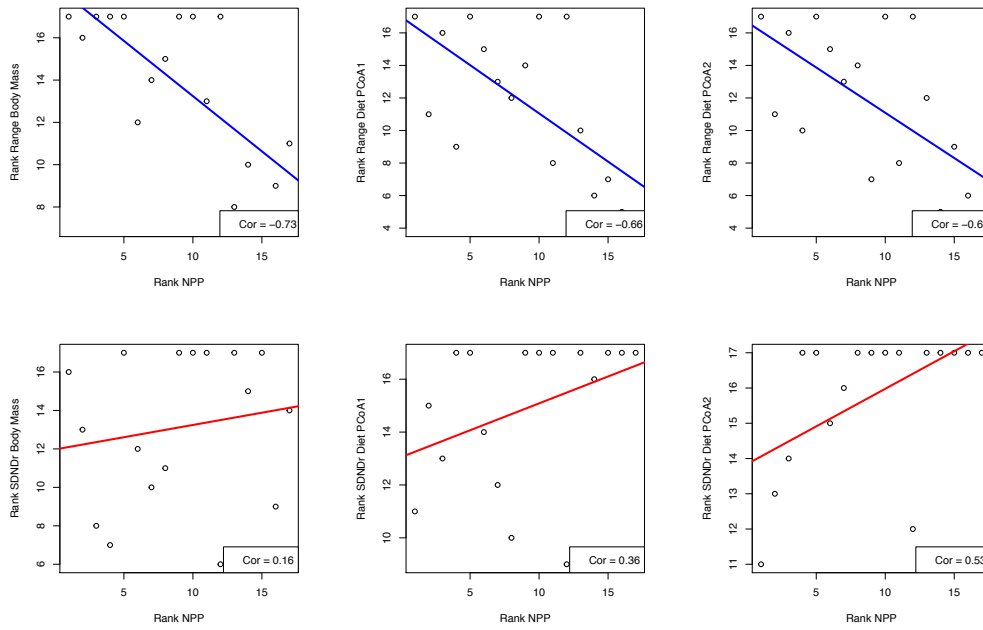
SI Figure 12. Percentage of variation explained (blue line), shown on the y-axis, across the first 15 axes of a principal coordinates analysis (PCoA), shown on the x-axis, for dietary data of primates. The first two components capture most of the variation in the dietary data and therefore are broadly representative of ‘dietary niche space’ across primates.



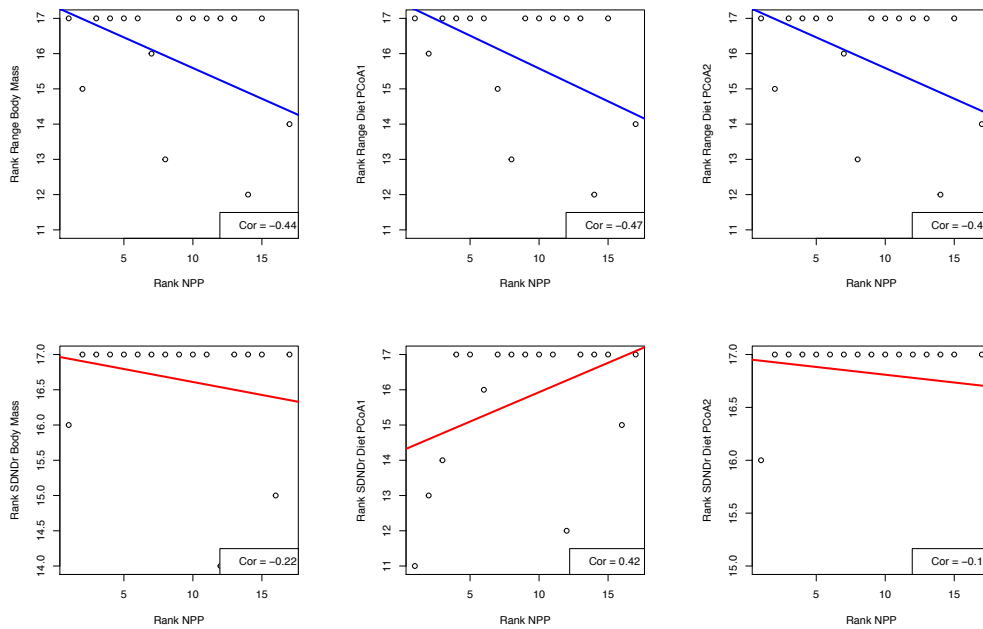
SI Figure 13. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for macromammals. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



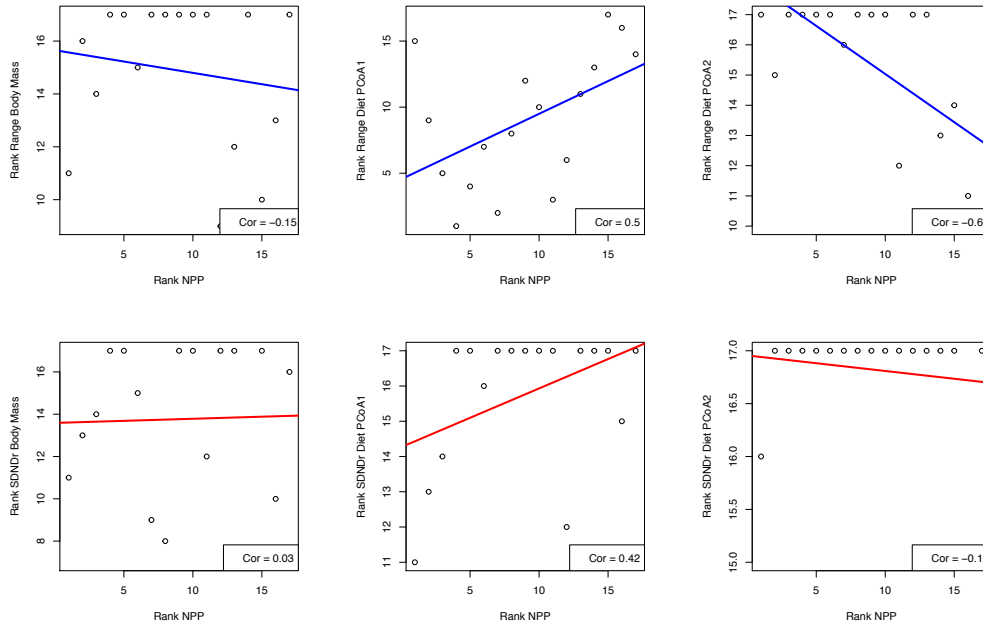
SI Figure 14. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for micromammals. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



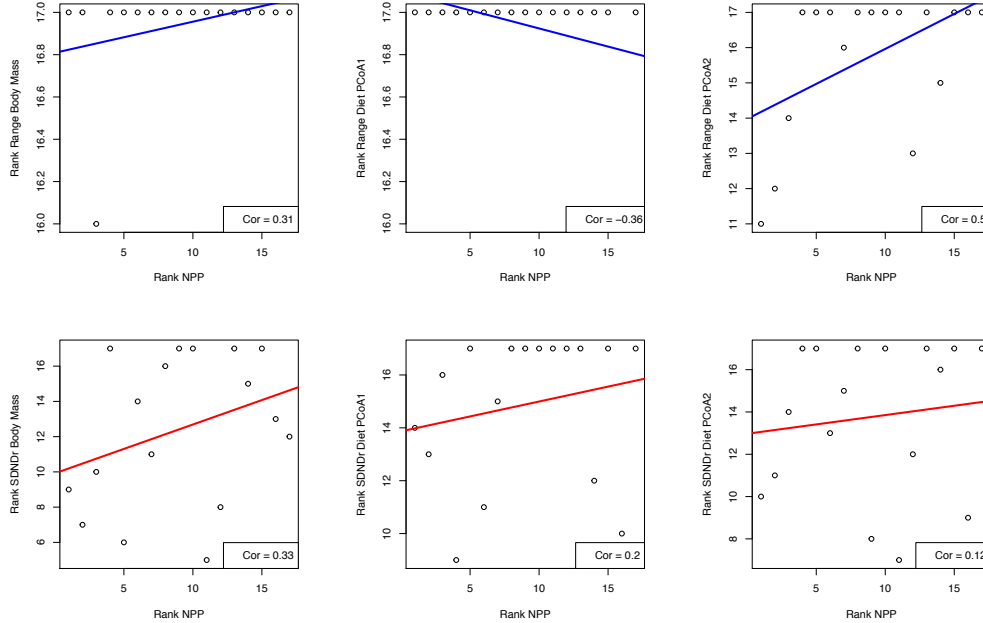
SI Figure 15. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for bats. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



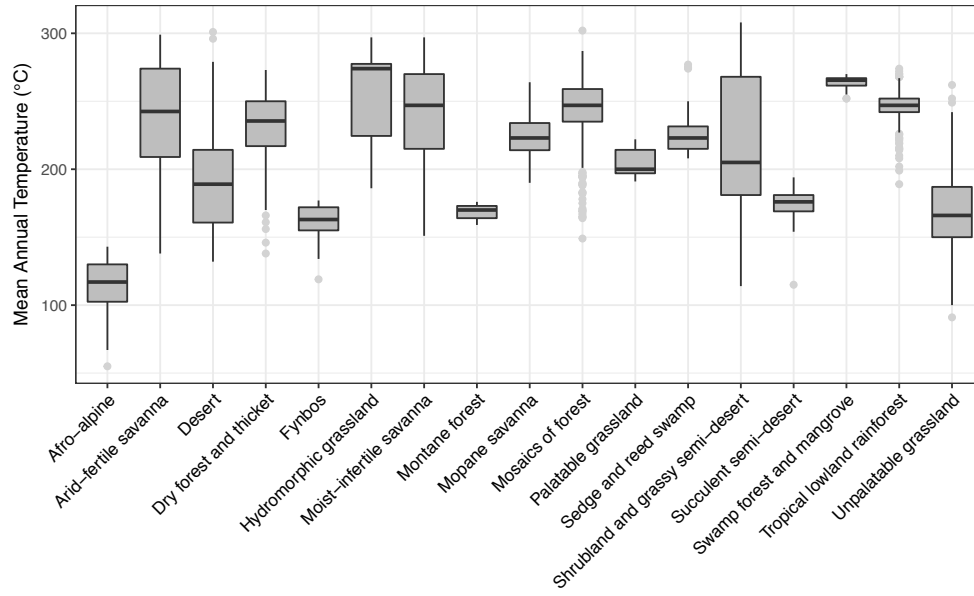
SI Figure 16. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for artiodactyls. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



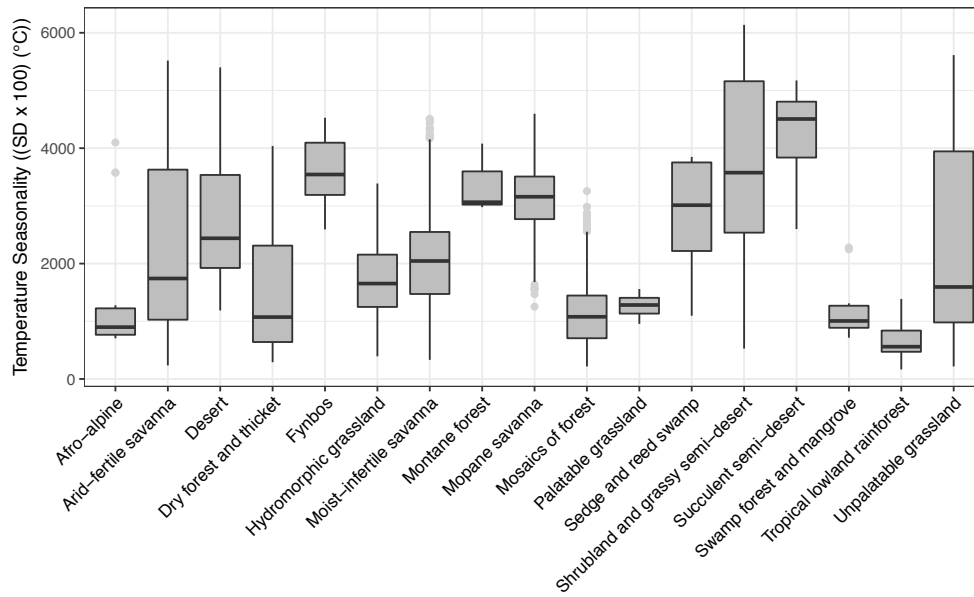
SI Figure 17. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for carnivorans. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



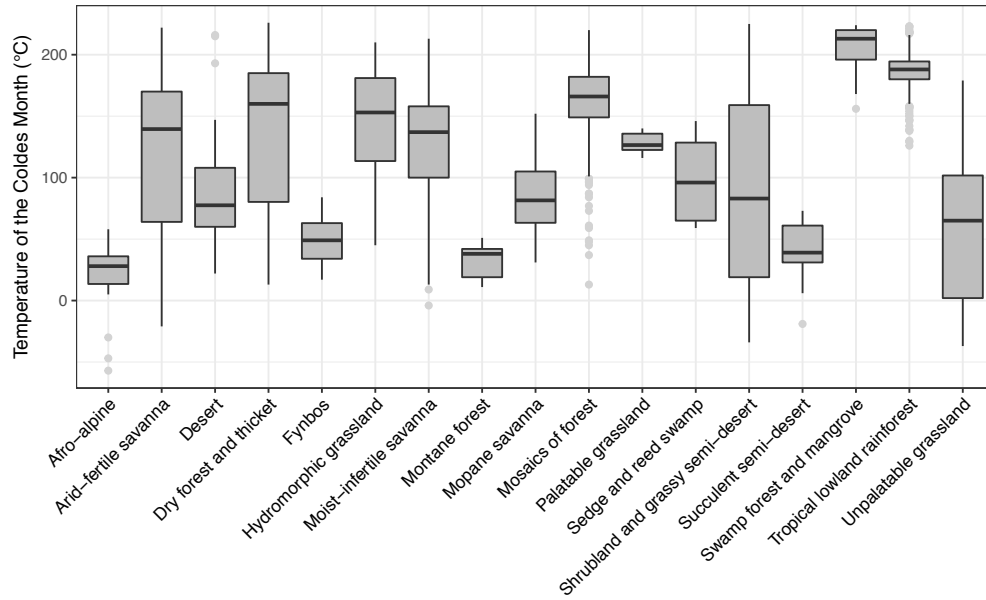
SI Figure 18. Rank correlations between mean net primary productivity (NPP) and community functional trait structure for primates. Biomes are ranked by the proportion of communities that were significant for a given functional trait metric.



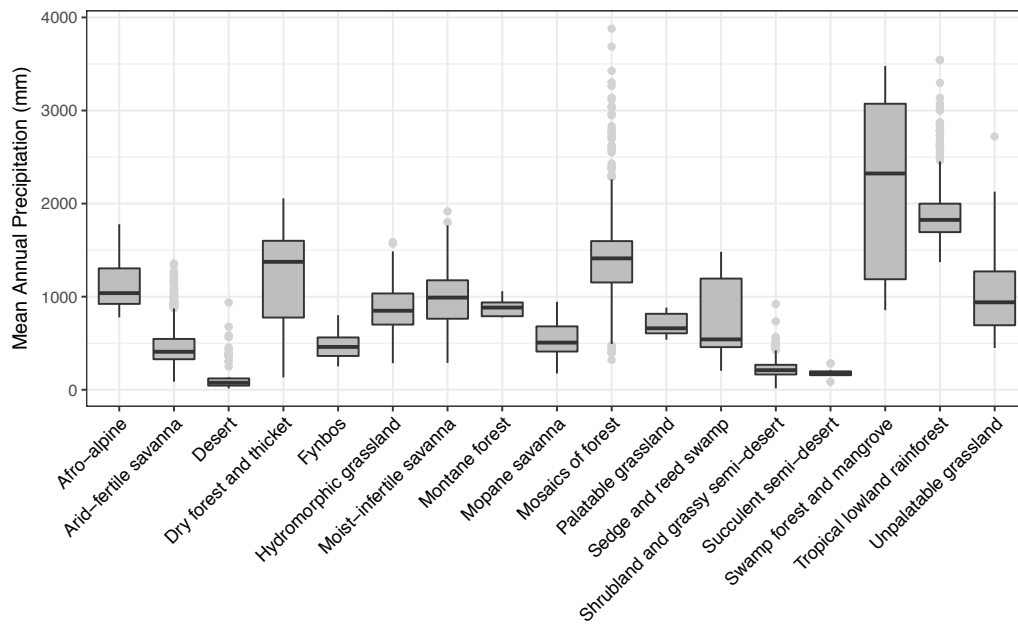
SI Figure 19. Boxplot of mean annual temperature (BIO 1) across White's (1983) biomes.



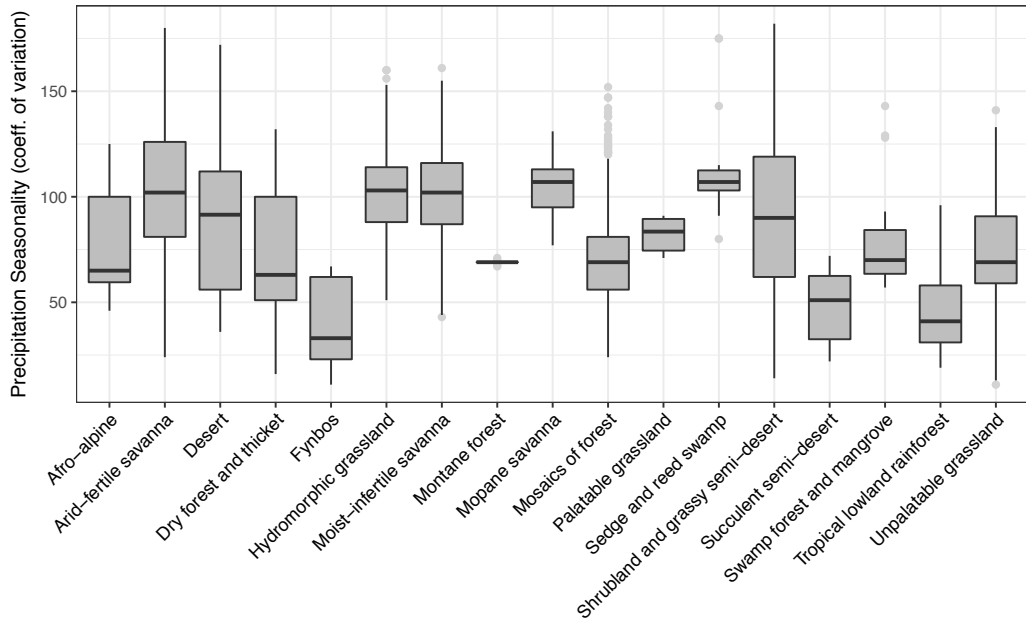
SI Figure 20. Boxplot of temperature seasonality (BIO 4) across White's (1983) biomes.



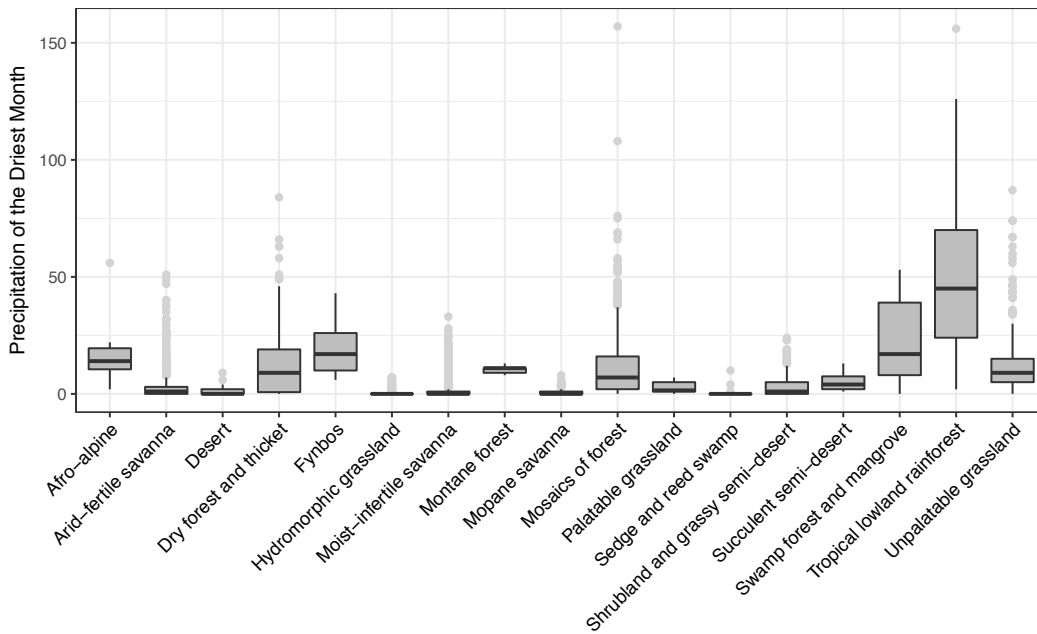
SI Figure 21. Boxplot of temperature of the coldest month (BIO 6) across White's (1983) biomes.



SI Figure 22. Boxplot of mean annual precipitation (BIO 12) across White's (1983) biomes.



SI Figure 23. Boxplot of precipitation seasonality (BI0 15) across White's (1983) biomes.



SI Figure 24. Boxplot of precipitation of the driest month (BI0 14) across White's (1983) biomes.

APPENDIX B

SUPPLEMENTARY MATERIALS FOR CHAPTER 4

Supplementary Materials for:

Strong influence of paleoclimate on the structure of modern African mammal communities

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1. SI Text

Supplementary information for Rowan et al. (2016) is permanently archived by *Proceedings of the Royal Society of London B: Biological Sciences*:

DOI: 10.1098/rspb.2016.1207

<http://rspb.royalsocietypublishing.org/content/283/1840/20161207.figures-only>