Dietary Ecology of Extant Artiodactyls: Biogeography, Ecomorphology, and Isotope Ecology, with Implications for Paleoecology

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Earth and Environmental Sciences)
in the University of Michigan
2021

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Dedication

To my grandmother

Acknowledgements

The work presented here was supported by funding from the Geological Society of America, the American Museum of Natural History, the Society of Vertebrate Paleontology, the Paleontological Society, University of Michigan Rackham Graduate School, and the University of Michigan Department of Earth and Environmental Sciences.

I would like to thank my advisor, Catherine Badgley, for all her guidance and support throughout the course of my graduate program. Catherine is a creative scientist, a caring mentor, and an inclusive leader. She is everything that I aspire to be. Her wealth of knowledge, wisdom, and kindness have nurtured me both intellectually and personally, and I have no doubt that I will continue to benefit from this experience for many years to come.

I feel extremely fortunate to have four other inspiring scientists in my committee: Miriam Zelditch, Laura MacLatchy, Matt Friedman, and Ben Passey. Through their course instructions and research, they have taken me to explore many wonders of vertebrate paleontology, functional morphology, and isotope geochemistry. I feel humbled by and grateful for their expertise. My committee has also been incredibly supportive and understanding as I navigated the COVID-19 pandemic and modified my research plans. I appreciate all their input on my work and their encouragements.

At the University of Michigan, I have had the privilege to work with and learn from many outstanding researchers, teachers, staff, and students. It has been a truly enriching and rewarding experience. I have been presented with many challenges as well as opportunities. I am

forever in debt to those who have helped me along the way, especially those who always believe in me and see me as who I am.

Lastly, I want to thank my family, especially my grandmother and mother, for always allowing me to make my own decisions, and my cat for the past eight years of affection and company.

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Abstract

The order Artiodactyla is a diverse group of terrestrial mammals that has been an important component of most terrestrial ecosystems since the Eocene. Understanding artiodactyl dietary ecology in relation to environmental gradients, morphological traits, and isotope ecology provides useful tools for making ecological inferences in the fossil record. I analyzed these topics for a wide range of extant species, utilizing a classification of herbivorous diets based on six rather than the usual three categories of dietary habits. The six-category scheme includes frugivores, browsers, browser-grazer intermediates, generalists, variable grazers, and obligate grazers. My dissertation research has three components.

First, I analyzed the ecological diversity represented in the diet and body size of artiodactyls in relation to climate and topography, using a global dataset of locality-based occurrence data for 161 extant species. Results show that higher species richness is associated with greater ecological diversity. The highest artiodactyl richness occurs in Africa and is achieved by accommodation of more ecological traits as well as more coexisting species with the same traits. A range of ecological diversity levels, however, can occur in different areas with comparable species richness. Among climatic variables, seasonal extremes of temperature and rainfall are important predictors of artiodactyl richness. The dietary extremes (frugivores and obligate grazers) occur in the most restricted climatic conditions. The occurrence of these dietary categories in the ungulate fossil record, as well as the ecological structure of fossil ungulate faunas, can be useful for inferring paleoclimatic conditions.

Next, I conducted an ecomorphological analysis of bovid mandibles with landmark-based geometric morphometrics. Mandibular morphology proves to be useful for differentiating dietary categories. Frugivores differ from browsers and obligate grazers from variable grazers. Notably, frugivorous bovids have a mandibular shape that is readily distinguished from all other dietary groups. The main differences in mandibular shape among dietary groups are related to the functional needs of species during forage prehension and mastication. Compared to browsers, both frugivores and grazers have mandibles that are adapted for higher biomechanical demand of chewing. Additionally, frugivore mandibles are adapted for selective cropping. These results offer an approach for reconstructing the diet of extinct bovids with mandibular morphology.

In the third study, I compiled a global dataset of carbon-isotope composition of artiodactyl tooth enamel to evaluate the isotopic composition of ingested forage ($\delta^{13}C_{diet}$). The herbivore dietary spectrum is expressed through increasing mean $\delta^{13}C_{diet}$ values from frugivores to obligate grazers, although the most depleted values occur in browsers that live under dense forest canopy. Grazing taxa generally have a wider range of $\delta^{13}C_{diet}$ values than browsing taxa. Variation in $\delta^{13}C_{diet}$ values also occurs among ecoregions, taxonomic groups, and geographic regions. Notably, variable grazers exhibit a bimodal distribution of $\delta^{13}C_{diet}$ values, with North American taxa consuming C_3 vegetation and African taxa consuming C_4 vegetation, reflecting the different amounts of C_4 biomass available in these regions today. Clarifying the contributing factors to variation in $\delta^{13}C_{diet}$ will refine paleoecological reconstructions.

These findings support use of the more detailed dietary classification in the study of artiodactyls. Identifying frugivory and obligate grazing, especially, will inform paleoenvironmental reconstructions. In addition, this work highlights the importance of integrating different data types in (paleo)ecological research. For example, stable-isotopic data showed strong separation of enriched and depleted values within morphospace for bovid mandibles, demonstrating the complementarity of different kinds of ecological data.

Chapter 1

Introduction

Ungulates are an important and diverse component of the Cenozoic mammalian fossil record. Both orders of ungulate mammals, the Artiodactyla and the Perissodactyla, have a long evolutionary history spanning the beginning of the Eocene to the present (Janis et al., 1998). The changing diversity and ecology of these ungulates through geologic time (Fig. 1.1) have long been investigated in relation to evolutionary adaptations, ecosystem change, and climate change. Key evolutionary events and dispersals of ungulates have been found to be associated with some of the most important environmental changes in the Cenozoic, including the Paleocene-Eocene Thermal Maximum, the Eocene-Oligocene Transition, the Mid-Miocene Climatic Optimum, and the expansion of C4 grasslands in the late Neogene (e.g., Janis, 1993; Gingerich, 2006; Bouchenak‐Khelladi et al., 2009; Fraser and Theodor, 2013).

Inferences about the ecology of extinct mammals rely heavily but not exclusively on what can be learned about their modern analogues, including their close relatives, and, therefore, a thorough understanding of the ecology of extant ungulates should better inform paleoecological research. Extant terrestrial ungulates are represented by over 250 species of (non-cetacean) artiodactyls and 18 species of perissodactyls (Burgin et al., 2018). Artiodactyls are widespread in the ecosystems of Africa, Eurasia, North America, and South America (Fig. 1.2). The taxonomic and ecological diversity of extant artiodactyls renders them good modern analogues for many extinct ungulates.

Understanding the dietary habits of ungulate mammals, which are predominantly herbivorous, is not only essential to reconstructing their paleoecology, but also has provided valuable insights into paleoenvironmental changes (e.g., DeMiguel et al., 2011; Rivals et al., 2011). Widely used methods for studying the diet of living and fossil herbivores include the dental hypsodonty index, dental microwear analysis, dental mesowear analysis, stable isotope analysis of body tissues, and ecomorphological analysis of craniomandibular features. These methods have been useful for differentiating browsing, grazing, and mixed feeding in herbivore dietary habits (e.g., Janis, 2008). Combining results from multiple methods improves accuracy of paleoecological reconstructions (e.g., Rivals and Ziegler, 2018).

The goal of my dissertation research is to understand the dietary habits of extant artiodactyls in relation to their general environment, mandibular morphology, and carbon-isotope composition of tooth enamel. Each of the three data chapters focuses on one of these topics. I adopt a classification scheme of herbivore diets that is more detailed than what is commonly used in the literature. This classification scheme includes seven feeding categories and provides more information about dietary habits than the three broad categories of browsing, grazing, and mixed feeding. In Chapter 2, I evaluate the geographic patterns of artiodactyl richness and ecological diversity in relation to climate and topography. In Chapter 3, I test whether artiodactyls (specifically bovids) with different diets can be differentiated by their mandibular morphology. In Chapter 4, I compare the stable-isotope composition of artiodactyls in different dietary categories using data derived from their tooth enamel. Findings of this research will not only give us better knowledge of the dietary ecology of living species, but also provide better tools for reconstructing ungulate paleoecology across space and through time.

1.1 Background: the herbivore dietary spectrum

Most artiodactyls are herbivorous, and they are typically classified as browsers, grazers, and mixed feeders. Browsers primarily feed on dicotyledonous material, such as leaves, fruits, and twigs; grazers primarily feed on monocotyledonous material, such as grasses or sedges, which are generally more abrasive than dicotyledonous material; and mixed feeders consume a mixture of dicotyledonous and monocotyledonous materials across space and seasons (Hofmann and Stewart, 1972). Much of the existing literature classifies living and fossil herbivores using these categories. Finer dietary classifications have been used in some studies to capture more details in the foraging selectivity and preference of various artiodactyls (Table 1.1). Analytical results of these studies show promise for differentiating artiodactyl feeding categories beyond three broad categories, giving consideration to the specialization or generality of species' diets, the canopy-cover of feeding environment, and sometimes the level (height from the ground) that species feed at. Other studies in recent years have used the percentage of grass in species' diets to quantitatively place species along a dietary continuum. This approach can overcome the potential weaknesses of categorical trait data and conceptualizes diet as a spectrum with two end members: browsers and grazers (e.g., Clauss et al., 2003).

It has been argued that the browser–grazer spectrum of ungulate diet should be, strictly speaking, a frugivore–browser–grazer spectrum (Bodmer, 1990). Later studies of dietary preference, enamel morphology, and tooth-wear also distinguished patterns in frugivorous ruminants that differ from those in other feeding categories, suggesting that frugivores should be considered as a distinct dietary group in ecomorphological analyses (Gagnon and Chew, 2000; Heywood, 2010; DeSantis, 2016). Identifying frugivory in the fossil record would enable refined paleoecological reconstructions, and it should also provide information about paleoclimate and paleoenvironment. The latter would be based on the relationship between frugivore occurrence and environmental variables in modern ungulates, a topic that has not been thoroughly investigated.

The dental morphology of fossil mammals is frequently used as an indicator of their feeding habits, based on similarity to that of modern mammals (Ungar, 2010). Common paleodietary proxies involve morphological and use-wear variables of teeth, including the hypsodonty index, dental mesowear, and dental microwear (e.g., Fortelius and Solounias, 2000; Damuth and Janis, 2011; Mihlbachler et al., 2016). Stable-isotope analysis and geometric morphometrics have furthered our understanding of the dietary adaptations of mammals. For example, the global expansion of C4 grasslands in the late Neogene was recorded in the teeth of a wide range of herbivorous mammals that incorporated the changes in vegetation into their diet (Wang et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997). Analyses of changes in mammalian dental morphology have revealed a shift toward plant-dominated diets during the Cretaceous angiosperm radiation (Grossnickle and Polly, 2013) and extinction selectivity against large-bodied dietary specialists through the K-Pg boundary (Wilson, 2013). In my research, I will use a combination of these methods to investigate the dietary ecology of extant artiodactyls.

1.2 Biogeography

The highest species richness of artiodactyls today occurs in East Africa. Species richness is generally higher in sub-Saharan Africa, the Indian subcontinent, and the Tibetan Plateau than other regions of the world (Fig. 1.2). Such a species-richness pattern differs considerably from those in the geological past as documented by the Cenozoic fossil record. Understanding the distribution of taxonomic richness along geographic, climatic, and topographic gradients through space and time requires investigating the ecological diversity and ecological structure of extant faunas.

Ecological diversity is an important component of biodiversity and provides a means of understanding how environmental factors shape and regulate taxonomic composition and species richness (Petchey and Gaston, 2006). Frequently investigated ecological traits in mammalian ecology include body size, locomotor adaptations, and feeding habits. These traits have been measured and analyzed independent of taxonomy in some studies, and different habitats are found to support different compositions and frequencies of traits (i.e., ecological structure; Andrews and Hixson, 2014). Understanding the variation in the ecological diversity of artiodactyls along environmental gradients should offer insights into the factors that regulate species richness.

In Chapter 2, I analyze trends in the frequency of two ecological traits of extant artiodactyls, dietary habit and body size, in relation to environmental gradients. Information about diet and body mass is well-documented for extant artiodactyls, allowing us to examine the relationship among species richness, ecological diversity, and environmental variables (climate and topography) in modern ecosystems. I also discuss implications of the findings for paleoenvironmental reconstruction.

1.3 Ecomorphology

Morphology has been used to assess many aspects of mammalian ecology, including dietary behavior, locomotor function, body size, and habitat preference. The approach of correlating osteological form and ecological function, known as ecomorphology, has been the basis for numerous paleoecological reconstructions (Polly et al., 2011). For example, comparative anatomical studies have shown that grazing and browsing ungulates can be distinguished by craniomandibular features, and these differences are used to evaluate the feeding ecology of extinct ungulates (e.g., Janis and Ehrhardt, 1998; Mendoza et al., 2002).

Studies using the craniodental features of ruminant artiodactyls have room for improvement in analytical methodology. Traditional morphological measurements include the length, width, and depth of features, and bear a number of limitations, including difficulties in separating shape from size, comparison of non-homologous features, and more importantly, the lack of information about the geometric structure of features. Geometric-morphometric methods provide solutions to these problems by placing sets of homologous anatomical loci—landmarks—on Cartesian geometric coordinates, enabling researchers to quantitatively determine variation in shape (Zelditch et al., 2012). This analytical method has been used to further our understanding of the dietary adaptations of early mammals during time intervals of substantial environmental changes (e.g., Grossnickle and Polly, 2013; Wilson, 2013).

In Chapter 3, I investigate the relationship between jaw morphology and dietary category in bovids by quantifying mandibular shape with landmark-based geometric morphometrics. The Bovidae is the most taxonomically, ecologically, and morphologically diverse group of artiodactyls today and offers useful analogues for extinct ungulates. Bovids have been widely studied in ecomorphological research using linear measurements, with important applications to paleoecological reconstructions of Plio-Pleistocene hominid sites in East Africa (Kovarovic and Andrew, 2007). Identifying craniomandibular morphological characteristics that are quantitatively correlated with the diets of the Bovidae will increase the utility of bovid ecomorphology for reconstructing dietary habits and interpreting paleoenvironments in the fossil record.

1.4 Stable isotope ecology

Stable isotope proxies have been used widely to study the dietary ecology, water-use strategy, habitat (and habitat changes), migration history, and life history of living and fossil animals (e.g., West, 2006). In mammals, the stable carbon-isotope composition of mammalian tooth enamel reliably records the carbon isotopic composition of ingested plants with a systematic enrichment in C-13. Teeth are also the hardest mineralized body tissue in mammals and are an abundant material in the mammalian fossil record. Carbon-isotope data derived from fossil teeth have been fundamental to our understanding of important evolutionary and environmental changes in the Cenozoic, including the global expansion of C_4 grasslands in the Neogene (e.g., Cerling et al., 1997).

The stable-isotope composition of mammalian tooth enamel records a combination of environmental parameters, ecological traits, and biological processes. Further increasing the utility of this tool as paleoecological and paleoenvironmental proxies requires thorough considerations of the interplay of these factors as well as the variability of isotopic composition that may be present in certain taxa or environmental settings. In Chapter 4, I compile published data from the literature, supplemented by new data from specimens at the University of Michigan Museum of Zoology, to compare the carbon-isotope values of artiodactyl tooth enamel in relation to their ecology (diet) and environment (biome).

1.5 Synthesis

The three research chapters of this dissertation utilize different types of data and analytical approaches but are united by two themes: a focus on the detailed classification of dietary ecology in extant artiodactyls and an overarching goal of applying what can be found in extant species to reconstructing the ecology of extinct species. I use quantitatively defined criteria to classify the feeding habits of extant artiodactyls, based on a large compilation of dietary data, which allows for comparison of a wider range of species than typically considered by previous studies. Chapter 2 examines the biogeography of different feeding groups, shedding light on the paleoclimatic and paleoenvironmental conditions that can potentially be inferred from each herbivore feeding category. Chapters 3 and 4 investigate the relationship between feeding category and paleodietary proxies, which test the possibility of identifying detailed dietary habits in the fossil record using these proxies. By comparing and combining findings from the three chapters, I draw conclusions on how the three research projects can jointly be applied to improved reconstruction of ungulate diets and habitats in the fossil record.

1.6 References

Andrews P, Hixson S, 2014. Taxon-free methods of paleoecology. *Ann Zool Fenn* **51**:269–284.

Badgley C, Barry JC, Morgan ME, Nelson SV, Behrensmeyer AK, Cerling TE, Pilbeam D, 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proc Nat Acad Sci USA* **105**:12145–12149.

Bodmer RE, 1990. Ungulate frugivores and the browser grazer continuum. *Oikos* **57**:319–325.

Bouchenak-Khelladi Y, Verboom GA, Hodkinson TR, Salamin N, Francois O, Chonghaile GN, Savolainen V, 2009. The origins and diversification of C4 grasses and savanna-adapted ungulates. *Glob Chang Biol* **15**:2397– 2417.

Burgin CJ, Colella JP, Kahn PL, Upham NS, 2018. How many species of mammals are there? *J Mammal* **99**:1–14.

Cerling TE, Harris JM, 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* **120**:347–363.

Cerling T, Harris J, MacFadden B, et al. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**:153–158.

Cerling TE, Harris JM, Passey BH, 2003. Diets of East African Bovidae based on stable isotope analysis. *J Mammal* **84**:456–470.

Clauss M, Lechner-Doll M, Streich WJ, 2003. Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. *Oikos* **102**:253–262.

Damuth J, Janis CM, 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol Rev* **86**:733–758.

DeMiguel D, Azanza B, Morales J, 2011. Paleoenvironments and paleoclimate of the Middle Miocene of central Spain: A reconstruction from dental wear of ruminants. *Palaeogeogr Palaeoclim Palaeoecol* **302**:452–463.

DeSantis LRG, 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surf Topogr: Metrol Prop* **4**:023002.

Fraser D, Theodor JM, 2013. Ungulate diets reveal patterns of grassland evolution in North America. *Palaeogeogr Palaeoclim Palaeoecol* **369**:409–421.

Forrest F, Plummer T, Raaum R, 2018. Ecomorphological analysis of bovid mandibles from Laetoli Tanzania using 3D geometric morphometrics: Implications for hominin paleoenvironmental reconstruction. *J Hum Evol* **114**:20–34.

Fortelius M, Solounias N, 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: A new method for reconstructing paleodiets. *Am Mus Novit* **3301**:1–36.

Gagnon M, Chew AE, 2000. Dietary preferences in extant African Bovidae. *J Mammal* **81**:490–511.

Gingerich PD, 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. *Trends Ecol Evol* **21**: 246–253.

Gordon IJ, Illius AW, 1988. Incisor arcade structure and diet selection in ruminants. *Funct Ecol* **2**:15–22.

Grossnickle DM, Polly DP, 2013. Mammal disparity decreases during the Cretaceous angiosperm radiation. *Proc Roy Soc B* **280**:20132110.

Heywood JJN, 2010. Functional anatomy of bovid upper molar occlusal surfaces with respect to diet. *J Zool* **281**:1–11.

Hofmann RR, Stewart DRM, 1972. Grazer or browser: A classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* **36**:226–240.

Janis CM, Ehrhardt D, 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool J Linn Soc* **92**:267–284.

Janis CM, 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu Rev Ecol Evol Syst* **24**:467–500.

Janis CM, 2008. An evolutionary history of browsing and grazing ungulates. In Gordon IJ, and Prins HHT, eds., *The Ecology of Browsing and Grazing: Ecological Studies* **195**:21–45.

Janis CM, Scott KM, Jacobs LL, 1998. Evolution of Tertiary Mammals of North America: Volume 1, Terrestrial Carnivores, Ungulates, and Ungulate Like Mammals. New York: Cambridge University Press.

Kingston JD, 2011. Stable isotopic analyses of Laetoli fossil herbivores. In: *Paleontology and geology of Laetoli: Human evolution in context*. Springer Netherlands, p 293–328.

Kovarovic K, Andrews P, 2007. Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *J Hum Evol* **52**:663–680.

MacFadden BJ, Cerling TE, 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: A 10 million-year sequence from the Neogene of Florida. *J Vertebr Paleontol* **16**:103-115.

Mendoza M, Janis CM, Palmqvist P, 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: A multivariate approach. *J Zool* **258**:223–246.

Mihlbachler MC, Campbell D, Ayoub M, Chen C, Ghani I, 2016. Comparative dental microwear of ruminant and perissodactyl molars: Implications for paleodietary analysis of rare and extinct ungulate clades. *Paleobiology* **42**:98–116.

Mendoza M, Janis CM, Palmqvist P, 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: A multivariate approach. *J Zool* **258**:223–246.

Petchey OL, Gaston KJ, 2006. Functional diversity: back to basics and looking forward: *Ecol Lett* **9**:741–758.

Polly PD, Eronen JT, Fred M, Dietl GP, Mosbrugger V, Scheidegger C, Frank DC, Damuth J, Stenseth NC, Fortelius M, 2011. History matters: ecometrics and integrative climate change biology. *Proc R Soc Lond B* **278**:1131–1140.

Rivals F, Ziegler R, 2018. High-resolution paleoenvironmental context for human occupations during the Middle Pleistocene in Europe (MIS 11, Germany). *Quat Sci Rev* **188**:136–142.

Rivals F, Gardeisen A, Cantuel J, 2011. Domestic and wild ungulate dietary traits at Kouphovouno (Sparta, Greece): implications for livestock management and paleoenvironment in the Neolithic. *J Archaeol Sci* **38**:528–537.

Spencer LM, 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. *J Mammal* **76**:448–471.

Sponheimer M, Reed KE, Lee-Thorp JA, 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J Hum Evol* **36**:705–718.

Ungar PS, 2010. Mammal Teeth: Origin, Evolution, and Diversity. Baltimore, Johns Hopkins University Press, 315 p.

Wang Y, Cerling TE, MacFadden BJ, 1994. Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeogr Palaeoclim Palaeoecol* **107**:269-279.

West JB, Bowen GJ, Cerling TE, Ehleringer JR, 2006. Stable isotopes as one of nature's ecological recorders. *Trend Ecol Evol* **21**:408–414.

Wilson GP, 2013. Mammals across the K/Pg boundary in northeastern Montana, U.S.A.: dental morphology and body-size patterns reveal extinction selectivity and immigrant-fueled ecospace filling. *Paleobiology* **39**: 429–469.

Zelditch ML, Swiderski DL, Sheets HD, 2012. Geometric Morphometrics for Biologists: A Primer. Academic Press.

Table 1.1 Herbivorous feeding categories of ungulates used in selected literature. Each column includes a classification scheme, generally ordered from browsing (selective feeding) on the top to grazing on the bottom, following by example studies that used the classification scheme.

Fruit and dicot foliage eater	Frugivore	Selective browser	Frugivore	Frugivore	Browser	Dicot feeder (ground level)	Hyperbrowser
Tree and shrub foliage eater	Browser	High level browser	Browser /frugivore	Browser	Mixed feeder preferring browse	Mixed-dicot feeder (ground level)	Browser
Intermediate eater preferring forbs and shrub and tree foliage	Intermediate feeder	Unspecialized browser	Browser	Browser-grazer intermediate	Mixed feeder preferring grass	Mixed-grass feeder (all levels)	Mixed feeder
Fresh grass grazer dependent upon water	Grazer	Mixed feeder (closed habitat)	Browser /grazer	Generalist	Fresh grass feeder	Grass feeder (tall plants)	Grazer
Roughage grazer		Mixed feeder (open habitat)	Grazer	Variable grazer	Grass feeder	Grass feeder (medium level)	Hypergrazer
Roughage grazer / Dry region grazer		Fresh grass grazer		Obligate grazer		Grass feeder (ground level)	
		Dry grass grazer					
Hofmann and Stewart (1972)	Gordon and Illius (1988); Badgley et al. (2008)	Janis and Ehrhardt (1988); Mendoza et al. (2002)	Bodmer (1990)	Gagnon and Chew (2000); Kingston (2011)	Sponheimer (1999); Forest et al. (2018)	Spencer (1995)	Cerling and Harris (1999); Cerling et al. (2003)

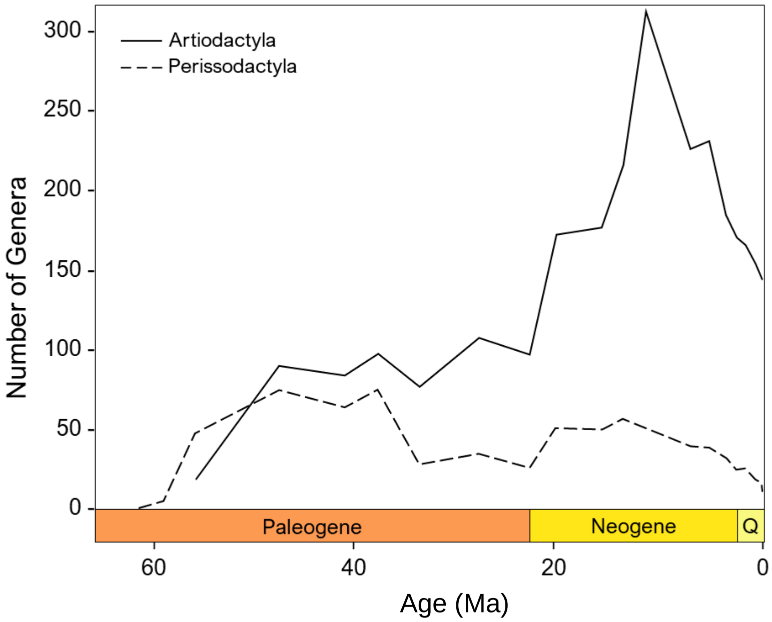


Figure 1.1 Generic richness of artiodactyls and perissodactyls in the Cenozoic (66 Ma to present). Global data from the Paleobiology Database (www.paleobiodb.org).

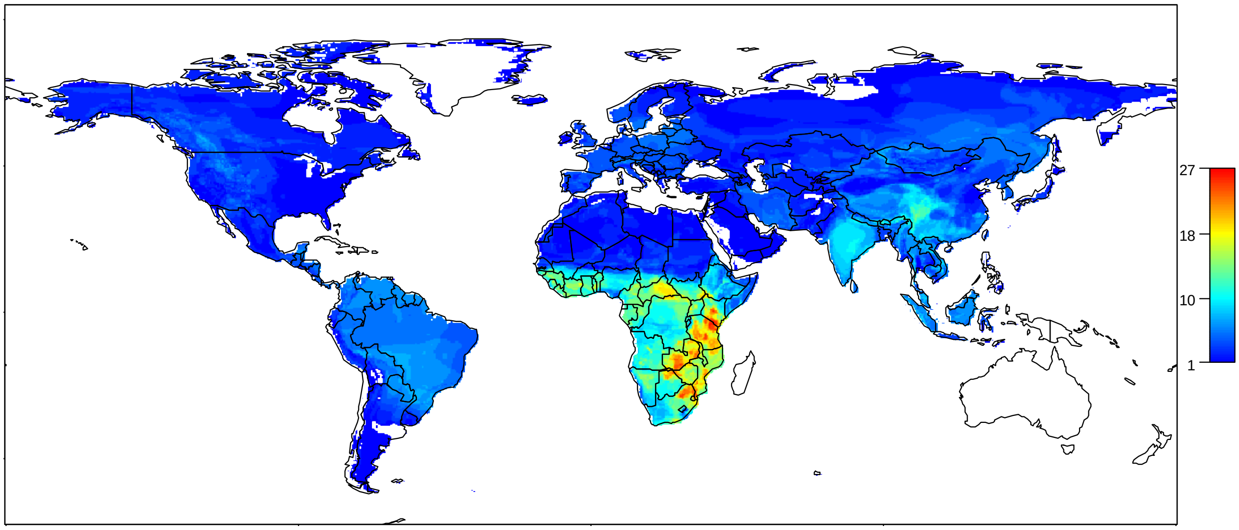


Figure 1.2 Map of species richness of artiodactyls in 100 × 100 km^2 grid cells. Data from the IUCN Red List (https://www.iucnredlist.org/resources/spatial-data-download).

Chapter 2

Ecological Diversity of Extant Artiodactyls in Relation to Climate and Topography

2.1 Introduction

The formation and causes of diversity patterns remain an exciting but challenging topic in ecological research. Much of the study of biodiversity has traditionally focused on understanding the geographic trends of species richness (e.g., Huston, 1994; Rosenzweig, 1995). This was typically done by associating variation in species richness with geographic gradients of the landscape, such as latitude and altitude. While this approach has provided fundamental observations for understanding large-scale patterns of biodiversity, it yields little information about the ecological processes that produce species-richness patterns over space and time. Species-richness gradients have also changed through geologic time, suggesting that the observed species-richness levels are insufficient for explaining the formation of species-richness patterns (e.g., Finarelli and Badgley, 2010; Rose et al., 2011; Marcot et al., 2016).

Disentangling the factors and processes that shape diversity gradients in modern ecosystems requires understanding the taxonomic diversity, phylogenetic diversity, and ecological diversity of the focal organisms (Swenson, 2006). Taxonomic diversity concerns the number and evenness of species represented by individual organisms in a community. Phylogenetic diversity depicts the amount of phylogenetic distance among species in a community. Ecological diversity entails the ecological roles and interactions of species in communities and ecosystems and is usually represented by ecological traits (Petchey and Gaston, 2006). The three types of diversity do not always exhibit the same trend across space and environmental gradients (e.g., Smiley et al., 2020). For example, two regions with similar species richness may differ in the structure and frequency of ecological traits and functions; on the other hand, two regions can accommodate different numbers of ecologically similar species, resulting in different species richness but similar levels of ecological diversity (Faith, 1992; Petchey and Gaston, 2006).

For the reasons above, a growing body of research has focused on evaluating the roles of ecological and evolutionary factors in shaping patterns of species richness (e.g., Graham et al., 2014). In mammalian ecology, frequently investigated traits include body size, feeding habits, and locomotor adaptations. These traits have been measured and analyzed independent of taxonomic richness in some studies (e.g., Blanco et al. 2021), and different habitats are found to support different combinations and frequencies of these traits (Andrews et al., 1979; Andrews and Hixson, 2014; Smiley et al. 2020). Understanding variation in the ecological diversity of mammals along environmental gradients should offer insights into the ecological and evolutionary factors that regulate taxonomic diversity, such as environmental filtering and speciation and extinction events. Environmental filtering refers to the absence of certain species in an ecosystem because they cannot tolerate particular biotic or abiotic factors, and it is thought to be a major mechanism that structures communities (Kraft et al., 2015). Speciation and extinction events are responsible for shaping taxonomic diversity over evolutionary time and are often associated with environmental changes, including tectonic changes in landscape. Previous studies of mammalian biogeography (e.g., Kerr and Packer, 1997; Badgley, 2010) have revealed that topographic complexity has a first-order impact on regional species richness of mammals. Changes in elevation create habitats with more heterogeneous environments, more variable microclimatic zones, and decreased connectivity. Therefore, areas of high topographic relief should have higher species diversity than adjacent areas of low relief through processes of accommodation and allopatric speciation (e.g., Hutchinson, 1959; Cracraft, 1985; Rosenzweig, 1995; Coblentz and Riitters, 2004; Badgley, 2010; Rahbek et al., 2019).

In this study, we investigate geographic patterns of species richness and ecological traits of extant artiodactyls and environmental variables. The order Artiodactyla is the most taxonomically diverse group of large-bodied terrestrial mammals today. Most artiodactyls are herbivores, and their presence and abundance in ecosystems should reflect the distribution of the vegetation they feed on. Because physical geography and climate determine the types of vegetation and the availability of different foods, the feeding adaptations of artiodactyls should be closely associated with physiographic and climatic variables (Eisenberg, 1981). Body size is closely tied to diet, home-range size, digestive physiology, as well as life history of artiodactyls (e.g., Jarman, 1974; Demment and van Soest, 1985).

We analyze the ecological diversity represented in the diet and body mass of artiodactyl species in relation to climatic and physiographic gradients. Specifically, we address the following questions: (1) Do areas with high species richness of artiodactyls support high ecological diversity? (2) Do species with different dietary habits differ in the climatic and physiographic niche space that they occupy? (3) Which environmental variables best predict the geographic distribution of species richness and ecological diversity? To address these questions, we use a global dataset of artiodactyl occurrences, ecological traits, and environmental conditions of their habitats to evaluate species richness and ecological diversity in relation to climate and topography.

2.2 Data and methods

We combined species richness and ecological data for artiodactyls with environmental data to analyze the relationship between taxonomic richness, ecological diversity, and the climate and physiography of their geographic ranges. We used locality-based data of species occurrences from a global dataset of mammalian faunas. Each species was assigned to one of seven feeding categories and to one of six body size classes (Fig. 2.1). Climatic data were directly measured from weather stations close to the localities, allowing us to avoid noise introduced by data interpolation, and capture annual and seasonal temperature and precipitation conditions. Topographic variables document the elevation and topographic relief of the localities (Fig. 2.2). The climatic and topographic data represent properties of the physical environment that determine vegetation types and affect the geographic ranges of artiodactyls, which are predominantly herbivorous.

2.2.1 Faunal data

We used three types of faunal data: species occurrence, body mass, and diet. Unpublished species-occurrence and body-mass data were obtained from John Damuth (NCES working group). Occurrence data include species lists of co-occurring mammals from 342 localities around the world. Artiodactyls occur in 328 of these faunas, distributed in Africa, Eurasia, North America, and South America. Occurrences of introduced species, domesticated species, and insular species were excluded. The data for analysis include 1984 occurrences of 161 species of artiodactyls, with representatives from all ten artiodactyl families, covering 62% of extant artiodactyl species (excluding Cetacea) (Burgin et al., 2018).

The adult body mass of these species ranges over three orders of magnitude, from 2.0 kg (*Neotragus pygmaeus*) to 1405.5 kg (*Hippopotamus amphibius*) (Fig. 2.1). Log_{10}-transformed body masses are normally distributed (Shapiro-Wilk W = 0.99, $p = 0.43$). We divided species into six size classes using statistical and physiological criteria (Table 2.1a). Size class 1 ranges from 2.0 kg to 9.9 kg; all species in this size class belong to the suborder Ruminantia, although some small-bodied species (specifically the tragulids) have a poorly developed omasum (Langer, 1974; Richardson et al. 1988). Size class 2 ranges from 10.0 kg to 20.9 kg (1st quartile). Size class 3 ranges from 21.0 kg to 53.9 kg (median) and includes some non-ruminants, specifically suiforms and camelids. Size class 4 ranges from 54.0 kg to 129.0 kg (3rd quartile). Size class 5 ranges from 130.0 kg to 599.9 kg and includes members of the Giraffidae and Hippopotamidae. Size class 6 ranges from 600.0 kg to 1405.5 kg; in this size range, retention times of food in the gut are sufficient to achieve relatively complete digestion of forage in the absence of elaborated stomach chambers (Demment and van Soest, 1985).

We compiled detailed dietary data for the 161 species included in this study (Appendix A). Most information came from primary sources with fecal or stomach-content analyses. Some review articles, such as those in the *Mammalian Species* series, and some stable-isotope studies of feces were also utilized. For each species that is predominantly herbivorous, we compiled the spatiotemporally averaged percentage of fruits, dicots, and monocots in its diet and assigned it to one of six feeding categories based on the classification of Gagnon and Chew (2000): frugivore, browser, browser-grazer intermediate, generalist, variable grazer, and obligate grazer. This classification scheme was originally developed for African bovids based on percent consumption of fruits, dicots, and monocots in the diet. We adopted this scheme because the quantitative nature of its classification criterion made it applicable to a large range of artiodactyl species.

When expanding this classification beyond African bovids, we also noted the combined proportions of lichen, mosses, fungi, and ferns, since these materials are consumed by a number of cervids, bovids, and moschids that inhabit tundra, temperate grassland, or boreal and temperate forests. For example, these food materials comprise over 50% of the diet of the Siberian musk deer (*Moschus mochiferus*) and over 30% of the diet of the caribou (*Rangifer tarand*us) (Appendix A). In previous studies of ungulate dietary ecology and ecomorphology, these species were considered as either a “browser” or a “mixed feeder” (e.g., Janis and Ehrhardt, 1988; Mendoza et al., 2002). For this study, we assigned both species to the browser category. Other artiodactyls consume little to no lichen, mosses, fungi, and ferns and can be directly assigned to a feeding category based on Gagnon and Chew (2000). Aside from the six herbivorous categories, species that consume both plant and animal materials were classified as omnivores, making a total of seven feeding categories (Table 2.1b).

For each locality, we recorded the following variables: (1) the total number of artiodactyl species, (2) the number of species in each ecological (diet or body size) category, and (3) the number of ecological categories occupied by artiodactyls. We computed the Shannon diversity index (H) of diet and of body size for each locality using the function “diversity” in the R package vegan (Oksanen et al., 2013). This index simultaneously accounts for the richness and evenness of distribution of species among ecological categories. We mapped these variables to visualize the geographic patterns of species richness and ecological diversity, and we generated bivariate plots of these variables against species richness to evaluate the relationship between ecological diversity and species richness (Figs. 2.3–2.8).

2.2.2 Environmental data

For each locality, we collected monthly climatic data from a nearby weather station using the following online databases: the Global Historical Climatology Network (Menne et al., 2018), the Food and Agriculture Organization of the United Nations (New et al., 2002), and the Climate Change Knowledge Portal (2020) of the World Bank Group. The data included four temperature variables (mean annual temperature, minimum monthly temperature, maximum monthly temperature, and annual range of monthly temperature) and three precipitation variables (mean annual precipitation, minimum monthly precipitation, and maximum monthly precipitation). Two other variables included in the analyses were derived from precipitation data: the total length of the dry season and the length of the longest continuous dry season. A “dry” month is defined as a month with total precipitation under 10 mm. These nine climatic variables capture the seasonal variation and annual average of temperature and precipitation experienced by species (Table 2.2).

We obtained continental topographic data from the GTOPO30 digital elevation model (US Geological Survey EROS Data Center, 1996). The model resolution is 30-arc seconds, which is roughly 1 km on Earth’s surface. Localities in our dataset represent areas ranging from 6 km^2 to 247000 km^2, with a median area of 2800 km^2. We computed the mean elevation and relief for each raster cell within a 50 km × 50 km rectangle (2500 km^2), then extracted the values for the coordinates of the 328 localities (Fig. 2.2). Because relief is highly sensitive to size of the input area, we also computed the standard deviation of elevation of the same grid cells. The two measures of landscape roughness yielded a high correlation ($r = 0.98$, $p < 0.001$). Therefore, we used relief for subsequent analyses, as the range of elevations is what species experience. Mean elevation and relief together represent the altitude and topographic complexity of the localities. Although they are moderately correlated ($r = 0.64$, $p < 0.001$), areas present in our dataset with high elevation but low relief (i.e., plateaus) and areas with steep mountain ranges adjacent to lowlands (moderate elevation and high relief) prevent the correlation from being higher (Fig. 2.2).

The 328 localities represent 13 of the 14 major terrestrial ecoregions of the Global 200 list (Olson and Dinerstein, 1998, 2002). These ecoregions are: 1) tropical and subtropical moist broadleaf forests, 2) tropical and subtropical dry broadleaf forests, 3) tropical and subtropical coniferous forests, 4) tropical and subtropical grasslands, savannas, and shrublands, 5) temperate broadleaf and mixed forests, 6) temperature coniferous forests, 7) boreal forests/taiga, 8) temperate grasslands, savannas, and shrublands, 9) flooded grasslands and savannas, 10) montane grasslands and shrublands, 11) tundra, 12) Mediterranean forests, woodlands, and scrub or sclerophyll forests, and 13) deserts and xeric shrublands. Table 2.3 reports the number of localities sampled from each ecoregion and the number of artiodactyl species occurring in each ecoregion as represented in these localities.

2.2.3 Climate envelopes for ecological traits

To evaluate the covariation among the nine climatic variables and to reduce the dimensionality of the data, we conducted a principal component analysis (PCA) using the software PAST 4.05 (Hammer et al., 2001) (Fig. 2.9). We used the built-in Broken Stick model to determine the number of significant principal components to be retained (Jackson, 1993). In the resulting ordination, we illustrated the distribution of each feeding category and each size class within the climate ordination space (Fig. 2.10). Localities with and without species in a particular ecological category are differentiated by colors, and the size of the data points is scaled to the richness of species in localities. We drew convex hulls around localities in which each ecological category occurred. These plots allowed us to compare on a two-dimensional (PC1-PC2) plane the range of climate envelopes occupied by species with different ecological traits.

2.2.4 Relationship between environmental variables and faunal variables

To visualize species-richness patterns along environmental gradients, we generated bivariate plots of locality-level species richness in each ecological category against four variables: PC1 score, PC2 score, mean elevation, and relief. Because species richness of feeding categories has a unimodal distribution along environmental gradients (Figs. 2.11–2.14), we used a canonical correspondence analysis (CCA) to detect relationships between environmental variables and diet. CCA is an effective ordination technique for analyzing unimodal species-environment relations (Ter Braak, 1987) (Fig. 2.15). The analysis was done with the function "cca" in the vegan R package (Oksanen et al., 2013).

We used multiple linear regression models to predict total species richness and richness of species in different ecological categories from environmental variables. From the PCA results (see sections 3.3), we chose four climatic variables to include in multiple linear regression analyses: minimum monthly temperature, maximum monthly temperature, total dry season length, and maximum monthly precipitation. Because elevation and relief are moderately positively correlated ($r = 0.64$; Fig. 2.2), we included elevation as the physiographic predictor variable, given results of the CCA (see section 3.4). These five variables were measured on different scales and units and, therefore, were each centered and standardized using the "scale" function in R before regression. For regression models that yielded an R-squared value of greater than 0.2, we re-ran the multiple regression analysis with stepwise removal of non-significant predictors ($p<0.05$) until all remaining predictors were significant. For these models, we additionally evaluated the spatial autocorrelation of environmental variables and faunal variables in the localities. We applied a spatial simultaneous autocorrelation (SAR) model to each original regression model, using the “errorsarlm” function in the spdep R package (Bivand and Wong, 2018). With the built-in “AIC” function in R, we used AIC model selection to identify the most appropriate distance for identifying cell neighborhoods and to select the most appropriate spatial weighting scheme. Combinations of cell distance and spatial weighting scheme that yielded the minimum AIC scores were selected.

2.2.5 Ecological structure and diversity of ecoregions

We counted the number of species in each combination of feeding category and size class to generate a matrix of ecological structure of extant artiodactyls. Then we repeated this for each of the eight most species-rich ecoregions, allowing for a comparison of ecological structure among these environmental settings (Fig. 2.16). To examine the range and frequency of occupied ecological categories in different ecoregions, we generated histograms of the number of ecological categories occupied by artiodactyls in each ecoregion (Fig. 2.17). This was done for all ecoregions except tropical and subtropical coniferous forests (2 localities) and flooded grasslands and savanna (3 localities) due to the number of localities in these ecoregions.

2.3 Result

The results are presented in six parts: (1) maps of the global distribution of total artiodactyl species richness, species richness in each ecological category, and diversity index values, (2) bivariate plots showing the relationship between species richness and measures of ecological diversity, (3) the ordination of climatic data, which reduced most of the variance in the original variables to two axes, and climate envelopes of ecological categories in the ordination plane, (4) ordination of dietary groups and environmental variables revealed by canonical correspondence analysis, (5) environmental predictors of diversity patterns, derived from multiple-regression analyses, and results of modified t-tests that account for spatial autocorrelation between environmental and faunal variables, and (6) variation in the ecological structure of artiodactyl faunas among ecoregions.

2.3.1 Geographic patterns of diversity

Artiodactyl species richness of localities ranges from 1 to 28, with a median of 6 species. The highest richness occurs in faunas of East Africa (Fig. 2.3). Sub-Saharan Africa in general has markedly higher richness than the rest of the world, with over 80% of the localities having at least 9 species. Outside Africa, the highest species richness occurs in northern India (11 species), but over 80% of the localities have fewer than 5 species. Species richness of localities is inversely correlated with latitude (r = -0.50, p < 0.001; Fig. 2.4a). The largest number of species in equal-interval latitudinal bands occurs between the equator and 10˚N (N = 69), and the number decreases largely progressively toward the poles (Fig. 2.3). However, it is notable that this latitudinal gradient is largely due to the high richness in African localities, which occur at low latitudes (<35˚ absolute latitude). When African localities are excluded, latitudinal bands with the most species are 20˚–30˚N (N=38) and 30˚–40˚N (N=37) (Fig. 2.3), and there is a flat richness gradient across latitudes (r = 0.04, p = 0.57; Fig. 2.4a).

The seven dietary groups exhibit different geographic patterns of species richness (Fig. 2.5). Frugivores are found at low latitudes (<30˚ absolute latitude) of sub-Saharan Africa, Latin America, South Asia, and Southeast Asia, with the highest richness (7–9 species) in western equatorial Africa (Fig. 2.5a). Browsers are the most species-rich dietary group (45 species, Table 2.1b) and have the widest geographic distribution among all dietary groups (Fig. 2.5b). They occur across Africa except in the Sahara Desert, Eurasia, North America, South America except in the Brazilian Highlands and Patagonian Plateau, and other sporadic localities. The highest richness of browsers occurs in East Africa (7 species). Other localities in East Africa, South Africa, and southwestern China also have high browser richness (5–6 species). Browser-grazer intermediates generally occur in low species richness (1–3 species), with the highest richness occurring in East Africa and southern Europe, as well as northern India (Fig. 2.5c). They are absent in western equatorial Africa, Siberia, Southeast Asia, the Amazon lowlands, and most of North America. Generalists are the least species-rich dietary group in our dataset (8 species; Table 2.1b) and coexist in few species (1–3). They are found over most of Africa (except the Congo Basin) and in restricted areas of South Asia, Southeast Asia, and South America (Fig. 2.5d). Variable grazers have a broad geographic range, occurring across Africa and most of Eurasia and North America, as well as in the central Andes (Fig. 2.5e). The highest richness of variable grazers (5 species) occurs in East Africa, South Africa, northern India, and Southeast Asia. Obligate grazers only occur in sub-Saharan Africa, with the highest richness (11 species) in East Africa and southern Africa (Fig. 2.5f). Omnivores occur in East Africa, western equatorial Africa, coastal North Africa, and across Eurasia and most of Latin America. Omnivores co-exist in relatively few species (1–3), with the highest richness of omnivores in eastern Congo Basin (Fig. 2.5g).

The six size classes also exhibit different geographic patterns of species richness (Fig. 2.6). Species in size class 1 (2.0–9.9 kg) occur in sub-Saharan Africa, southern and eastern regions of Asia, and subtropical South America (Fig. 2.6a). They co-exist in few species (1–3), with the highest richness in western equatorial Africa. Other size classes have wider geographic distributions. Size class 2 (10.0–20.9 kg) is present in sub-Saharan Africa, some localities in Asia, and tropical to temperate regions of South America (Fig. 2.6b); its highest richness (5 species) occurs in equatorial Africa. Size class 3 (21.0–53.9 kg) occurs throughout Africa, Eurasia, and much of South America and North America, with the highest richness (5 species) in East Africa (Fig. 2.5c). Size class 4 (54.0–129.9 kg) has the widest geographic distribution of all size classes, being absent only from localities in eastern Brazil and Patagonia in South America and sporadic areas of Eurasia (Fig. 2.6d). The highest richness of size class 4 (8 species) occurs in East Africa. Size class 5 (130.0–599.9 kg) is also widely distributed across the continents; species of this size are absent in the Sahara Desert, Central America, and the Amazon lowlands. The highest richness,10 species, occurs in southern Africa (Fig. 2.6e). Size class 6 (600.0–1405.5 kg) occurs in most areas of Africa and Eurasia and in the Intermountain West of North America (Fig. 2.6f). These large artiodactyls coexist in relatively few species (1–3 species), although one locality in Southeast Asia has four species.

The geographic variation in the richness and evenness of species among ecological categories is reflected in the Shannon diversity index. The highest Shannon index values of diet occur in the East African Rift System; moderately high values occur in other parts of Africa, Europe, and tropical and subtropical Asia (Fig. 2.7a). Interestingly, although many localities in North America have artiodactyl species richness that is comparable to that of Europe and central Asia (Fig. 2.3), the dietary diversity is lower in North America (Fig. 2.7a), reflecting a less even distribution of dietary groups in North America dominated by browsers and variable grazers (Fig. 2.5). Although localities in tropical and subtropical Asia have fewer artiodactyl species than those in sub-Saharan Africa, their Shannon index values of diet are comparable (Fig. 2.7a), reflecting an even distribution of species among feeding categories. As a result, the Shannon index of diet shows a moderate latitudinal gradient with and without African sites (Fig. 2.4b), unlike the patterns of species richness (Fig. 2.4a). The Shannon index values of size are generally high in sub-Saharan Africa and tropical and subtropical Asia, with the highest values occurring in East Africa, western equatorial Africa, southwestern China, and northern India (Fig. 2.7b). Moderate size diversity is found in Europe and the Intermountain West of North America. Shannon index values of size exhibit a weak latitudinal gradient, with high diversity occurring through low- to mid-latitudes with and without African localities, but the Shannon values do decrease poleward beyond 50˚ absolute latitude (Fig. 2.4c). Combining feeding and body-size categories, the geographic pattern of the number of ecological categories occupied by artiodactyls (Fig. 2.7c) is similar to that of species richness (Fig. 2.3).

2.3.2 Species richness and ecological diversity

The artiodactyl species richness of localities is positively correlated with the number of ecological categories occupied ($r = 0.87$, $p < 0.001$), the Shannon diversity index of diet ($r = 0.68$, $p < 0.001$), and the Shannon diversity index of size ($r = 0.72$, $p < 0.001$) (Fig. 2.8). The number of ecological categories occupied by co-occurring artiodactyls ranges from two (all species in the locality are in the same feeding category and same size class) to 13 (species in the locality represent all seven feeding categories and all six size classes). Among localities with 10 or fewer species of artiodactyls, the number of ecological categories generally increases linearly with increasing species richness; as species richness approaches the sum of feeding categories and size classes, the number of ecological categories occupied by artiodactyls reaches a plateau (Fig. 2.8a). This asymptotic relationship also characterizes the relationship between species richness and Shannon index values of diet and of size (Fig. 2.8b-c). However, several localities notably deviate from the general trend. Consistent with observations from maps of ecological diversity (Fig. 2.7), localities in tropical and subtropical Asia, namely in Sri Lanka and Vietnam, have some of the highest dietary diversity of the world, even though their species richness is lower than that of most African localities (Fig. 2.8b). Southwestern China (Sichuan) and the Tibetan Plateau have notably high size diversity, especially considering their moderate level of species richness (Fig. 2.8c). Jasper National Park of the Canadian Rockies, dominated by browsers and variable grazers of size classes 4 and 5, has considerably lower size diversity and fewer occupied ecological categories than other localities with comparable species richness. Guadalupe Mountains National Park of the southern Great Plains also has relatively few occupied ecological categories (Fig. 2.8a). In general, North American localities have lower ecological diversity represented in the diet and body size of artiodactyls compared with Eurasian localities with similar species richness. Most African localities are characterized by both high species richness and high ecological diversity (Fig. 2.8). The one African locality with relatively low ecological diversity, Okavango Delta, has notably low relief relative to its elevation (Fig. 2.2b).

2.4 Principal component analysis and climate envelopes of ecological categories

The principal component analysis of nine climatic variables resulted in two significant principal components (PCs), which explain 45.5% and 34.0% of the variance, respectively (Table 2.4; Fig. 2.9). PC1 largely corresponds to variation in temperature, with localities dominated by cold climates on the left and localities in warm climates on the right. PC2 corresponds to variation in precipitation, with high annual precipitation and no dry season on the negative end and low precipitation and long dry seasons on the positive end of the vertical axis. Minimum monthly temperature is highly correlated with mean annual temperature ($r = 0.97$, $p < 0.001$) and annual temperature range ($r = -0.94$, $p < 0.001$). Total dry season length is highly correlated with continuous dry season length ($r = 0.99$, $p < 0.001$) and moderately correlated with minimum monthly precipitation ($r = -0.52$, $p < 0.001$).

This ordination pattern corresponds to geographic variation among regions. African localities are characterized by moderate to high temperature and low to moderate precipitation conditions; localities with the longest dry seasons occur in Africa. Eurasian localities have a wide range of temperature and precipitation conditions, reflecting the large area and latitudinal span of the continent; localities in Malaysia are among the warmest localities and have the highest annual precipitation among all localities. North American localities have moderate precipitation and a wide range of temperature conditions, although most of them have relatively low mean annual temperature with high seasonality. South America has the fewest localities in our dataset; these localities have moderate to high levels of annual temperature and precipitation.

Comparing the convex hulls enclosing localities with different ecological traits, it is evident that obligate grazers, frugivores, generalists, and species in size class 1 occupy relatively small ranges of climate space, all restricted to localities with warm winters and low seasonality of temperature (Fig. 2.10). These groups, however, occupy different precipitation conditions. Obligate grazers occur in localities with intermediate precipitation conditions; they are absent in areas with a long dry season or with high precipitation throughout the year, reflecting their dependence on a year-long supply of grasses. Frugivores and size class 1 occur in intermediate to high precipitation conditions but are absent from areas with a long dry season. Generalists are present over the whole range of precipitation conditions. Other ecological categories occur in nearly all climatic conditions. However, higher species richness generally occurs in localities with higher temperature (high PC1 scores) and moderate precipitation (intermediate PC2 scores).

2.4.1 Correspondence analysis

The canonical correspondence analysis (CCA) depicts climatic and physiographic variables, faunal variables, and localities in the same ordination space (Fig. 2.15). The first two axes explain 57.5% and 28.5% of the constrained inertia, respectively (Table 2.5). Correlations among the nine climatic variables are similar to results of the principal component analysis (Fig. 2.9), but CCA reveals variation in the relative importance of the environmental variables in predicting species richness. Among the climatic variables, maximum monthly temperature is less important than minimum monthly temperature (winter temperature) and range of annual temperature (seasonality of temperature). Among the precipitation variables, mean annual precipitation is more important than other variables. The two physiographic variables are not as useful as the climatic variables in predicting species richness, although elevation is slightly more important than relief.

Frugivore is the most distant faunal variable from the origin of the ordination space, followed by obligate grazers; these feeding categories can be best predicted by the included environmental variables. High frugivore richness is associated with high temperature, high precipitation, low elevation and low relief. High richness of obligate grazers and generalists is associated with high annual temperature, relatively precipitation, and relatively high elevation. Omnivore richness is associated with relatively high precipitation, moderate temperature, and low elevation. Predictability of browser, browser-grazer intermediate, and variable grazer richness is low; these feeding categories are associated with moderate seasonality of temperature and of precipitation, high elevation, and high relief.

2.4.2 Multiple linear regression and spatial autocorrelation

Multiple linear regressions model the relationship between a set of explanatory variables and a single response variable. We chose minimum monthly temperature, maximum monthly temperature, total dry season length, and maximum monthly precipitation as climatic predictors in multiple linear regression. These variables capture the most variation in the climate data

(Tables 2.4, 2.5; Figs. 2.9, 2.15) and represent seasonal climatic conditions that are biologically meaningful. We also included elevation as the physiographic predictor. The response variables are the species richness for individual ecological categories and the Shannon diversity indices of localities.

Minimum monthly temperature is the single most effective predictor of total artiodactyl species richness (Table 2.6a) and Shannon index of diet (Table 2.6p). It is also a significant ($p <$ 0.05) predictor for species richness in all dietary categories except browsers and variable grazers (Table 2.6b–i) and for species richness in all size classes (Table 2.6j–o). Additionally, elevation is a significant predictor for frugivores, browsers, variable grazers, size classes 3 and 4, and the Shannon index of size. Maximum precipitation is a significant predictor for frugivores, browser-grazer intermediates, omnivores, and size class 1. Dry season length and maximum temperature are significant predictors for relatively few categories. Ecological categories that can be best predicted by combinations of environmental variables are frugivores ($r^2 = 0.25$), omnivores ($r^2 = 0.25$), size class 3 ($r^2 = 0.25$), and size class 1 ($r^2 = 0.21$).

Accounting for the spatial autocorrelation among the variables, frugivores, size class 1, and size class 3 have the highest numbers of significant environmental predictors, including minimum monthly temperature, maximum monthly temperature, and maximum monthly precipitation (Table 2.7). Maximum monthly precipitation explains the highest number of ecological categories as well as the Shannon values of both diet and size. Elevation remains a significant predictor of variable grazer richness.

Models for four ecological groups yielded an R-squared value of 0.2 or greater: frugivores, omnivores, size class 1, and size class 3. For all four groups, minimum monthly temperature remains a significant predictor ($p<0.05$) in the final regression model (Table 2.7).

Dry season length and maximum monthly precipitation are also significant predictors for frugivores and omnivores, maximum monthly temperature is a significant predictor for size class 1, and elevation is a significant predictor for size class 3. SAR models led to an improvement in AIC score compared to the multiple linear regression models (Table 2.7). Fitting the SAR model removed the significant correlations ($p < 0.05$) between maximum monthly temperature with the richness of frugivores and size class 1 and between elevation and the richness of size class 3. Minimum monthly temperature remains a significant predictor for all four groups, and dry season length remains a significant predictor for frugivores and omnivores.

2.4.3 Ecological structure of ecoregions

The ecological structure of extant artiodactyls among localities is characterized by the association of small body size with browsing and fruit-eating species and the association of large body size with grazing species (Fig. 2.16a, Table 2.8a). This relationship between diet and body mass is largely consistent across ecoregions with at least 30 species (Fig. 2.16b–d; Table 2.5b–d). However, additional variation in ecological structure exists among ecoregions. Tropical forests support higher proportions of small, browsing species and lower proportions of large, grazing species than other ecoregions (Fig. 2.16b). Grassland, savanna, and shrubland biomes support relatively high proportions of large grazers, especially obligate grazers, but tropical and subtropical grasslands also support high proportions of frugivores while montane grasslands do not (Fig. 2.16c–d). Desert and xeric shrublands, despite having similar number of artiodactyl species as montane grasslands and shrublands, have a notably different ecological structure, with no frugivores, fewer small-bodied species (size classes 1 and 2), and more medium-size species (size class 4) (Fig. 2.16e). The ecological structure of temperate broadleaf and mixed forests is characterized by the absence of frugivores and obligate grazers and the dominance of small to large browsers and medium-sized intermediate feeders (Fig. 2.16f).

There is no consistent distribution of occupied ecological categories among ecoregions; some exhibit a unimodal distribution, some bimodal distribution, and some unitary distribution. Two ecoregions have a bimodal distribution of numbers of occupied ecological categories: tropical and subtropical most broadleaf forests and tropical and subtropical grasslands, savannas, and shrublands (Fig. 2.17a–b). The higher peaks in both ecoregions are primarily or entirely associated with African localities, while the lower peaks are associated with South American localities. These two ecoregions support comparable species richness to two other ecoregions: temperate broadleaf and mixed forests and desert and xeric shrublands. However, the latter two ecoregions primarily exhibit unimodal distributions in the frequency of occupied ecological categories, with lower peak and mean values (Fig. 2.17d–e), suggesting lower ecological diversity in these regions than tropical and subtropical ones. Localities in montane grasslands and shrublands, primarily in Africa, support a wide range of ecological diversity despite relatively a relatively low number of species occurring in this ecoregion (Fig. 2.17h). In general, within a given ecoregion, African localities support higher ecological diversity than other localities (Fig. 2.17a, b, d), while Eurasian localities support higher ecological diversity than North American and South American localities (Fig. 2.17a, c, d, e, f, j, k). One exception to this is the Mediterranean forests, woodlands, and scrub ecoregion, in which Eurasian localities (in the Mediterranean) have higher ecological diversity than African localities (in coastal South Africa) (Fig. 2.17i).

2.5 Discussion

Multiple species-richness patterns exist in subsets of artiodactyls, combining into the observed total richness pattern around the world. Species with different ecological traits have markedly different geographic patterns of presence, absence, and richness hotspots, highlighting the importance of understanding the role that dietary ecology and body mass play in shaping taxonomic diversity patterns. Below, we revisit the research questions we posed regarding (1) the relationship between species richness and ecological diversity, (2) the variation in climate envelopes of different ecological categories, (3) the relationship between environmental variables and faunal variables, and (4) the variation in ecological structure and ecological diversity among different environmental settings. Then we discuss the implication of our findings on extant artiodactyls for ungulate paleoecology.

2.5.1 Species richness and ecological diversity

The highest richness of extant artiodactyls occurs in localities in the East African Rift System, and the richness of sub-Saharan Africa is generally higher than in the rest of the world (Fig. 2.3). The high species richness in sub-Saharan Africa results from the accommodation of more species in all ecological categories (Figs. 2.5, 2.6). Most categories have their peak species richness in East Africa. Western equatorial Africa, particularly the Congo Basin, hosts high richness of small-bodied (size classes 1–2) species and frugivores (Figs. 2.5a, 2.6a–b). Other regions of the world, such as southern Europe and northern India, host many coexisting species with certain ecological traits, but not for all trait categories.

Geographic patterns of ecological diversity share similarities as well as differences with those of species richness. Higher species richness is generally associated with more ecological categories occupied, higher Shannon diversity of diet, and higher Shannon diversity of size (Fig. 2.8). In faunas with low species richness (fewer than ~10 species, occurring in all continents), ecological diversity increases with increasing species richness in a largely linear fashion. In faunas with relatively high species richness (over ~10 species, occurring mostly in Africa), ecological diversity increases little with increasing richness and eventually approaches saturation level. Consequently, there is an asymptotic relationship between species richness and ecological diversity.

It is also worth noting that some localities, mostly with richness in the range of 5 to 10 species, deviate from the general pattern in Fig. 2.8. For example, high dietary and size diversity occurs in localities of tropical and subtropical Asia, even though fewer species occur there than in African localities, indicating more even distribution of species among ecological categories in this region (Figs. 2.3, 2.7, 2.8). The only feeding category missing from tropical and subtropical Asia is obligate grazer, which occurs only in sub-Saharan Africa (Fig. 2.5f). As a result of the high ecological diversity in tropical and subtropical Asia, the Shannon diversity indices of diet and of size exhibit moderate latitudinal gradients both in Africa and in other continents (Fig. 2.4b–c). This contrasts with the pattern in species richness, which varies little with latitude outside Africa (Fig. 2.4a).

Another discrepancy between species richness and dietary diversity occurs between the Intermountain West of North America and Europe. The United States and Canada have similar ranges of temperature and precipitation and comparable species richness to those of Europe. Ten species occur in the US and Canada, including cervids, bovids, an antilocaprid, and a tayassuid. Eight species occur in Europe, including cervids, bovids, and a suid. The North American artiodactyl fauna is dominated by browsers and variable grazers (with a few occurrences of omnivores in the southern Rockies), while the European fauna additionally supports browser-grazer intermediates and more widespread omnivores (Fig. 2.5). The North American continent is considerably larger than the area of Europe, and most artiodactyl species have large geographic ranges in North America, while several European species are restricted to small areas in montane regions.

2.5.2 Climate envelopes of ecological categories

Species with different ecological traits vary in the total range of their climate envelope and preference of climatic conditions. Frugivores and obligate grazers are the two dietary extremes in our herbivore classification scheme; their dietary specializations restrict them to limited geographic ranges and climatic conditions (Figs. 2.5, 2.10). Both dietary groups have high species richness in tropical Africa; they are absent from temperate and boreal regions and occupy the warm region of climate space. However, they prefer different precipitation conditions (Fig. 2.10). Frugivores tolerate a relatively wide range of precipitation conditions; they occur in higher richness in wetter environments with no dry season. Obligate grazers occupy intermediate precipitation conditions and are absent from areas with a prolonged dry season (deserts) or with year-round high precipitation (rainforests). Generalists occupy a climate envelope that is slightly larger than those of the dietary extremes but notably smaller than those of other dietary groups (Fig. 2.10d). This may reflect two factors: the smaller number of species in this group and their partial dependence on fruits (Table 2.1b). By definition, generalists consume higher proportions of fruits than all other feeding categories except frugivores, which restricts them to warm climates. However, generalists are capable of consuming leafy dicots and monocots when fruits are not seasonally available, allowing them to tolerate a wider range of precipitation as well as temperature conditions than the dietary extremes.

Among the size classes, size class 1 has the most restricted climate envelope, occurring only in warm environments with moderate to high rainfall (Fig. 2.10i). Size class 2 also has a concentrated distribution in climate space, mostly occurring in warm environments with moderate rainfall, although a few sporadic occurrences in very cold and very dry environments considerably expands its climate envelope (Fig. 2.10j). The rest of the size classes are widely distributed over the full range of climate space. Differences in the climate envelopes correspond to different areas and latitudinal spans that species in different ecological categories inhabit (Figs. 2.5, 2.6).

There is a left-skewed unimodal distribution of species richness along PC1 for most ecological categories (Fig. 2.11). This pattern largely reflects the high species richness of African localities, which occur in warm climates (Fig. 2.9). Frugivores, obligate grazers, and generalists, and size class 1 occur almost exclusively in warm climates. Browsers, intermediate feeders, generalist, and variable grazers have a slightly left-skewed unimodal distribution along PC1, with more species in warmer climates. Browser-grazer intermediates have a symmetric unimodal distribution along the temperature gradient (Fig. 2.11c).

The species richness of most ecological categories has a generally symmetric unimodal distribution along PC2, with the highest values associated with intermediate precipitation conditions in Africa (Fig. 2.12). Among African localities, frugivores (Fig. 2.12a) favor wetter climate (lower PC2 scores) than obligate grazers (Fig. 2.12f).

In general, higher species richness is found in localities with lower elevation (Fig. 2.13) and lower relief (Fig. 2.14). This trend is especially strong for frugivores: the highest species richness occurs below 1000 m and they are absent in areas above ~2300 m mean elevation (Fig. 2.13a). Size class 1 has similar upper limits of elevation and relief to those of frugivores (Figs.

2.13h, 2.14h). Obligate grazers prefer low to intermediate elevations with low relief; they are absent in areas with a mean elevation above ~3000 m. Browsers, browser-grazer intermediates, variable grazers, obligate grazers, and omnivores all have peak species richness at around 1000 m above sea level with a local relief of ~500 m.

2.5.3 Environmental predictors of faunal variables

Canonical correspondence analysis and regression models show that temperature of the coldest month is the most useful environmental predictor of species richness on a global scale (Tables 2.6, 2.7; Fig. 2.11). This result corresponds to the observed latitudinal gradient of artiodactyl species richness (Fig. 2.3). Minimum monthly temperature is additionally useful for predicting species richness of most ecological categories. Seasonal extremes of precipitation (maximum monthly precipitation and dry season) are also useful predictors of certain ecological categories.

We did not find strong evidence for a topographic diversity gradient in this group of mammals on a global scale (Table 2.6a). On the continental scale, higher richness is observed in topographically complex areas of Africa, North America, and Asia than in their adjacent lowlands (Table 2.3, Fig. 2.3). A locality in Africa with low relief relative to its elevation (Okavango Delta; Fig. 2.2b) has markedly lower ecological diversity than other localities with comparable or fewer species (Fig. 2.8), suggesting that topographic complexity can be important at the local to regional scale. Elevation is moderately useful for explaining species richness of artiodactyls for certain ecological traits (Tables 2.6, 2.7). The regression models indicate that elevation is a significant positive predictor of the richness of browser, generalist, variable grazer, and omnivores, but a significant negative predictor of frugivore species richness.

Fitted SAR models accounted for spatial autocorrelation and show that minimum monthly temperature is a significant predictor for species richness of both geographically restricted groups (such as frugivores and size class 1) and widespread groups (such as omnivores and size class 3) (Table 2.7). This climatic variable is likely a primary control on the richness of artiodactyls by directly or indirectly influencing the metabolic demands and food resources of artiodactyls (Tables 2.6, 2.7). Dry season length, a measure of the seasonal extreme of precipitation, remains a significant predictor of frugivores and omnivores. Maximum monthly temperature and elevations have little impact on the richness of ecological groups of artiodactyls after accounting for spatial autocorrelation.

2.5.4 Ecological structure and ecological diversity of ecoregions

Different ecoregions vary in the richness of artiodactyls (Table 2.3), in the ecological structure of artiodactyl faunas (Fig. 2.12), and in the ecological diversity (Fig. 2.13) that they support. Tropical forests support high proportions of small, browsing species (Fig. 2.12b). Grasslands support higher proportions of large grazers than forests (Fig. 2.12b–d). Temperate forests are dominated by browsers and browser-grazer intermediates of small and medium body sizes (Fig. 2.12f). Frugivores are absent from deserts and temperate regions (Fig. 2.12e–f). Within a given ecoregion, localities on different continents vary in the range and frequency of occupied ecological categories (Fig. 2.13). In general, tropical and subtropical areas of Africa and Eurasia accommodate a wider and more even distribution of ecological traits and thereby higher ecological diversity than other regions of the world (Figs. 2.4, 2.7). All size classes occur in these areas (Fig. 2.6). Such environments involve high primary productivity, high plant diversity, and complex vegetation structure (e.g., Rosenzweig, 1995; Waide et al., 1999). In contrast, tropical and subtropical South America occupies similar regions of climate space but hosts considerably fewer artiodactyl species (Figs. 2.3) and supports lower ecological diversity (Figs, 2.5–2.8, 2.13). North America and Europe have many localities with similar climatic conditions (Fig. 2.9) and share many of the same ecoregions, but North American localities support lower ecological diversity than European localities (Figs. 2.8, 2.13). These findings suggest that the different evolutionary and biogeographic histories of continents influence the ecological structure and diversity of their extant faunas. The current species composition, richness patterns, and ecological diversity not only reflect the climatic and physiographic conditions of their environment today, but also are influenced by the speciation, extinction, and range-shift events of ancestral species in response to past environmental changes.

2.5.5 Considerations for the ungulate fossil record

Ungulates are an important component of the Cenozoic mammalian fossil record. Reconstructing their ecology is essential for understanding the evolutionary changes and ecological structure of ancient mammalian communities. In addition, their dietary and locomotory adaptations provide information about the vegetation and climatic conditions of their paleoenvironment (e.g., Kappelman, 1991; Janis et al., 2002; Mihlbachler et al., 2011). Our results show that the herbivore dietary extremes, frugivores and obligate grazers, have the most restricted climate envelopes among all ecological categories, reflecting their narrow dietary niche breaths. Identifying frugivory and obligate grazing in the fossil record would be useful for recognizing their associated paleoclimates and paleoenvironments.

Diversity patterns of artiodactyls varied considerably over the Cenozoic. In the geological past, high taxonomic and ecological diversity has occurred in regions that are depauperate in both today. Fossil data from the Great Plains of North America and the Siwalik Group of Asia, for example, show a regional ungulate species richness of over 20 species (e.g., Morgan et al., 1995; Janis, 1998; Janis et al., 2000; Khan et al., 2006; Flynn et al., 2014). The documented loss of diversity over the Neogene contributed to the relatively low species richness in these regions today. In addition, many aspects of the South American mammalian faunas notably differ from those in other continents, reflecting the long history of geographic isolation of this continent and its unique evolutionary history. South American faunas are also affected by large-scale extinction of large-bodied herbivores in the Pleistocene (Barnosky et al., 2016). A deeper evaluation of the formation of modern diversity gradients requires incorporation of paleontological, biogeographic, phylogenetic, and ecological data (e.g., Badgley et al., 2017).

2.6 Conclusion

By analyzing the ecological diversity represented in the diet and body size of 161 extant artiodactyl species and comparing the geographic patterns of diversity in relation to climate and topography, we found that higher species richness is generally associated with greater ecological diversity. High species richness of artiodactyls in low latitudes, particularly in Africa, is achieved by accommodation of more ecological traits as well as more coexisting species with the same traits. A range of ecological diversity, however, can be present in localities with comparable species richness or in the same ecoregions. Tropical and subtropical Asia supports high Shannon diversity values comparable to those of sub-Saharan Africa, despite having considerably fewer species, corresponding to more even distribution of species among ecological categories.

Species with different ecological traits occupy different regions of climate space, and different ecoregions support different richness and diversity levels of artiodactyls. Dietary extremes (frugivores and obligate grazers) and size class 1 (body mass under 10 kg) have restricted climate envelopes compared to other groups, occurring in regions with warm climates and no prolonged dry season. Seasonal extremes of temperature (mean temperature of the coldest month) and rainfall (maximum monthly precipitation) are the most important climatic predictors of diversity patterns for living artiodactyls. The occurrence of these ecological traits in the ungulate fossil record, as well as the ecological structure of fossil ungulate faunas, can be useful for inferring paleoclimatic conditions and paleoenvironments.

2.7 Acknowledgements

We thank Miriam Zelditch, Don Swiderski, and Matt Friedman for their helpful comments on this work. R code for spatial autocorrelation regression models provided by Pascal Title. Occurrence data were compiled by a working group of the National Center for Ecological Analysis and Synthesis (NCEAS) led by John Damuth and colleagues.

2.8 References

Andrews P, Hixson S, 2014. Taxon-free methods of paleoecology. *Ann Zool Fenn* **51**:269–284.

Andrews P, Lord JM, Evans EMN, 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol J Linn Soc* **11**:177–205.

Badgley C, Smiley TM, Terry R, Davis EB, DeSantis LRG, Fox DL, Hopkins SSB, Jezkova T, Matocq MD, Matzke N, McGuire JL, Mulch A, Riddle BR, Roth VL, Samuels JX, Strömberg CAE, Yanites BJ, 2017. Biodiversity and topographic complexity: modern and geohistorical perspectives. *Trends Ecol Evol* **32**:211–226.

Barnosky AD, Lindsey EL, Villavicencio NA, Bostelmann E, Hadly EA, Wanket J, Marshall CR, 2016. Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proc Natl Acad Sci USA* **113**:856–861.

Bivand R, Wong DWS, 2018. Comparing implementations of global and local indicators of spatial association. *TEST* **27**:716–748.

Blanco F, Calatayud J, Martín-Perea DM, Domingo MS, Menéndez I, Müller J, Fernández MH, Cantalapiedra JL, 2021. Punctuated ecological equilibrium in mammal communities over evolutionary time scales. *Science* **372**:300–303.

Climate Change Knowledge Portal, 2020. The World Bank Group. Retrieved from https://climateknowledgeportal.worldbank.org. Accessed 2020.

Demment MW, Van Soest PJ, 1985. A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. *Am Nat* **125**:641–672.

Faith DP, 1992. Conservation evaluation and phylogenetic diversity: *Biol Conserv* **61**:1–10.

Gagnon M, Chew AE, 2000. Dietary preferences in extant African Bovidae. *J Mammal* **81**:490–511.

Graham CH, Carnaval AC, Cadena CD, Zamudio KR, Roberts TE, Parra JL, McCain CM, Bowie RCK, Moritz C, Baines SB, Schneider CJ, Van Der Wal J, Rahbek C, Kozak KH, Sanders NJ, 2014. The origin and maintenance of montane diversity: integrating evolutionary and ecological processes: *Ecography* **37**: 001–009.

Finarelli JA, Badgley C, 2010. Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate. *Proc R Soc London B* **277**:2721–2726.

Flynn LJ, Pilbeam D, Barry JC, Morgan ME, Raza SM, 2014. Siwalik synopsis: A long stratigraphic sequence for the Later Cenozoic of South Asia. *C R Palevol* **15**:877–887.

Hammer Ø, Harper DAT, Ryan PD, 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron* **4**:1–9.

Huston M, 1994. *Biological Diversity*. Cambridge: Cambridge University Press, 681 p.

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM, 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct Ecol* **29**:592–599.

Jackson DA, 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* **74**:2204–2214.

Janis CM, 1998. *Evolution of tertiary mammals of North America: Volume 1, terrestrial carnivores, ungulates, and ungulate like mammals*. Cambridge: Cambridge University Press.

Janis CM, Damuth J, Theodor JM, 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc Natl Acad Sci USA* **97**:7899–7904.

Janis CM, Damuth J, Theodor JM, 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeogr Palaeoclimatol Palaeoecol* **177**:183–198.

Jarman PJ, 1974. The social organization of antelope in relation to their ecology. *Behaviour* **48**:215–267.

Kappelman J, 1991. The paleoenvironment of *Kenyapithecus* at Fort Ternan. *J Hum Evol* **20**:95–129.

Khan MA, Abdul G, Umar F, Muhammad A, 2006. Ruminant Fauna from the Tertiary Hills (Neogene) of the Siwaliks of Pakistan. *J Appl Sci* **6**:131–137

Langer P, 1974. Stomach evolution in the Artiodactyla. *Mammalia* **38**:295–314.

Marcot JD, Fox DL, Niebuhr SR, 2016. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. *Proc Nat Acad Sci* **113**:7189–7194.

Menne MJ, Williams CN, Gleason BE, Rennie JJ, Lawrimore JH, 2018. The Global Historical Climatology Network monthly temperature dataset, version 4. Journal of Climate, 31, 9835–9854. https://www.ncdc.noaa.gov/data-access/land-based-station-data/land-based-datasets/global-historical-climatology-network-monthly-version-4. Accessed 2019.

Mihlbachler MC, Rivals F, Solounias N, Semprebon GM, 2011. Dietary change and evolution of horses in North America. *Science* **311**:1178–1181.

Morgan ME, Badgley C, Gunnell GF, Gingerich PD, Kappelman JW, Maas MC, 1995. Comparative paleoecology of Paleogene and Neogene mammalian faunas: body-size structure. *Palaeogeogr Palaeoclimatol Palaeoecol* **115**:287–317.

New M, Lister D, Hulme M, Makin I. 2002. A high-resolution data set of surface climate over global land areas. *Clim Res* **21**:1–25. Retrieved from http://www.fao.org/aquastat/en/climate-info-tool/. Accessed 2019.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. 2011. vegan: Community ecology package. R package version 2.0-0. http://cran.r-project.org/web/packages/vegan/index.html.

Olson DM, Dinerstein E, 1998. The Global 200: A representation approach to conserving the Earth’s most biologically valuable ecoregions. *Conservation Biol* 12:502–515.

Olson, D. M., Dinerstein, E. 2002. The Global 200: Priority ecoregions for global conservation. *Ann Missouri Bot Gard* **89**:199–224.

Petchey OL, Gaston KJ, 2006. Functional diversity: back to basics and looking forward. *Ecol Lett* **9**:741–758.

Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, Rasmussen CMØ, Richardson K, Rosing MT, Whittaker RJ, Fjeldså J, 2018. Building mountain biodiversity: Geological and evolutionary processes. *Science* **365**:1114–1119.

Richardson KC, Vidyadaran MK, Azmi TI, Fuzinz NH, 1988. The radiographic anatomy of the gastrointestinal tract of the lesser mouse deer (*Tragulus javanicus*). *Pertanika* **11**: 427-435.

Rose PJ, Fox DL, Marcot J, and Badgley C, 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology* **39**:163–166.

Rosenzweig ML, 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press, 436 p.

Smiley TM, Title PO, Zelditch ML, Terry RC, 2020. Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological and phylogenetic diversity: A case study of North American rodents. *Glob Ecol Biogeogr* **29**:516–533.

Swenson NG, 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional, and phylogenetic biodiversity. *Am J Bot* **98**:472–480.

Ter Braak CJF, 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* **69**: 69–77.

US Geological Survey EROS Data Center, 1996. Global 30 arc-second elevation (GTOPO30). US Geological Survey, Sioux Falls, SD. https://doi.org/10.5066/F7DF6PQS. Accessed 2021.

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R, 1999. The relationship between productivity and species richness. *Annu Rev Ecol Syst* **30**:257–300.

Table 2.1 Classification of ecological traits for 161 species of artiodactyls. Criteria for the six herbivore feeding categories follow Gagnon and Chew (2000).

Ecological category	**N species**	**Defining criteria**
(a) Body size class		
Size class 1	15	2.0–9.9 kg
Size class 2	24	10.0–20.9 kg
Size class 3	42	21.0–53.9 kg
Size class 4	40	54.0–129.9 kg
Size class 5	29	130.0–599.9kg
Size class 6	11	600.0–1405.5kg
(b) Feeding category		
Frugivore	23	>60% fruits, little or no monocots
Browser	45	>70% dicots
Browser-grazer intermediate	25	30-70% dicots and monocots, <20% fruits
Generalist	8	>20% of all plant types
Variable grazer	36	60-90% monocots, variable
Obligate grazer	16	>90% monocots, not variable
Omnivore	8	Plants, animals, algae, or fungi

Table 2.2 Environmental variables documented for 328 artiodactyl localities.

Variables	**Definition**
(a) Temperature variables	
Mean temp	Mean annual temperature, averaged across 12 months
Min temp	Mean temperature of the coldest month
Max temp	Mean temperature of the warmest month
Temp range	Difference between mean temperatures of the coldest and warmest months
(b) Precipitation variables	
Mean ppt	Mean annual precipitation, averaged across 12 months
Min ppt	Mean precipitation of the driest month
Max ppt	Mean precipitation of the wettest month
Dry season length (continuous)	Number of consecutive months with precipitation < 10 mm/month
Dry season length (total)	Total number of months with precipitation < 10 mm/month
(c) Topographic variables	
Elevation	Mean elevation within a 50 km × 50 km grid centered on the locality
Relief	Difference between highest and lowest elevation within a 50 km × 50 km grid centered on the locality

Table 2.3 Numbers of artiodactyl localities and species occurring in terrestrial ecoregions of the world. Ecoregion classification follows Olsen and Dinerstein (1998, 2002).

Ecoregion	N Localities	N Species	Description [a]
1) Tropical and subtropical moist broadleaf forests	57	85	High temperature and high precipitation year-round (AF, EA, NA, SA)
2) Tropical and subtropical dry broadleaf forests	8	17	High temperature year-round, relatively high annual rainfall but with seasonal droughts (EA, NA)
3) Tropical and subtropical coniferous forests	2	3	Moderately variable seasonal temperature, relatively low precipitation (NA)
4) Temperate broadleaf and mixed forests	50	30	Moderate mean annual temperature with distinct warm and cool seasons; relatively rainy in wet season, sometimes with a dry season (EA, NA, SA)
5) Temperate coniferous forests	25	24	Warm summer, cool winter; moderate rainfall (EA, NA)
6) Boreal forests/taiga	19	13	Low mean annual temperature with high seasonal variability; relatively low precipitation; some areas with recent glaciation history (EA, NA)
7) Tropical and subtropical grasslands, savannas, and shrublands	48	74	Warm year-round; semi-arid to semi-humid, highly seasonal rainfall (AF, SA)
8) Temperate grasslands, savannas, and shrublands	24	18	Warm summer, cool winter; semi-arid to semi-humid, highly seasonal rainfall (EA, NA, SA)
9) Flooded grasslands and savannas	3	28	Unique rain-fed hydrologic regimes and soil conditions (AF)
10) Montane grasslands and shrublands	17	55	High-altitude (above treeline) (AF, EA)
11) Tundra	10	8	Low annual temperature, short growing season, low potential evapotranspiration (EA, NA)
12) Mediterranean forests, woodlands, and scrub	24	17	Dry summer and rainy winter (AF, EA, NA)
13) Deserts and xeric shrublands	41	51	Low precipitation, temperature varies among regions (AF, EA, NA)

[a] Abbreviations in parentheses describe the geographic distribution of artiodactyl localities in the ecoregion. AF, Africa; EA, Eurasia; NA, North America, SA, South America.

Table 2.4 Results from the principal component analysis (PCA) of nine climatic variables. The analysis was based on covariation matrix and yielded two significant principal components (PCs) that together explain 79.55% of the variation in the original variables.

(a) Eigenvalues of the PCs

Principal component	PC1	PC2
Eigenvalue	4.10	3.06
% Variance	45.54	34.01

(b) Loadings of variables on the PCs

Climatic variable	PC 1	PC 2
Mean Temp	0.459	0.169
Max Temp	0.328	0.254
Min Temp	0.471	0.114
Temp Range	-0.438	-0.020
Mean Ppt	0.346	-0.350
Max. Ppt	0.365	-0.227
Min Ppt	0.114	-0.404
Dry Season (continuous)	0.025	0.525
Dry Season (total)	0.025	0.530

Table 2.5 Result of the canonical correspondence analysis for eleven environmental variables and seven faunal variables.

(a) Summary statistics

	CCA1	CCA2	CCA3
Eigenvalue	0.243	0.120	0.042
Constrained inertia (%)	57.53	28.41	9.94
Cumulative %	57.53	85.94	95.88
Total inertia (%)	19.85	9.80	3.43
Cumulative %	19.85	29.65	33.08

(b) Loadings of environmental variables

	CCA1	CCA2	CCA3
Mean Ppt	0.779	-0.499	0.034
Max Ppt	0.704	-0.186	0.130
Min Ppt	0.209	-0.695	-0.328
Dry Season cont	-0.122	0.618	-0.277
Dry Season tot	-0.133	0.625	-0.328
Mean Temp	0.751	0.452	-0.258
Max Temp	0.430	0.322	-0.297
Min Temp	0.817	0.454	-0.234
Temp Range	-0.831	-0.423	0.155
Elevation	-0.281	0.225	0.227
Relief	-0.206	-0.187	-0.229

(c) Loadings of faunal variables

	CCA1	CCA2	CCA3
Browser	-0.344	-0.203	0.162
Frugivore	1.255	-0.461	0.002
Generalist	0.159	0.414	-0.408
Intermediate	-0.363	0.181	-0.358
Obligate Grazer	0.386	0.632	0.206
Variable Grazer	-0.390	-0.030	0.007
Omnivore	0.241	-0.319	-0.175

Table 2.6 Coefficients from multiple linear regression models. For each model, the environmental variables are the predictor (independent) variables, and the dependent variable is the number of species in the ecological category or Shannon diversity index. R-squared values of the regression models are reported in table headings. All models yielded p < 0.05.

(a) Total species richness ($r^2 = 0.14$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	5.80	0.27	21.16	**0.00**
Elevation	0.54	0.31	1.78	0.08
Dry Season	0.12	0.32	0.36	0.72
Max Ppt	0.30	0.36	0.83	0.41
Max Temp	-0.44	0.44	-0.99	0.32
Min Temp	2.07	0.46	4.47	**0.00**

(b) Frugivore ($r^2 = 0.25$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.50	0.06	7.99	**0.00**
Elevation	-0.14	0.07	-2.08	**0.04**
Dry Season	-0.12	0.07	-1.63	0.10
Max Ppt	0.33	0.08	4.07	**0.00**
Max Temp	-0.15	0.10	-1.45	0.15
Min Temp	0.45	0.11	4.30	**0.00**

(c) Browser ($r^2 = 0.04$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	1.76	0.08	22.05	**0.00**
Elevation	0.28	0.09	3.20	**0.00**
Dry Season	-0.16	0.09	-1.70	0.09
Max Ppt	0.07	0.10	0.63	0.53
Max Temp	0.07	0.13	0.55	0.58
Min Temp	-0.10	0.13	-0.72	0.47

(d) Browser-grazer intermediate ($r^2 = 0.11$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.61	0.04	14.62	**0.00**
Elevation	0.01	0.05	0.13	0.89
Dry Season	0.10	0.05	2.08	**0.04**
Max Ppt	-0.24	0.05	-4.42	**0.00**
Max Temp	-0.12	0.07	-1.80	0.07
Min Temp	0.30	0.07	4.30	**0.00**

(e) Generalist ($r^2 = 0.17$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.36	0.03	10.42	**0.00**
Elevation	0.03	0.04	0.82	0.42
Dry Season	0.12	0.04	3.03	**0.00**
Max Ppt	0.00	0.04	0.05	0.96
Max Temp	-0.04	0.06	-0.65	0.52
Min Temp	0.26	0.06	4.48	**0.00**

(f) Variable grazer ($r^2 = 0.07$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.97	0.06	16.52	**0.00**
Elevation	0.29	0.07	4.39	**0.00**
Dry Season	0.10	0.07	1.42	0.16
Max Ppt	0.05	0.08	0.66	0.51
Max Temp	0.17	0.09	1.83	0.07
Min Temp	-0.09	0.10	-0.89	0.37

(g) Obligate grazer ($r^2 = 0.13$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.92	0.11	8.13	**0.00**
Elevation	0.11	0.13	0.89	0.37
Dry Season	0.17	0.13	1.31	0.19
Max Ppt	-0.05	0.15	-0.34	0.73
Max Temp	-0.31	0.18	-1.68	0.09
Min Temp	0.96	0.19	5.03	**0.00**

(i) Omnivore ($r^2 = 0.25$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.69	0.03	20.87	**0.00**
Elevation	-0.03	0.04	-0.87	0.38
Dry Season	-0.10	0.04	-2.55	**0.01**
Max Ppt	0.13	0.04	3.13	**0.00**
Max Temp	-0.08	0.05	-1.42	0.16
Min Temp	0.28	0.06	5.04	**0.00**

(j) Size class 1 ($r^2 = 0.21$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.29	0.03	9.20	**0.00**
Elevation	-0.02	0.03	-0.48	0.63
Dry Season	-0.05	0.04	-1.45	0.15
Max Ppt	0.15	0.04	3.61	**0.00**
Max Temp	0.01	0.05	0.19	0.85
Min Temp	0.18	0.05	3.40	**0.00**

(k) Size class 2 ($r^2 = 0.19$)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.70	0.06	11.13	**0.00**
Elevation	0.09	0.07	1.27	0.21
Dry Season	0.08	0.07	1.09	0.28
Max Ppt	0.05	0.08	0.59	0.56
Max Temp	-0.24	0.10	-2.41	**0.02**
Min Temp	0.64	0.11	6.00	**0.00**

(l) Size class 3 (r^2 = 0.25)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	1.30	0.05	25.38	**0.00**
Elevation	0.19	0.06	3.27	**0.00**
Dry Season	0.03	0.06	0.56	0.58
Max Ppt	0.12	0.07	1.81	0.07
Max Temp	0.15	0.08	1.83	0.07
Min Temp	0.34	0.09	3.94	**0.00**

(m) Size class 4 (r^2 = 0.05)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	1.55	0.09	17.51	**0.00**
Elevation	0.22	0.10	2.19	**0.03**
Dry Season	-0.03	0.10	-0.31	0.76
Max Ppt	-0.01	0.11	-0.09	0.93
Max Temp	0.00	0.14	-0.02	0.98
Min Temp	0.32	0.15	2.11	**0.04**

(n) Size class 5 (r^2 = 0.04)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	1.19	0.08	14.28	**0.00**
Elevation	0.05	0.09	0.54	0.59
Dry Season	0.12	0.10	1.27	0.20
Max Ppt	-0.08	0.11	-0.71	0.48
Max Temp	-0.32	0.13	-2.42	**0.02**
Min Temp	0.43	0.14	3.06	**0.00**

(o) Size class 6 (r^2 = 0.05)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.77	0.05	16.66	**0.00**
Elevation	0.02	0.05	0.40	0.69
Dry Season	-0.04	0.05	-0.65	0.51
Max Ppt	0.07	0.06	1.11	0.27
Max Temp	-0.03	0.07	-0.37	0.71
Min Temp	0.17	0.08	2.11	**0.04**

(p) Shannon index of diet (r^2 = 0.16)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.90	0.03	33.55	**0.00**
Elevation	0.02	0.03	0.51	0.61
Dry Season	0.05	0.03	1.61	0.11
Max Ppt	0.03	0.03	0.83	0.41
Max Temp	-0.05	0.04	-1.11	0.27
Min Temp	0.21	0.05	4.75	**0.00**

(q) Shannon index of size (r^2 = 0.07)

	Estimate	S.E.	t value	Pr(>|t|)
(Intercept)	0.94	0.03	33.13	**0.00**
Elevation	0.07	0.03	2.22	**0.03**
Dry Season	-0.01	0.03	-0.25	0.81
Max Ppt	0.04	0.04	0.98	0.33
Max Temp	0.02	0.05	0.53	0.59
Min Temp	0.09	0.05	1.92	0.06

Table 2.7 Comparison of multiple linear regression (MLR) models and spatial simultaneous autoregressive (SAR) models for four ecological groups. MLR models include only significant predictors. For all four groups, accounting for spatial autocorrelation led to an improvement in AIC of the model.

(a) Frugivore

	MLR model (AIC = 1079.6)				SAR model (AIC = 734.0)			
	Estimate	S.E.	t value	Pr(>|t|)	Estimate	S.E.	z value	Pr(>|t|)
(Intercept)	0.50	0.06	7.95	**0.00**	0.32	0.10	3.08	**0.00**
Dry Season	-0.16	0.07	-2.35	**0.02**	-0.13	0.05	-2.58	**0.01**
Max Ppt	0.35	0.08	4.30	**0.00**	0.02	0.05	0.51	0.61
Min Temp	0.37	0.08	4.57	**0.00**	0.18	0.06	2.84	**0.00**

(b) Omnivore

	MLR model (AIC = 640.3)				SAR model (AIC = 515.8)			
	Estimate	S.E.	t value	Pr(>|t|)	Estimate	S.E.	z value	Pr(>|t|)
(Intercept)	0.69	0.03	20.87	**0.00**	0.57	0.05	12.35	**0.00**
Dry Season	-0.11	0.04	-3.17	**0.01**	-0.11	0.04	-2.98	**0.00**
Max Ppt	0.14	0.04	3.34	**0.00**	0.12	0.04	2.95	**0.00**
Min Temp	0.23	0.04	5.48	**0.00**	0.17	0.04	4.00	**0.00**

(c) Size class 1

	MLR model (AIC = 604.9)				SAR model (AIC = 405.8)			
	Estimate	S.E.	t value	Pr(>|t|)	Estimate	S.E.	z value	Pr(>|t|)
(Intercept)	0.29	0.03	9.20	**0.00**	0.26	0.07	3.77	**0.00**
Max Ppt	0.17	0.04	4.56	**0.00**	-0.01	0.03	-0.27	0.79
Min Temp	0.17	0.04	4.47	**0.00**	0.18	0.05	3.89	**0.00**

(d) Size class 3

	MLR model (AIC = 942.0)				SAR model (AIC = 845.5)			
	Estimate	S.E.	t value	Pr(>|t|)	Estimate	S.E.	z value	Pr(>|t|)
(Intercept)	1.30	0.05	25.26	**0.00**	1.12	0.09	12.95	**0.00**
Elevation	0.15	0.05	2.85	**0.00**	0.04	0.05	0.85	0.39
Min Temp	0.51	0.05	9.91	**0.00**	0.38	0.06	5.91	**0.00**

Table 2.8 Number of species in each joint feeding-size category, counted for all localities and for the eight most species-rich ecoregions.

(a) World

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	5	8	1	1	0	0	0
Size class 2	10	10	1	1	2	0	0
Size class 3	6	11	12	2	6	2	2
Size class 4	2	8	6	1	15	5	4
Size class 5	0	6	5	3	7	7	1
Size class 6	0	1	0	0	7	2	1

(b) Tropical and subtropical moist broadleaf forests (N = 57 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	5	8	1	1	0	0	0
Size class 2	10	4	0	1	2	0	0
Size class 3	5	6	4	1	2	2	2
Size class 4	2	2	3	1	3	3	4
Size class 5	0	3	0	3	3	6	1
Size class 6	0	1	0	0	3	2	1

(c) Tropical and subtropical grasslands, savannas, and shrublands (N = 48 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	1	5	1	0	0	0	0
Size class 2	8	2	0	1	2	0	0
Size class 3	3	3	5	2	0	2	2
Size class 4	1	1	2	1	3	4	2
Size class 5	0	4	2	2	1	7	1
Size class 6	0	1	0	0	0	2	0

(d) Montane grasslands and shrublands (N = 17 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	1	1	1	0	0	0	0
Size class 2	1	5	0	1	1	0	0
Size class 3	0	3	4	1	2	2	0
Size class 4	0	2	1	1	4	3	2
Size class 5	0	1	5	1	3	7	0
Size class 6	0	1	0	0	1	2	1

(e) Deserts and xeric shrublands (N = 41 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	0	2	0	0	0	0	0
Size class 2	0	3	1	1	0	0	0
Size class 3	0	5	7	1	2	0	1
Size class 4	0	4	2	0	8	4	0
Size class 5	0	2	3	1	5	5	0
Size class 6	0	1	0	0	1	2	1

(f) Temperate broadleaf and mixed forests (N = 50 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	0	2	0	0	0	0	0
Size class 2	0	3	0	0	0	0	0
Size class 3	0	3	4	0	2	0	0
Size class 4	0	4	1	0	1	0	0
Size class 5	0	2	2	1	2	0	0
Size class 6	0	0	0	0	2	0	1

(g) Flooded grasslands and savannas (N = 3 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	0	1	0	0	0	0	0
Size class 2	0	3	0	0	0	0	0
Size class 3	0	2	2	0	0	0	0
Size class 4	0	0	0	0	3	3	0
Size class 5	0	2	0	1	2	5	0
Size class 6	0	1	0	0	0	2	1

(h) Temperate coniferous forests (N = 19 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	0	0	0	0	0	0	0
Size class 2	0	2	0	0	0	0	0
Size class 3	0	4	1	0	1	0	1
Size class 4	0	4	0	0	4	0	0
Size class 5	0	2	1	0	1	0	0
Size class 6	0	0	0	0	2	0	1

(i) Temperate grasslands, savannas, and shrublands (N = 24 localities)

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Size class 1	0	0	0	0	0	0	0
Size class 2	0	0	0	0	0	0	0
Size class 3	0	4	1	0	0	0	0
Size class 4	0	3	0	0	2	0	0
Size class 5	0	1	2	0	2	0	0
Size class 6	0	0	0	0	2	0	1

Table 2.S 1 Location, principal component scores from ordination of nine climatic variables, and physiographic variables of the 328 artiodactyl localities.

ID	Locality Name	Country	Continent	PC 1	PC 2	Elevation (m)	Relief (m)
1	Kgalagadi Transfrontier Park	Botswana	Africa	0.04	1.49	1001	100
2	Okavango Delta	Botswana	Africa	0.72	2.14	955	10
3	Sangmelima	Cameroon	Africa	2.42	-1.24	624	321
4	La Maboke	Central African Republic	Africa	2.48	-0.62	360	49
5	Makokou	Gabon	Africa	2.51	-1.08	327	231
6	Lamto	Ivory Coast	Africa	2.47	-0.75	87	131
7	Tai National Park	Ivory Coast	Africa	3.91	-2.18	181	114
8	Amboseli National Reserve	Kenya	Africa	1.26	1.52	1159	50
9	South Turkana National Reserve	Kenya	Africa	1.69	2.35	631	429
10	Mount Nimba Strict Nature Reserve	Liberia & Guinea	Africa	3.32	-1.22	628	944
11	Kasungu National Park	Malawi	Africa	1.00	1.90	1087	224
12	Lengwe Nature Park/Mwabvi Game Reserve	Malawi	Africa	2.17	-1.30	131	217
13	Nyika National Park	Malawi	Africa	1.08	1.76	2159	705
14	Zinave National Park	Mozambique	Africa	1.28	1.35	128	46
15	Benin City	Nigeria	Africa	2.93	-0.93	76	90
17	Lake Chad Game Reserve	Nigeria	Africa	1.95	2.51	292	31
18	Cross River National Park	Nigeria	Africa	2.63	1.33	297	426
19	Yankari National Park	Nigeria	Africa	2.55	1.53	267	79
20	Akagera National Park	Rwanda	Africa	1.09	-0.48	1355	564
21	Ihema	Rwanda	Africa	1.09	-0.48	1528	400
22	Bandia	Senegal	Africa	1.70	2.64	42	125
23	Golden Gate Highlands National Park	South Africa	Africa	0.14	0.71	2053	1194
24	Bethal	South Africa	Africa	-0.02	0.57	1644	135
25	Bloemhof	South Africa	Africa	0.07	1.21	1240	67
26	Germiston	South Africa	Africa	0.16	0.73	1634	330
27	Komatipoort	South Africa	Africa	0.85	0.13	191	351
28	Messina	South Africa	Africa	0.79	2.27	527	307
29	Nelspruit	South Africa	Africa	0.85	0.13	794	708
30	Pietersburg	South Africa	Africa	0.13	1.09	1300	328
31	Potchefstroom	South Africa	Africa	0.04	0.87	1364	211
32	Pretoria	South Africa	Africa	0.39	0.82	1330	380
33	Punda Milia	South Africa	Africa	1.03	1.62	457	324
34	Thabazimbi	South Africa	Africa	0.68	0.79	1061	835
35	Wakkerstroom	South Africa	Africa	-0.02	0.57	1863	659
36	Zeerust	South Africa	Africa	0.21	1.09	1289	419
37	Jebel Marra	Sudan	Africa	1.13	3.29	2073	1631
38	Lake Rukwa Valley	Tanzania	Africa	1.61	1.83	919	361
39	Serengeti National Park	Tanzania	Africa	1.55	-0.34	1515	445
40	Bagbele	Zaire	Africa	2.19	-0.86	791	127
41	Garamba National Park	Zaire	Africa	2.19	-0.86	731	75
42	Kibara Plateau, Upemba National Park	Zaire	Africa	1.39	0.51	1100	1052
43	Lake Upemba, Upemba National Park	Zaire	Africa	2.05	0.96	685	401
44	Kivu Lake, Kahuzi-Bie ga National Park	Zaire	Africa	1.38	-1.14	1152	360
45	Rwindi-Rutshuru Plain, Virunga National Park	Zaire	Africa	1.45	-0.73	1080	523
46	Algiers	Algeria	Africa	0.38	0.72	99	527
47	Biskra	Algeria	Africa	0.08	2.72	138	60
48	Djelfa	Algeria	Africa	-0.85	0.80	1177	480
49	Ain Sefra	Algeria	Africa	-0.55	1.65	1291	835
50	El Golea	Algeria	Africa	-0.01	4.94	423	15
51	Beni Abbes	Algeria	Africa	-0.16	3.57	494	150
52	Tamanrassett	Algeria	Africa	0.02	5.09	1339	286

53	Kafue National Park	Zambia	Africa	1.07	1.59	1021	339
54	Maputo Elephant Reserve	Mozambique	Africa	1.34	-0.57	56	71
55	Gile Wildlife Reserve	Mozambique	Africa	1.93	-0.01	124	156
56	Northern Tete District	Mozambique	Africa	2.05	0.05	1159	581
67	Aghbolagh Morched	Iran	Eurasia	-0.77	1.51	2171	1572
68	Bialowieza National Park	Poland	Eurasia	-1.52	-0.88	170	61
69	Central Vietnam	Vietnam	Eurasia	3.83	-2.19	335	365
70	Cesky les	Czechoslovakia	Eurasia	-1.42	-0.76	437	388
71	Dalsland	Sweden	Eurasia	-1.52	-1.38	145	115
72	Donana National Park	Spain	Eurasia	0.21	0.91	22	52
73	Geh	Iran	Eurasia	0.98	4.56	952	762
74	Gorgan Province	Iran	Eurasia	0.98	4.56	952	762
75	Malaysian Lowland Rain Forest	Malaysia	Eurasia	4.40	-3.42	42	62
76	Lyallpur	Pakistan	Eurasia	0.64	1.96	163	26
77	Lowland Sabah	Malaysia	Eurasia	5.05	-3.87	432	406
78	South-Central Vietnam	Vietnam	Eurasia	2.92	-1.40	553	1276
79	Nowy Targ Valley	Poland	Eurasia	-1.23	-1.84	696	658
80	Rhone Valley, Ardeche	France	Eurasia	0.24	-1.52	1150	627
81	Seistan	Iran	Eurasia	0.03	4.93	512	154
82	Shush	Iran	Eurasia	0.49	3.17	15	24
83	Lowland Dry Zone	Sri Lanka	Eurasia	3.08	-0.68	59	63
84	Lowland Wet Zone	Sri Lanka	Eurasia	2.88	-1.99	177	558
85	Mid-Elevation Wet Zone	Sri Lanka	Eurasia	2.35	-1.11	625	970
86	Montane Zone	Sri Lanka	Eurasia	1.90	-2.50	1732	1255
87	Trzebnickie Hills	Poland	Eurasia	-1.30	-0.86	157	116
88	Tatras	Poland	Eurasia	-1.17	-1.54	1130	1641
89	Bieszczady Mountains	Poland	Eurasia	-1.44	-1.51	451	357
90	Lebanon	Lebanon	Eurasia	-0.26	1.96	1066	1063
91	Greater Caucausus Mountains	Georgia and Azerbaijan	Eurasia	-1.64	-1.85	1122	1472
92	Dagestan Caucasus	Russia	Eurasia	-1.56	-0.66	2752	2371
93	Talysh Mountains, Forest Region	Iran	Eurasia	-1.20	1.02	1872	1553
94	Sevan Lake	Armenia	Eurasia	-2.09	-0.99	2046	800
95	Terek-Kuma, Northern Dagestan	Russia	Eurasia	-1.16	-0.21	-18	9
96	Hortobagy National Park	Hungary	Eurasia	-1.00	-0.77	100	95
97	Kiskunsag National Park	Hungary	Eurasia	-1.06	-0.73	136	128
98	Nanking	China	Eurasia	0.43	-1.22	45	218
99	Lincang	China	Eurasia	1.49	-1.29	1855	1111
100	Dhofar	Oman	Eurasia	1.09	4.51	935	395
101	Kelabit Plateau, Sarawak	Sarawak, Malaysia	Eurasia	4.54	-4.98	799	1198
102	Medog County	China	Eurasia	0.95	-1.28	2427	3459
103	Azraq	Jordan	Eurasia	-0.33	3.34	548	136
104	Kuwait	Kuwait	Eurasia	0.51	3.67	192	98
105	United Arab Emirates	United Arab Emirates	Eurasia	0.92	4.36	16	63
106	Low Gunung Benom	Malaya	Eurasia	3.53	-2.34	471	1904
107	Middle Gunung Benom	Malaya	Eurasia	3.53	-2.34	471	1904
108	High Gunung Benom	Malaya	Eurasia	2.76	-3.55	471	1904
109	Langtang National Park	Nepal	Eurasia	-0.73	-1.04	4881	3279
110	Royal Chitwan National Park	Nepal	Eurasia	3.24	-0.15	230	438
111	Xishuangbanna	China	Eurasia	1.49	-1.29	843	814
112	Southwestern Guangxi	China	Eurasia	1.45	-0.63	224	351
113	Tarim Basin	China	Eurasia	-1.79	3.46	1234	40
114	Northern Tibetan Plateau	China	Eurasia	-2.67	0.99	5577	1750
115	Central Shaanxi Province	China	Eurasia	-1.12	0.76	986	919
116	Daba Shan	China	Eurasia	0.32	-0.90	1170	1141
117	Dong Ujimqin Qi	China	Eurasia	-2.87	1.59	1157	877
118	Changchun Plain	China	Eurasia	-1.75	-1.14	1318	917
119	Chang Bai Shan	China	Eurasia	-3.53	0.91	1530	753
120	Xianxia Ling	China	Eurasia	0.59	-1.07	773	1097
121	Northern Da Hinggan Ling	China	Eurasia	-3.07	1.75	837	646

122	Red Basin	China	Eurasia	0.12	-0.31	425	155
123	Northern Denali National Park	USA	N. America	-3.25	-1.19	677	802
124	Seward Peninsula	USA	N. America	-3.53	-1.16	328	840
125	Eastern Azuero Peninsula	Panama	N. America	2.80	0.41	21	120
126	Sierra de la Laguna	Mexico	N. America	1.97	-0.63	1081	1625
127	McKittrick, Western Kern County	USA	N. America	0.19	-0.60	460	1108
128	Western Mohave Desert	USA	N. America	0.05	-0.65	815	675
129	Colima	Mexico	N. America	2.10	0.75	407	1046
130	Colon Province	Panama	N. America	3.95	-1.62	37	164
131	Palm Valley	USA	N. America	0.67	-0.62	5	20
132	Ripley and Jefferson Counties	USA	N. America	-1.25	-0.62	264	124
133	Meade County	USA	N. America	-0.90	-0.58	771	109
135	Northeastern Louisiana	USA	N. America	0.26	-0.63	23	6
136	Washtenaw County	USA	N. America	-1.50	-0.68	270	84
137	Charlevoix County	USA	N. America	-2.03	-0.77	242	199
138	Michoacan	Mexico	N. America	1.23	0.55	917	1184
139	Western Missouri	USA	N. America	-0.88	-0.58	252	75
140	Savannah River	USA	N. America	0.09	-0.65	71	94
141	Morelos	Mexico	N. America	1.16	1.81	1130	640
142	Charleston Mountains	USA	N. America	-1.01	-0.68	2441	2049
143	Siskiyou Mountains	USA	N. America	-1.16	-0.77	792	1071
144	Quetico Provincial Park	Canada	N. America	-2.55	-1.24	420	113
145	Sierra de Chama	Guatemala	N. America	4.79	-2.71	395	706
146	Carlsbad Caverns National Park	USA	N. America	-0.55	-0.75	1371	783
147	Great Smoky Mountains National Park	USA	N. America	-0.85	-0.68	823	1519
148	Big Bend National Park	USA	N. America	0.08	-0.67	922	1194
149	Guadalupe Mountains National Park	USA	N. America	0.04	-0.71	1715	1445
150	Buffalo National River	USA	N. America	-0.43	-0.56	314	463
151	Little Missouri National Grassland	USA	N. America	-2.11	-0.58	757	172
152	Cook County	USA	N. America	-2.39	-0.32	547	280
153	Wichita Mountains Wildlife Refuge	USA	N. America	-0.24	-0.54	443	333
154	Jasper National Park	Canada	N. America	-2.24	-1.97	1456	1592
155	Bighorn Basin	USA	N. America	-1.96	-0.59	1425	532
156	Black Hills	USA	N. America	-1.56	-0.62	1447	731
157	Goshen County	USA	N. America	-1.56	-0.62	1333	287
158	Jackson Hole	USA	N. America	-2.64	-0.95	2111	1432
159	Lower Green River	USA	N. America	-2.03	-0.62	1995	354
160	Uinta Mountains	USA	N. America	-2.28	-1.07	3052	1161
161	Yellowstone National Park	USA	N. America	-2.71	-0.56	2448	291
162	Yucatan	Mexico	N. America	1.25	0.33	25	15
163	Monteverde, Pacific Seasonal Forest	Costa Rica	N. America	2.15	-0.38	1028	1465
164	Monteverde, Cloud Forest	Costa Rica	N. America	1.99	-2.42	1054	1459
165	Monteverde, Atlantic Slope Rainforest	Costa Rica	N. America	2.15	-0.38	1202	1377
166	La Selva Biological Station and Reserve	Costa Rica	N. America	3.05	0.59	90	381
167	Tug Hill Plateau	USA	N. America	-1.74	-0.77	531	303
168	Adelaide Peninsula	Canada	N. America	-5.25	1.60	30	56
169	Okefinokee Swamp	USA	N. America	0.37	-0.61	36	10
170	Wood Buffalo National Park	Canada	N. America	-3.71	-0.99	280	55
171	Lacreek National Wildlife Refuge	USA	N. America	-1.60	-0.55	952	138
172	Prince Albert National Park	Canada	N. America	-2.98	-0.99	554	180
173	Riding Mountain National Park	Canada	N. America	-2.79	-0.90	629	346
174	Western San Luis Potosi	Mexico	N. America	0.14	1.96	1874	739
175	Eastern San Luis Potosi	Mexico	N. America	0.63	1.58	314	626
176	Mackenzie River Delta	Canada	N. America	-4.40	-1.13	51	162
177	Western Durango	Mexico	N. America	0.14	1.66	1762	1002
178	Eastern Durango	Mexico	N. America	0.09	2.43	1423	502
179	Medicine Hat	Canada	N. America	-2.27	-0.50	747	141
180	Guatopo National Park	Venezuela	S. America	1.74	1.08	746	933
181	Chaco Boreal	Paraguay	S. America	1.39	0.12	114	14
182	Central Plateau-Paraguay	Paraguay	S. America	2.11	-1.95	188	149

183	Salta Puna	Argentina	S. America	-1.05	2.06	4230	2073
184	Monte Desert, Salta	Argentina	S. America	-0.97	2.41	2889	1000
185	Caatinga	Brazil	S. America	1.54	1.66	478	186
186	Cocha Cashu, Manu National Park	Peru	S. America	3.04	-1.35	417	93
187	Masaguaral, Fundo Pecuario Masaguaral	Venezuela	S. America	2.47	1.49	80	15
188	Manaus-MCSE	Brazil	S. America	3.44	-1.49	99	12
189	Lower Rio Cenepa	Peru	S. America	3.31	-2.39	353	727
190	Rio Santiago Basin	Peru	S. America	3.31	-2.39	270	532
191	Torres del Paine National Park	Chile	S. America	-1.58	-0.72	223	411
192	Paramaribo	Surinam	S. America	3.35	-1.56	4	10
193	Chapada do Araripe	Brazil	S. America	1.54	1.66	829	174
194	Paraguay River Valley	Paraguay	S. America	1.75	-0.66	104	117
195	Alto Paran?° River Valley	Paraguay	S. America	2.11	-1.95	255	167
196	Cuzco Amaz??nico	Peru	S. America	3.04	-1.35	199	38
197	Igauzu National Park	Argentina	S. America	1.87	-1.92	215	229
198	Rio Doce National Park	Brazil	S. America	1.78	-0.76	298	210
199	Altiplano	Bolivia	S. America	-0.87	1.04	3907	893
200	Pando Department	Bolivia	S. America	2.28	-0.60	232	120
201	Cabassou	French Guiana	S. America	4.91	-3.20	67	129
202	Etosha National Park	Namibia	Africa	0.82	2.05	1073	41
203	Namib-Naukluft National Park	Namibia	Africa	-0.31	4.63	516	151
204	Lunda Norte	Angola	Africa	1.72	0.28	1013	134
205	Huila Plateau	Angola	Africa	0.94	1.42	1434	190
206	Gebel Auenat	Libya	Africa	0.27	5.32	1091	933
207	Gebel Elba	Egypt	Africa	0.72	5.54	469	1300
208	Halfaya Pass	Egypt	Africa	0.06	3.04	158	235
209	El Fayum	Egypt	Africa	0.18	5.19	3	100
210	Ticino Park	Italy	Eurasia	-0.14	-1.58	108	70
211	Babia Gora Biosphere Reserve, Lower Forest Belt	Poland	Eurasia	-1.17	-1.54	798	1066
215	Hak Valley	Papua New Guinea	Eurasia	2.15	-1.77	783	1942
216	Telefomin	Papua New Guinea	Eurasia	2.15	-1.77	1608	1871
217	Fariman	Iran	Eurasia	-0.69	1.58	1549	1870
218	Talysh Mountains, Steppe	Azerbaijan	Eurasia	-1.55	0.57	1636	992
219	Turgai Basin	Kazakhstan	Eurasia	-2.71	-0.26	124	189
220	Central Kirgizia	Kyrgyzstan	Eurasia	-1.62	-0.33	920	830
221	Araks Sector	Armenia	Eurasia	-1.29	1.11	1085	1221
222	Neusiedler See National Park	Austria	Eurasia	-1.09	-0.93	135	180
223	Kura Region	Azerbaijan	Eurasia	-1.31	-0.70	41	376
224	Armorique	France	Eurasia	-0.16	-1.57	173	183
225	Bayonne	France	Eurasia	-0.16	-1.55	46	173
226	Camargues	France	Eurasia	-0.18	-0.50	2	12
227	Cevennes, Southern Massif Central	France	Eurasia	-0.64	-1.79	928	1242
228	Colmar	France	Eurasia	-0.63	-1.55	176	83
229	Hautes-Pyrenees	France	Eurasia	-1.81	-2.58	1899	2396
230	Landes de Gascogne	France	Eurasia	-0.16	-1.20	68	52
231	Livradois-Forez, Northern Massif Central	France	Eurasia	-0.62	-1.73	889	894
232	Marais Poitevin	France	Eurasia	-0.42	-1.00	7	39
233	Nord-Pas-de-Calais	France	Eurasia	-0.75	-1.20	50	85
234	Normandie-Maine	France	Eurasia	-0.68	-1.39	192	253
235	Quercy	France	Eurasia	-0.34	-0.87	270	257
236	Saint-Vidal, Haute-Loire	France	Eurasia	-0.62	-1.73	955	700
237	Sologne	France	Eurasia	-0.72	-1.01	98	79
238	Vercors	France	Eurasia	-0.57	-1.83	698	1255
239	Vosges du Nord	France	Eurasia	-0.79	-1.59	606	889
240	Lesser Caucasus Mountains	Georgia, Azerbaijan	Eurasia	-1.53	-1.86	1920	1284
241	Partenio Mountains	Italy	Eurasia	0.15	-0.49	278	1145

243	Liechtenstein	Liechtenstein	Eurasia	-0.23	-2.62	944	1811
245	Pila Region	Poland	Eurasia	-1.48	-0.89	117	82
246	Suwalki Region	Poland	Eurasia	-1.73	-1.01	158	91
247	Swietokrzyski National Park	Poland	Eurasia	-1.39	-1.03	312	314
248	Anadyr Region	Russia	Eurasia	-3.84	-1.33	15	82
249	Ciscaucasian Subdistrict	Russia	Eurasia	-1.36	-0.57	98	74
250	Khabarovsk	Russia	Eurasia	-2.59	-0.61	52	89
251	Lower Ienissei River	Russia	Eurasia	-4.20	-1.56	48	144
252	Lower Khatanga River	Russia	Eurasia	-4.87	-1.26	63	131
253	Lower Kolyma River	Russia	Eurasia	-5.02	-0.10	53	74
254	Lower Lena River	Russia	Eurasia	-5.16	-1.30	134	354
255	Novosibirsk	Russia	Eurasia	-2.90	-0.90	127	121
256	Southern Lake Baikal	Russia	Eurasia	-2.78	-1.03	477	170
257	St. Petersburg	Russia	Eurasia	-1.89	-1.20	9	55
258	Yakutsk	Russia	Eurasia	-5.11	0.12	119	165
259	Aiguamolls de l'Emporda	Spain	Eurasia	-0.41	-0.62	162	493
260	Alto Tajo	Spain	Eurasia	-1.02	-0.74	1341	722
261	Cazorla	Spain	Eurasia	-0.43	0.78	829	992
262	Sierra de Gredos	Spain	Eurasia	-1.09	-0.54	1392	1049
263	Annaba	Algeria	Africa	0.35	0.68	151	587
264	Brezina	Algeria	Africa	-0.48	1.19	886	297
265	Djanet	Algeria	Africa	0.26	5.29	1147	353
266	Ghardaia	Algeria	Africa	0.08	4.93	546	167
267	Northern Savannah Cameroon	Cameroon	Africa	2.40	2.09	306	20
268	Mayombe, Kouilou Basin	Congo	Africa	2.07	0.85	10	97
269	Tadjura-Obock	Djibouti	Africa	1.57	3.25	265	891
270	Addis Ababa	Ethiopia	Africa	1.08	-1.57	2480	988
271	Arba Minch	Ethiopia	Africa	1.63	0.57	1342	990
272	Asmara	Eritrea	Africa	0.65	0.98	2240	1020
273	Awash National Park	Ethiopia	Africa	1.43	0.87	1145	1090
274	Backo, Wollega	Ethiopia	Africa	1.32	-0.13	1946	451
275	Dire Dawa	Ethiopia	Africa	1.39	0.58	1321	821
276	Dohonta	Ethiopia	Africa	1.54	2.46	717	378
277	Gondaraba	Ethiopia	Africa	1.63	-0.76	840	1182
278	Southern Lake Tana	Ethiopia	Africa	1.84	1.25	1826	299
279	Lake Ziway	Ethiopia	Africa	0.70	0.59	1685	205
280	Simien Mountains	Ethiopia	Africa	0.27	0.73	3045	2765
281	Lake Malombe	Malawi	Africa	1.34	1.69	505	379
282	Agadir	Morocco	Africa	0.05	2.12	207	1172
283	Figuig	Morocco	Africa	-0.15	1.00	885	548
284	Jbel Ouarkziz	Morocco	Africa	0.06	1.98	653	830
285	Middle Atlas Mountains	Morocco	Africa	-0.36	-0.44	1710	1786
286	Oujda	Morocco	Africa	-0.15	1.00	608	571
287	Tarfaya	Morocco	Africa	0.12	4.46	38	29
288	Kaokoveld Desert	Namibia	Africa	0.82	2.05	1031	891
289	Kainji Lake National Park	Nigeria	Africa	2.49	1.97	174	167
290	Nyungwe National Park	Rwanda	Africa	1.18	-0.36	2333	1265
291	Nord Ferlo	Senegal	Africa	1.45	3.29	51	17
292	Swartwater, Transvaal	South Africa	Africa	0.79	2.27	774	225
293	Ituri Forest	Zaire	Africa	1.80	-1.16	904	116
294	Southwestern Kivu Lake	Zaire	Africa	1.30	-1.43	1728	1136
295	Cockscomb Basin	Belize	N. America	2.84	-1.98	250	730
296	Hamilton Inlet	Canada	N. America	-2.34	-2.01	217	280
297	Northwestern Nueltin Lake, Keewatin	Canada	N. America	-4.42	-0.81	301	36
298	Lac St. Jean	Canada	N. America	-2.16	-1.69	132	209
299	Bonnet Plume Lake	Canada	N. America	-4.46	0.49	1552	1082
300	Dawson	Canada	N. America	-3.86	-0.22	675	688
301	Kluane Lake	Canada	N. America	-3.61	-0.31	1288	1648
302	Lapierre House/Summit Lake	Canada	N. America	-4.38	0.66	423	708
303	Mayo/Keno	Canada	N. America	-3.86	-0.22	796	573
304	Old Crow	Canada	N. America	-4.26	0.59	344	501
305	Teslin Lake	Canada	N. America	-3.38	-0.97	908	834

306	Watson Lake	Canada	N. America	-3.64	-1.10	786	470
307	Whitehorse	Canada	N. America	-3.30	-0.47	906	1038
308	Mexico City Basin	Mexico	N. America	-0.30	0.28	2412	1030
309	Jalpa, Zacatecas	Mexico	N. America	1.23	0.55	1501	1382
310	Northern Zacatecas	Mexico	N. America	0.14	1.66	1835	545
311	Pinos, Zacatecas	Mexico	N. America	0.50	0.65	2347	723
312	Barro Colorado Island	Panama	N. America	4.73	-2.48	44	114
313	Katmai National Park	United States	N. America	-2.13	-1.75	499	1252
314	Colorado Desert	United States	N. America	1.10	-0.41	45	321
315	Colusa County	United States	N. America	0.08	-0.66	151	524
316	Del Norte County	United States	N. America	-0.69	-0.78	605	1097
317	Eastern Kern County	United States	N. America	-0.65	-0.76	1442	1439
318	Modoc Plateau	United States	N. America	-1.14	-0.74	1432	561
319	Mono Lake	United States	N. America	-1.47	-0.98	2099	732
320	San Joaquin Valley	United States	N. America	0.13	-1.01	89	68
321	Santa Barbara County	United States	N. America	-2.56	-2.32	568	1037
322	Lake Tahoe	United States	N. America	-1.47	-0.98	2163	976
323	Yosemite National Park	United States	N. America	-1.47	-0.98	2425	1898
324	Grand Mesa	United States	N. America	-2.50	-0.45	2807	1452
325	Mesa Verde National Park	United States	N. America	-1.89	-0.85	2119	793
326	Pocatello	United States	N. America	-2.08	-0.79	1660	825
327	Cheyenne County	United States	N. America	-1.02	-0.60	1035	135
328	Republic County	United States	N. America	-0.90	-0.52	478	88
329	Carter County	United States	N. America	-1.92	-0.66	1030	105
330	Chadron	United States	N. America	-1.35	-0.65	1048	176
331	Wildcat Hills	United States	N. America	-1.69	-0.67	1319	315
332	Pembina Hills	United States	N. America	-2.51	-0.16	341	188
333	McCurtain County	United States	N. America	-0.40	-0.57	231	249
334	Harding County	United States	N. America	-1.55	-0.72	912	166
335	Minnehaha County	United States	N. America	-1.80	-0.51	467	79
336	Southern Culberson County	United States	N. America	0.04	-0.71	1374	463
337	Concepcion, Tucuman	Argentina	S. America	-0.28	2.89	309	60
338	Nahuel Huapi National Park	Argentina	S. America	-0.75	-1.14	878	1239
339	Tierra del Fuego	Argentina	S. America	-1.45	-1.25	119	201
340	Urundel, Salta	Argentina	S. America	0.94	1.25	315	173
341	Federal District	Brazil	S. America	2.15	0.12	1151	177
342	Sipaliwini	Surinam	S. America	3.62	-1.47	389	146
343	Fort Chimo	Quebec	N. America	-3.64	-1.56	69	157
344	Gamba	Gabon	Africa	2.47	1.05	52	55
345	Udzungwa Mountains	Tanzania	Africa	1.80	-0.45	1674	1806

Table 2.S 2 Species counts for ecological categories and Shannon diversity index values (H) for the 328 artiodactyl localities. N, total species richness; FR, frugivore; BR, browser; IM, browser-grazer intermediate; GN, generalist; VG, variable grazer; OG, obligate grazer; OM, omnivore; S1–S6, size class 1–size class 6.

Id	N	BR	FR	GN	IM	OG	VG	OM	S1	S2	S3	S4	S5	S6	H (diet)	H (size)
1	10	3	0	1	1	2	3	0	0	2	1	2	5	0	1.50	1.22
2	21	5	0	1	1	10	4	0	0	2	2	6	8	3	1.30	1.45
3	14	4	6	0	0	1	1	2	3	4	1	3	2	1	1.38	1.67
4	14	2	6	0	0	2	3	1	1	4	1	5	1	2	1.44	1.57
5	16	3	8	0	0	2	1	2	2	5	2	3	2	2	1.35	1.72
6	21	3	7	0	0	6	3	2	3	5	2	6	3	2	1.50	1.70
7	17	3	9	1	0	1	1	2	3	3	4	3	3	1	1.39	1.73
8	23	7	1	1	3	7	4	0	1	5	5	4	5	3	1.57	1.70
9	10	1	0	2	3	1	3	0	1	2	1	3	2	1	1.50	1.70
10	10	1	5	1	0	1	1	1	2	3	1	2	1	1	1.50	1.70
11	21	3	0	2	2	9	3	2	1	3	2	6	7	2	1.59	1.59
12	20	4	0	3	2	7	2	2	2	2	2	7	5	2	1.66	1.64
13	21	3	2	2	2	8	2	2	2	3	2	6	6	2	1.77	1.67
14	23	6	0	2	2	8	3	2	2	3	2	7	6	3	1.62	1.67
15	7	1	5	0	0	0	0	1	2	2	1	2	0	0	0.80	1.35
17	9	1	0	1	2	3	2	0	0	1	2	3	1	2	1.52	1.52
18	13	2	5	1	0	3	1	1	2	2	2	4	1	2	1.59	1.71
19	15	3	1	0	1	7	3	0	0	3	2	3	4	3	1.36	1.59
20	21	3	2	1	1	7	4	3	0	5	3	7	4	2	1.75	1.53
21	12	2	0	1	1	4	3	1	0	3	2	3	2	2	1.63	1.59
22	4	2	0	0	0	0	2	0	0	1	1	2	0	0	0.69	1.04
23	14	4	0	0	1	5	4	0	0	3	3	4	3	1	1.27	1.54
24	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0.00	0.00
25	9	3	0	0	1	4	1	0	0	2	1	1	5	0	1.21	1.15
26	13	5	0	0	1	5	2	0	0	3	3	1	4	2	1.22	1.52
27	26	6	1	3	2	9	3	2	1	5	4	7	6	3	1.72	1.67
28	20	5	1	3	2	6	1	2	1	4	3	5	4	3	1.75	1.71
29	16	4	1	2	1	4	2	2	0	5	3	5	2	1	1.82	1.47
30	9	5	0	1	2	1	0	0	0	2	3	0	3	1	1.15	1.31
31	7	4	0	0	0	2	1	0	0	2	0	1	3	1	0.96	1.28
32	23	6	0	2	2	8	5	0	0	3	4	5	10	1	1.47	1.40
33	23	6	0	3	2	9	1	2	2	3	2	6	7	3	1.54	1.67
34	16	5	0	2	2	3	2	2	1	3	3	5	4	0	1.72	1.51
35	7	4	0	0	0	3	0	0	0	2	2	1	2	0	0.68	1.35
36	16	5	0	2	1	4	2	2	0	3	3	5	4	1	1.66	1.51
37	3	1	0	1	1	0	0	0	0	1	0	0	2	0	1.10	0.64
38	28	6	1	2	2	11	4	2	2	4	4	8	7	3	1.66	1.69
39	28	6	1	1	3	10	5	2	2	5	4	8	6	3	1.67	1.70
40	15	3	2	0	0	6	3	1	1	3	2	5	1	3	1.46	1.64
41	16	3	2	0	0	7	3	1	1	3	2	5	2	3	1.42	1.68
42	17	3	2	1	0	6	3	2	1	3	1	6	5	1	1.65	1.53
43	18	3	2	1	0	8	2	2	1	2	1	7	5	2	1.55	1.53
44	6	1	3	0	0	1	0	1	0	2	1	1	1	1	1.24	1.56
45	22	5	4	1	0	6	3	3	2	4	2	8	4	2	1.68	1.64
46	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0.00	0.00
47	4	0	0	1	1	0	1	1	0	0	2	1	0	1	1.39	1.04
48	4	0	0	1	1	0	1	1	0	0	2	1	0	1	1.39	1.04
49	5	0	0	1	2	0	1	1	0	0	3	1	0	1	1.33	0.95
50	3	0	0	1	1	0	1	0	0	0	2	1	0	0	1.10	0.64
51	4	0	0	1	2	0	1	0	0	0	3	1	0	0	1.04	0.56
52	4	0	0	1	1	0	2	0	0	0	2	2	0	0	1.04	0.69
53	20	3	0	1	2	10	3	1	1	2	2	6	7	2	1.45	1.57
54	15	4	1	3	2	3	1	1	2	4	3	4	1	1	1.81	1.66
55	16	4	1	2	0	7	1	1	1	3	1	4	5	2	1.49	1.63
56	15	3	0	2	2	6	1	1	2	2	2	4	3	2	1.59	1.75
67	4	2	0	0	0	0	1	1	0	0	2	0	1	1	1.04	1.04
68	5	2	0	0	1	0	1	1	0	0	1	0	2	2	1.33	1.05
69	8	2	1	1	1	0	2	1	1	0	1	2	1	3	1.73	1.49
70	6	2	0	0	2	0	1	1	0	0	1	1	2	2	1.33	1.33
71	3	2	0	0	1	0	0	0	0	0	1	0	2	0	0.64	0.64
72	4	1	0	0	2	0	0	1	0	0	1	1	1	1	1.04	1.39

73	4	1	0	0	1	0	1	1	0	1	1	0	1	1	1.39	1.39
74	5	2	0	0	1	0	1	1	0	0	2	0	2	1	1.33	1.05
75	8	2	2	1	0	0	1	2	2	0	1	2	1	2	1.56	1.56
76	6	0	0	0	3	0	2	1	0	1	2	1	1	1	1.01	1.56
77	7	2	2	1	0	0	1	1	2	0	2	1	1	1	1.55	1.55
78	10	2	2	1	0	0	4	1	2	0	1	2	1	4	1.47	1.47
79	6	2	0	0	1	0	2	1	0	0	2	0	2	2	1.33	1.10
80	5	1	0	0	1	0	2	1	0	0	2	1	1	1	1.33	1.33
81	3	1	0	0	0	0	1	1	0	0	1	0	1	1	1.10	1.10
82	4	1	0	0	1	0	1	1	0	0	1	1	1	1	1.39	1.39
83	6	1	1	1	0	0	2	1	1	0	2	0	1	2	1.56	1.33
84	6	1	1	1	1	0	1	1	1	0	2	1	1	1	1.79	1.56
85	4	1	1	1	0	0	0	1	1	0	1	0	1	1	1.39	1.39
86	3	1	0	1	0	0	0	1	0	0	1	0	1	1	1.10	1.10
87	6	2	0	0	2	0	1	1	0	0	1	1	2	2	1.33	1.33
88	5	2	0	0	1	0	1	1	0	0	2	0	2	1	1.33	1.05
89	4	1	0	0	1	0	1	1	0	0	1	0	1	2	1.39	1.04
90	5	1	0	0	2	0	1	1	0	1	1	2	0	1	1.33	1.33
91	7	2	0	0	1	0	3	1	0	0	2	1	2	2	1.28	1.35
92	9	3	0	0	2	0	3	1	0	0	4	1	2	2	1.31	1.27
93	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
94	6	3	0	0	1	0	1	1	0	0	2	0	2	2	1.24	1.10
95	4	1	0	0	2	0	0	1	0	0	2	0	1	1	1.04	1.04
96	4	1	0	0	1	0	1	1	0	0	1	0	1	2	1.39	1.04
97	5	1	0	0	2	0	1	1	0	0	1	1	1	2	1.33	1.33
98	4	2	0	0	1	0	0	1	1	1	1	0	0	1	1.04	1.39
99	8	3	0	1	2	0	1	1	1	0	3	2	1	1	1.49	1.49
100	3	1	0	0	1	0	1	0	0	1	1	1	0	0	1.10	1.10
101	7	2	2	1	0	0	1	1	2	0	2	1	1	1	1.55	1.55
102	8	5	0	0	1	0	1	1	0	1	3	2	1	1	1.07	1.49
103	5	1	0	0	1	0	2	1	0	1	1	2	0	1	1.33	1.33
104	2	1	0	0	0	0	1	0	0	0	1	1	0	0	0.69	0.69
105	4	2	0	0	1	0	1	0	0	1	1	2	0	0	1.04	1.04
106	6	2	2	1	0	0	0	1	2	0	1	2	1	0	1.33	1.33
107	6	2	2	1	0	0	0	1	2	0	1	2	1	0	1.33	1.33
108	4	0	2	1	0	0	0	1	2	0	0	1	1	0	1.04	1.04
109	8	3	0	0	0	0	4	1	0	1	2	2	1	2	0.97	1.56
110	11	3	0	1	1	0	5	1	0	1	3	2	2	3	1.37	1.55
111	5	2	0	1	0	0	1	1	0	0	1	1	1	2	1.33	1.33
112	7	4	0	1	1	0	0	1	2	0	2	1	1	1	1.15	1.55
113	3	1	0	0	0	0	1	1	0	0	1	0	1	1	1.10	1.10
114	5	1	0	0	1	0	3	0	0	1	1	1	1	1	0.95	1.61
115	7	4	0	0	1	0	1	1	1	0	3	1	1	1	1.15	1.48
116	7	5	0	0	1	0	0	1	2	1	2	1	0	1	0.80	1.55
117	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0.00	0.00
118	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0.00	0.00
119	2	1	0	0	0	0	0	1	0	0	1	0	0	1	0.69	0.69
120	5	3	0	0	1	0	0	1	1	0	2	1	0	1	0.95	1.33
121	4	2	0	0	0	0	1	1	0	1	0	0	2	1	1.04	1.04
122	9	6	0	1	1	0	0	1	2	1	2	1	2	1	1.00	1.74
123	4	2	0	0	0	0	2	0	0	0	0	3	1	0	0.69	0.56
124	4	2	0	0	1	0	1	0	0	0	0	2	2	0	1.04	0.69
125	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
126	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
127	4	2	0	0	0	0	2	0	0	0	1	2	1	0	0.69	1.04
128	2	1	0	0	0	0	1	0	0	0	1	1	0	0	0.69	0.69
129	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
130	2	0	1	0	0	0	0	1	0	0	2	0	0	0	0.69	0.00
131	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
132	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
133	5	3	0	0	0	0	2	0	0	0	1	2	1	1	0.67	1.33
135	3	1	0	0	0	0	2	0	0	0	0	1	1	1	0.64	1.10
136	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
137	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
138	3	1	0	0	0	0	0	2	0	0	2	1	0	0	0.64	0.64
139	3	1	0	0	0	0	2	0	0	0	0	1	1	1	0.64	1.10
140	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
141	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
142	3	1	0	0	0	0	2	0	0	0	0	2	1	0	0.64	0.64

143	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
144	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
145	4	1	1	0	0	0	0	2	0	0	3	1	0	0	1.04	0.56
146	3	2	0	0	0	0	1	0	0	0	1	1	1	0	0.64	1.10
147	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
148	6	3	0	0	0	0	2	1	0	0	2	3	0	1	1.01	1.01
149	7	3	0	0	0	0	3	1	0	0	2	3	1	1	1.00	1.28
150	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
151	5	3	0	0	0	0	2	0	0	0	1	3	0	1	0.67	0.95
152	3	3	0	0	0	0	0	0	0	0	0	2	1	0	0.00	0.64
153	6	3	0	0	0	0	3	0	0	0	1	3	1	1	0.69	1.24
154	7	4	0	0	0	0	3	0	0	0	0	5	2	0	0.68	0.60
155	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
156	5	3	0	0	0	0	2	0	0	0	1	3	1	0	0.67	0.95
157	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
158	7	4	0	0	0	0	3	0	0	0	1	3	2	1	0.68	1.28
159	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
160	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
161	7	4	0	0	0	0	3	0	0	0	1	3	2	1	0.68	1.28
162	4	1	1	0	0	0	0	2	0	0	3	1	0	0	1.04	0.56
163	4	1	1	0	0	0	0	2	0	0	3	1	0	0	1.04	0.56
164	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1.10	0.64
165	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1.10	0.64
166	4	1	1	0	0	0	0	2	0	0	3	1	0	0	1.04	0.56
167	3	2	0	0	0	0	1	0	0	0	0	1	2	0	0.64	0.64
168	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0.69	0.69
169	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
170	4	3	0	0	0	0	1	0	0	0	0	2	1	1	0.56	1.04
171	4	2	0	0	0	0	2	0	0	0	0	2	1	1	0.69	1.04
172	6	4	0	0	0	0	2	0	0	0	0	3	2	1	0.64	1.01
173	4	2	0	0	0	0	2	0	0	0	0	1	2	1	0.69	1.04
174	4	3	0	0	0	0	0	1	0	0	2	2	0	0	0.56	0.69
175	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1.10	0.64
176	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
177	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
178	3	2	0	0	0	0	0	1	0	0	2	1	0	0	0.64	0.64
179	6	4	0	0	0	0	2	0	0	0	1	2	2	1	0.64	1.33
180	2	0	1	0	0	0	0	1	0	0	2	0	0	0	0.69	0.00
181	4	0	0	1	1	0	0	2	0	0	3	0	1	0	1.04	0.56
182	4	0	2	0	0	0	0	2	0	1	3	0	0	0	0.69	0.56
183	2	0	0	0	1	0	1	0	0	0	1	0	1	0	0.69	0.69
184	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0.00	0.00
185	2	0	1	0	1	0	0	0	0	1	1	0	0	0	0.69	0.69
186	4	0	2	0	0	0	0	2	0	1	3	0	0	0	0.69	0.56
187	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
188	4	0	2	0	0	0	0	2	0	1	3	0	0	0	0.69	0.56
189	3	0	1	0	0	0	0	2	0	0	3	0	0	0	0.64	0.00
190	4	1	2	0	0	0	0	1	0	1	2	1	0	0	1.04	1.04
191	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0.69	0.69
192	4	1	2	0	0	0	0	1	0	1	2	1	0	0	1.04	1.04
193	2	0	1	0	1	0	0	0	0	1	1	0	0	0	0.69	0.69
194	4	0	2	0	0	0	0	2	0	1	3	0	0	0	0.69	0.56
195	4	0	1	1	0	0	0	2	1	0	3	0	0	0	1.04	0.56
196	5	1	2	0	0	0	0	2	0	1	3	1	0	0	1.05	0.95
197	4	0	1	1	0	0	0	2	1	0	3	0	0	0	1.04	0.56
198	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0.00	0.00
199	4	1	0	0	2	0	1	0	0	0	1	2	1	0	1.04	1.04
200	4	0	2	0	0	0	0	2	0	1	3	0	0	0	0.69	0.56
201	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0.00	0.00
202	12	5	0	1	2	2	2	0	1	2	2	1	5	1	1.47	1.58
203	6	2	0	2	1	0	1	0	0	3	1	0	2	0	1.33	1.01
204	7	2	2	0	0	3	0	0	1	1	1	3	1	0	1.08	1.48
205	14	6	0	2	2	3	1	0	1	3	3	1	4	2	1.44	1.67
206	5	0	0	1	1	0	3	0	0	0	2	2	1	0	0.95	1.05
207	3	1	0	1	0	0	1	0	0	0	1	2	0	0	1.10	0.64
208	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0.00	0.00
209	6	0	0	1	1	0	3	1	0	0	2	2	1	1	1.24	1.33
210	4	1	0	0	2	0	0	1	0	0	1	1	1	1	1.04	1.39
211	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10

215	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0.00	0.00
216	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0.00	0.00
217	5	2	0	0	1	0	1	1	0	0	2	1	1	1	1.33	1.33
218	3	1	0	0	0	0	1	1	0	0	1	0	0	2	1.10	0.64
219	3	1	0	0	1	0	0	1	0	0	2	0	0	1	1.10	0.64
220	5	1	0	0	1	0	2	1	0	0	1	1	2	1	1.33	1.33
221	4	2	0	0	1	0	0	1	0	0	2	0	1	1	1.04	1.04
222	4	1	0	0	2	0	0	1	0	0	1	1	1	1	1.04	1.39
223	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
224	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
225	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
226	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0.00	0.00
227	4	1	0	0	2	0	0	1	0	0	1	1	1	1	1.04	1.39
228	6	1	0	0	2	0	2	1	0	0	2	1	1	2	1.33	1.33
229	4	1	0	0	2	0	0	1	0	0	2	0	1	1	1.04	1.04
230	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
231	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
232	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
233	3	1	0	0	0	0	1	1	0	0	1	0	0	2	1.10	0.64
234	4	1	0	0	1	0	1	1	0	0	1	0	1	2	1.39	1.04
235	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
236	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
237	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
238	4	1	0	0	1	0	1	1	0	0	2	0	1	1	1.39	1.04
239	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
240	5	1	0	0	2	0	1	1	0	0	3	0	1	1	1.33	0.95
241	3	1	0	0	1	0	0	1	0	0	1	0	1	1	1.10	1.10
243	6	2	0	0	1	0	2	1	0	0	2	1	2	1	1.33	1.33
245	6	2	0	0	2	0	1	1	0	0	1	1	2	2	1.33	1.33
246	5	2	0	0	1	0	1	1	0	0	1	0	2	2	1.33	1.05
247	7	2	0	0	2	0	2	1	0	0	1	1	3	2	1.35	1.28
248	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
249	7	3	0	0	2	0	1	1	0	0	3	0	2	2	1.28	1.08
250	5	3	0	0	0	0	1	1	0	1	1	0	2	1	0.95	1.33
251	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
252	4	3	0	0	0	0	1	0	0	1	0	2	1	0	0.56	1.04
253	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
254	3	2	0	0	0	0	1	0	0	0	0	2	1	0	0.64	0.64
255	4	2	0	0	0	0	1	1	0	0	1	0	2	1	1.04	1.04
256	6	4	0	0	0	0	1	1	0	1	1	1	2	1	0.87	1.56
257	4	3	0	0	0	0	0	1	0	0	1	1	1	1	0.56	1.39
258	4	4	0	0	0	0	0	0	0	1	1	1	1	0	0.00	1.39
259	3	1	0	0	1	0	0	1	0	0	1	1	0	1	1.10	1.10
260	5	1	0	0	3	0	0	1	0	0	1	2	1	1	0.95	1.33
261	5	1	0	0	3	0	0	1	0	0	1	2	1	1	0.95	1.33
262	5	1	0	0	3	0	0	1	0	0	1	2	1	1	0.95	1.33
263	3	0	0	0	2	0	0	1	0	0	1	0	1	1	0.64	1.10
264	4	0	0	1	1	0	1	1	0	0	2	1	0	1	1.39	1.04
265	4	0	0	1	1	0	2	0	0	0	2	2	0	0	1.04	0.69
266	5	0	0	1	2	0	2	0	0	0	3	2	0	0	1.05	0.67
267	11	2	0	0	1	7	1	0	0	1	1	3	4	2	1.03	1.47
268	11	1	7	0	0	1	1	1	1	5	1	3	0	1	1.16	1.37
269	4	1	0	1	1	0	1	0	1	0	2	1	0	0	1.39	1.04
270	7	2	0	1	0	1	2	1	0	3	2	2	0	0	1.55	1.08
271	14	3	0	1	1	6	2	1	1	1	3	4	3	2	1.54	1.67
272	13	3	0	3	2	1	3	1	1	3	3	2	3	1	1.70	1.70
273	17	4	0	2	2	5	3	1	1	3	4	4	3	2	1.68	1.71
274	6	2	0	1	0	2	1	0	0	2	1	1	1	1	1.33	1.56
275	14	5	0	3	2	1	2	1	2	2	4	3	3	0	1.63	1.57
276	13	5	0	1	2	3	2	0	2	0	3	3	2	3	1.48	1.59
277	16	4	0	2	2	6	2	0	1	1	3	4	4	3	1.49	1.67
278	11	2	0	2	0	4	2	1	0	3	2	3	1	2	1.52	1.55
279	15	3	0	2	2	5	2	1	0	3	3	5	3	1	1.67	1.51
280	10	3	0	2	0	2	2	1	0	4	2	2	1	1	1.56	1.47
281	15	2	0	2	2	6	2	1	1	3	2	4	3	2	1.62	1.71
282	4	0	0	1	1	0	1	1	0	0	2	1	0	1	1.39	1.04
283	4	0	0	1	1	0	1	1	0	0	2	1	0	1	1.39	1.04
284	3	0	0	0	2	0	1	0	0	0	2	1	0	0	0.64	0.64
285	3	0	0	0	1	0	1	1	0	0	1	1	0	1	1.10	1.10

286	3	0	0	1	1	0	0	1	0	0	2	0	0	1	1.10	0.64
287	2	0	0	0	1	0	0	1	0	0	1	0	0	1	0.69	0.69
288	13	5	0	2	2	2	2	0	1	3	2	1	4	2	1.52	1.67
289	12	2	1	0	0	7	2	0	0	3	2	3	2	2	1.12	1.59
290	7	1	3	0	0	1	0	2	0	2	1	2	1	1	1.28	1.55
291	6	1	0	1	2	1	1	0	0	0	3	1	1	1	1.56	1.24
292	14	4	0	2	1	5	1	1	0	1	2	4	5	2	1.57	1.47
293	16	4	7	0	0	2	1	2	2	5	1	3	3	2	1.40	1.68
294	6	1	3	0	0	0	0	2	0	2	1	2	1	0	1.01	1.33
295	3	0	1	0	0	0	0	2	0	0	3	0	0	0	0.64	0.00
296	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
297	3	3	0	0	0	0	0	0	0	0	0	2	1	0	0.00	0.64
298	2	2	0	0	0	0	0	0	0	0	0	1	1	0	0.00	0.69
299	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0.00	0.00
300	3	1	0	0	0	0	2	0	0	0	0	2	1	0	0.64	0.64
301	2	0	0	0	0	0	2	0	0	0	0	2	0	0	0.00	0.00
302	4	2	0	0	0	0	2	0	0	0	0	3	1	0	0.69	0.56
303	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0.00	0.00
304	2	2	0	0	0	0	0	0	0	0	0	1	1	0	0.00	0.69
305	4	3	0	0	0	0	1	0	0	0	0	3	1	0	0.56	0.56
306	2	2	0	0	0	0	0	0	0	0	0	2	0	0	0.00	0.00
307	2	1	0	0	0	0	1	0	0	0	0	2	0	0	0.69	0.00
308	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
309	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
310	3	2	0	0	0	0	0	1	0	0	1	2	0	0	0.64	0.64
311	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0.00	0.00
312	4	1	1	0	0	0	0	2	0	0	3	1	0	0	1.04	0.56
313	2	2	0	0	0	0	0	0	0	0	0	1	1	0	0.00	0.69
314	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
315	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
316	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
317	2	1	0	0	0	0	1	0	0	0	0	1	1	0	0.69	0.69
318	2	2	0	0	0	0	0	0	0	0	1	1	0	0	0.00	0.69
319	2	2	0	0	0	0	0	0	0	0	1	1	0	0	0.00	0.69
320	3	2	0	0	0	0	1	0	0	0	1	1	1	0	0.64	1.10
321	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
322	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
323	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
324	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
325	3	1	0	0	0	0	2	0	0	0	0	2	1	0	0.64	0.64
326	4	1	0	0	0	0	3	0	0	0	0	2	1	1	0.56	1.04
327	2	2	0	0	0	0	0	0	0	0	0	2	0	0	0.00	0.00
328	4	2	0	0	0	0	2	0	0	0	1	1	1	1	0.69	1.39
329	6	3	0	0	0	0	3	0	0	0	1	3	1	1	0.69	1.24
330	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
331	3	3	0	0	0	0	0	0	0	0	1	2	0	0	0.00	0.64
332	3	3	0	0	0	0	0	0	0	0	0	2	1	0	0.00	0.64
333	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
334	6	3	0	0	0	0	3	0	0	0	1	3	1	1	0.69	1.24
335	2	2	0	0	0	0	0	0	0	0	0	2	0	0	0.00	0.00
336	2	1	0	0	0	0	0	1	0	0	1	1	0	0	0.69	0.69
337	2	0	1	0	0	0	0	1	0	0	2	0	0	0	0.69	0.00
338	3	2	0	0	1	0	0	0	0	1	0	1	1	0	0.64	1.10
339	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0.00	0.00
340	2	0	2	0	0	0	0	0	0	1	1	0	0	0	0.00	0.69
341	4	0	1	0	1	0	0	2	0	0	4	0	0	0	1.04	0.00
342	5	1	2	0	0	0	0	2	0	1	3	1	0	0	1.05	0.95
343	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0.00	0.00
344	13	1	8	0	0	2	1	1	2	5	1	3	0	2	1.18	1.48
345	10	2	3	0	0	3	1	1	2	1	1	4	0	2	1.50	1.47

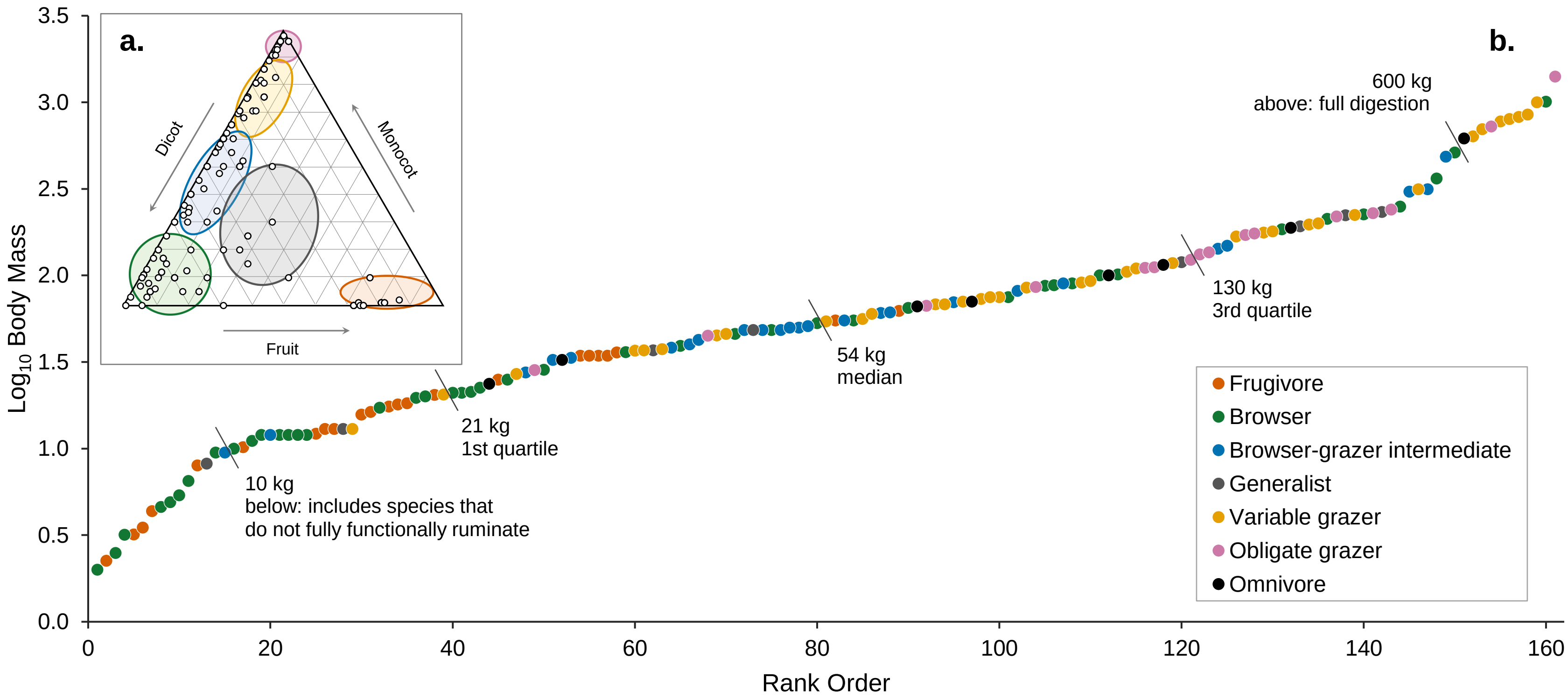


Figure 2.1 Two types of ecological data are used in this study: diet and body mass. (a) Classification of herbivorous artiodactyls into six categories based on percent consumption of fruits, dicots, and monocots following Gagnon and Chew (2000). Data points represent individual species. Circles roughly outline the boundaries of the six feeding categories. (b) Ranked log10-transformed body masses (in kg) of 161 artiodactyl species analyzed in this study, color coded by feeding category. Species are divided into six size classes based on physiological and statistical criteria. Diagonal lines indicate boundaries between size classes.

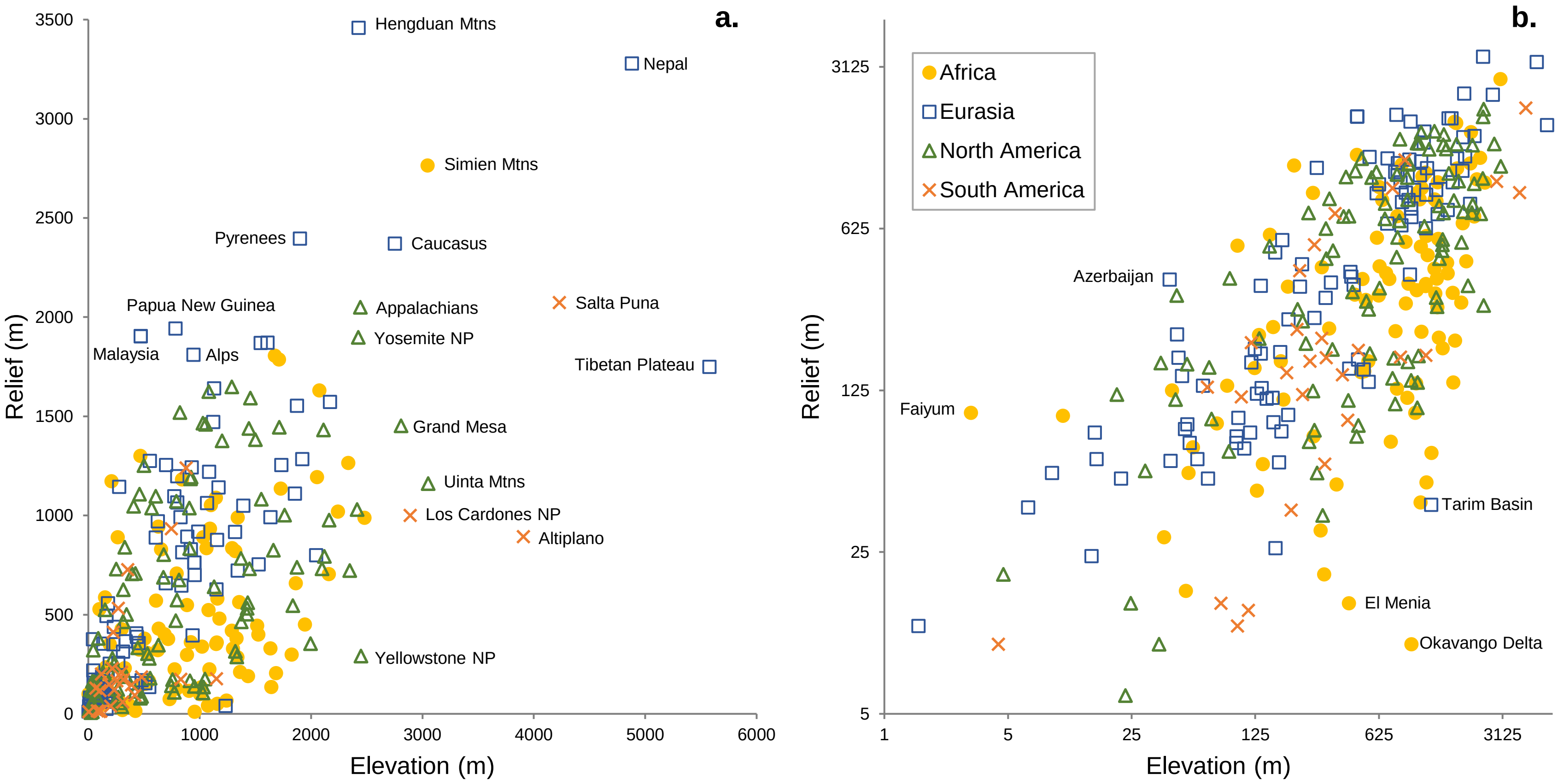


Figure 2.2 Mean elevation and local relief of localities are positively correlated ($r = 0.64$, $p < 0.001$, $N = 328$). Data computed for 50 km × 50 km grid cells centered on each locality. The two panels show data plotted on (a) a linear scale and (b) a logarithmic scale to highlight localities with very high and very low values, respectively.

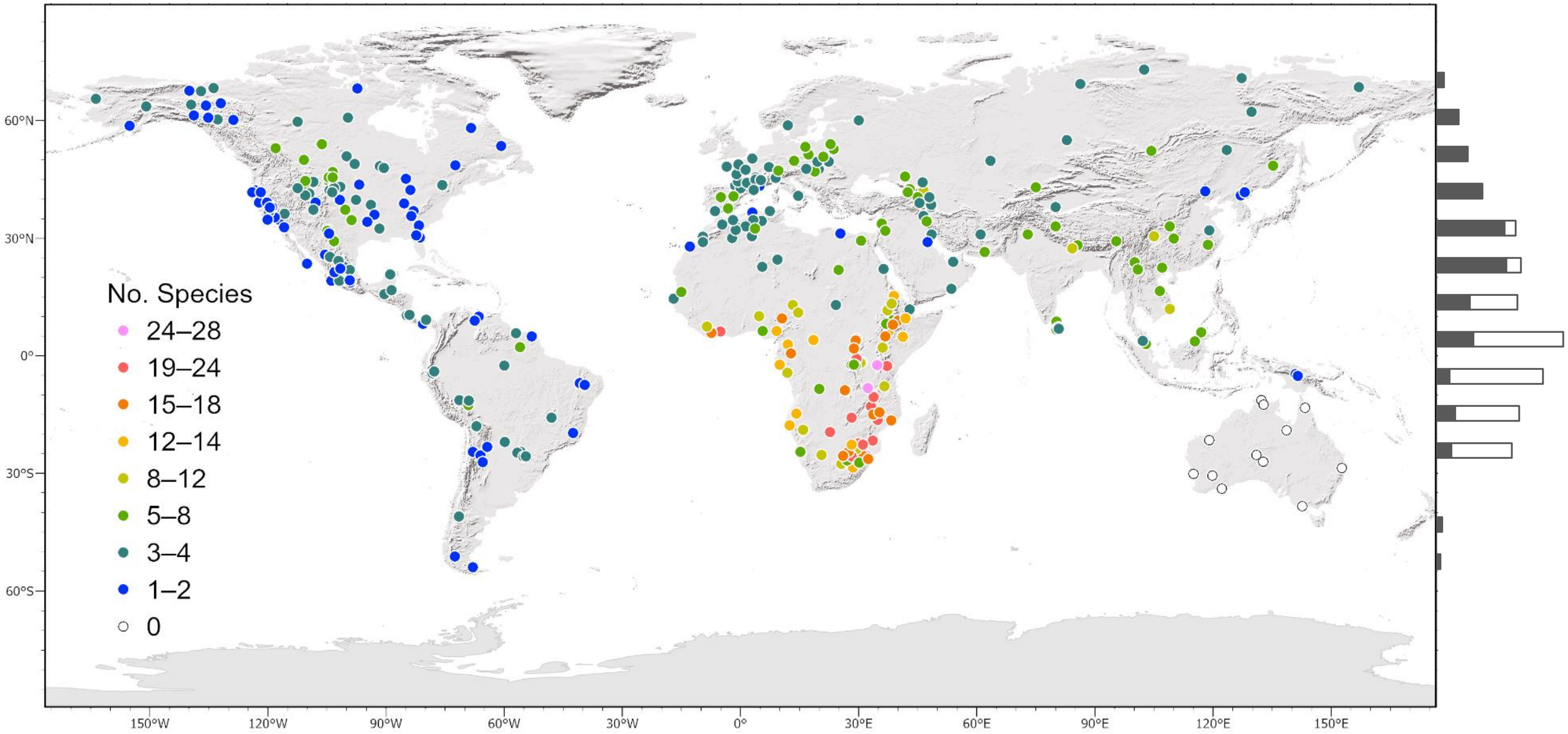


Figure 2.3 Species richness of artiodactyls in 342 mammal localities around the world. Subsequent analyses include 328 artiodactyl-bearing localities, as no native species occur in Australia. Histogram on the right axis represent the numbers of artiodactyl species occurring in 10˚ bands of latitude, showing a unimodal distribution with the highest richness occurring between the equator and 10˚N (N = 69). Open bars represent species that occur only in Africa.

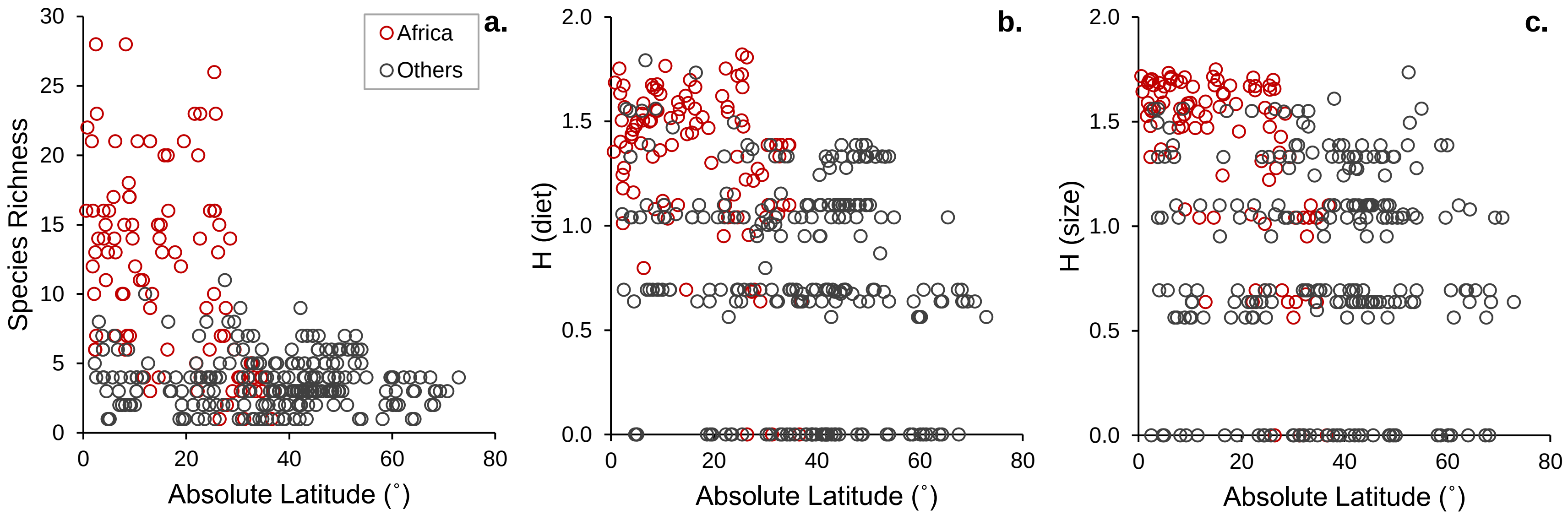


Figure 2.4 Latitudinal gradients of (a) species richness, (b) Shannon diversity index (H) of diet, and (c) Shannon diversity index (H) of size. Each data point represents a locality (N=328).

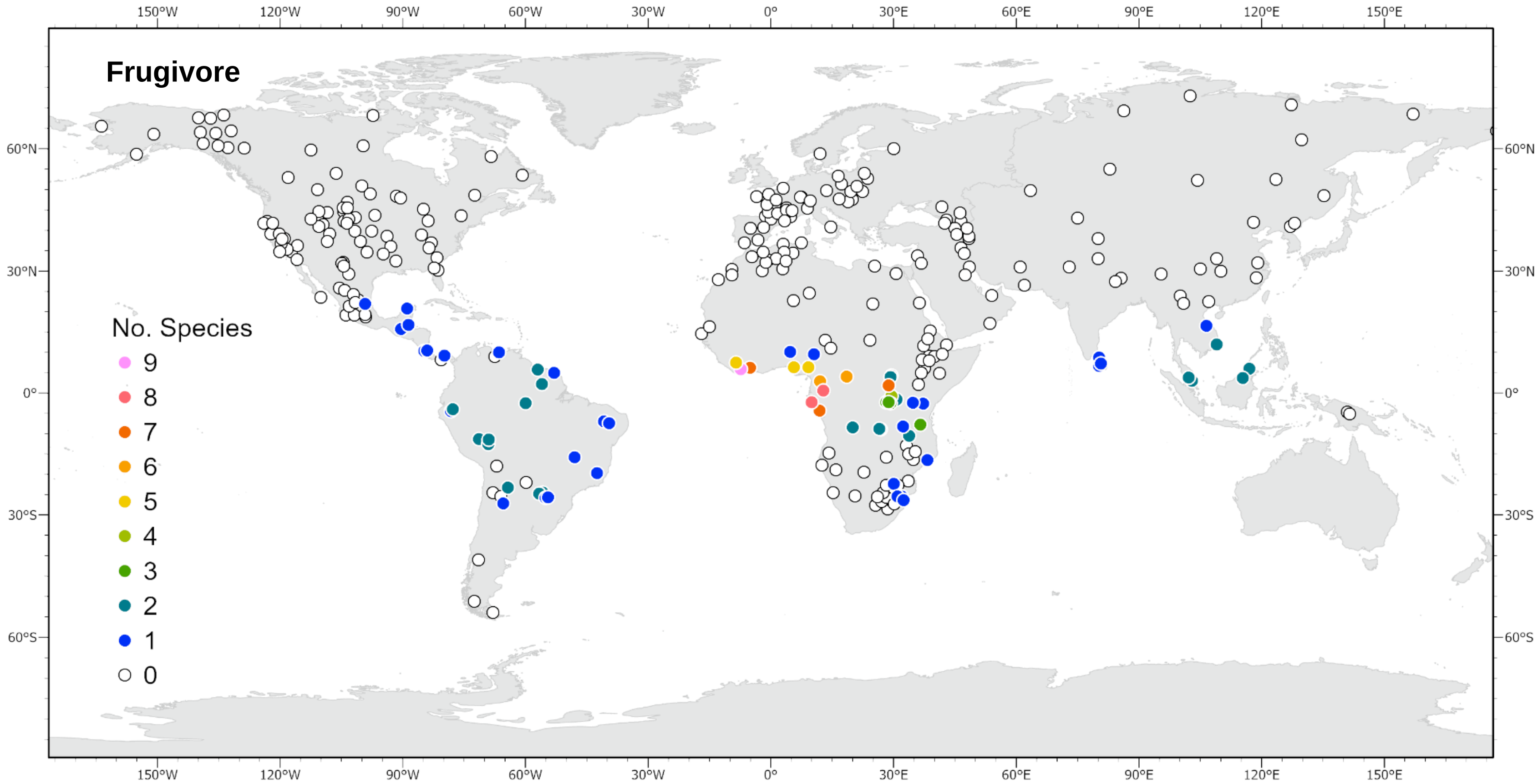


Figure 2.5 a Species richness pattern of frugivores.

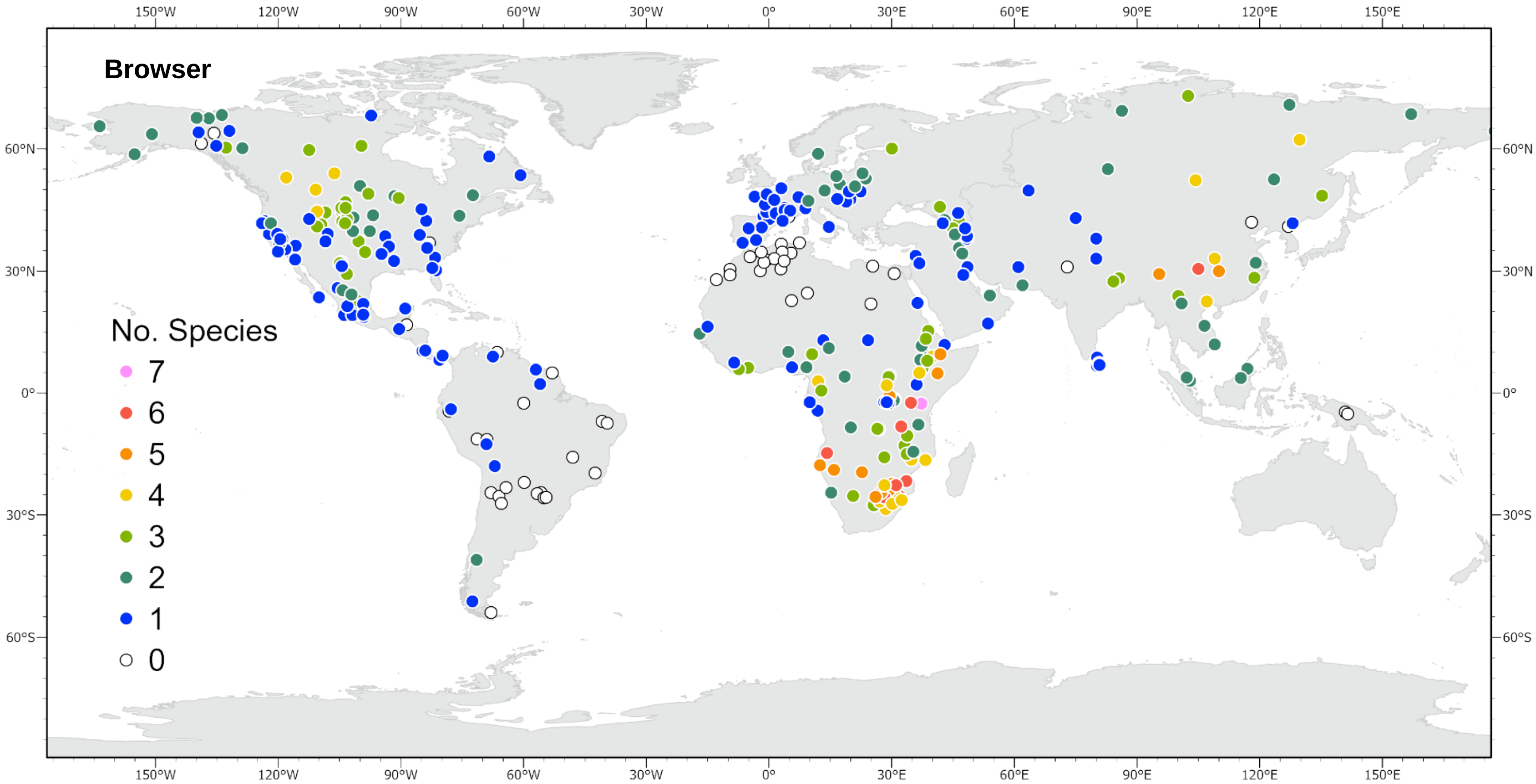


Figure 2.5 b Species richness pattern of browsers.

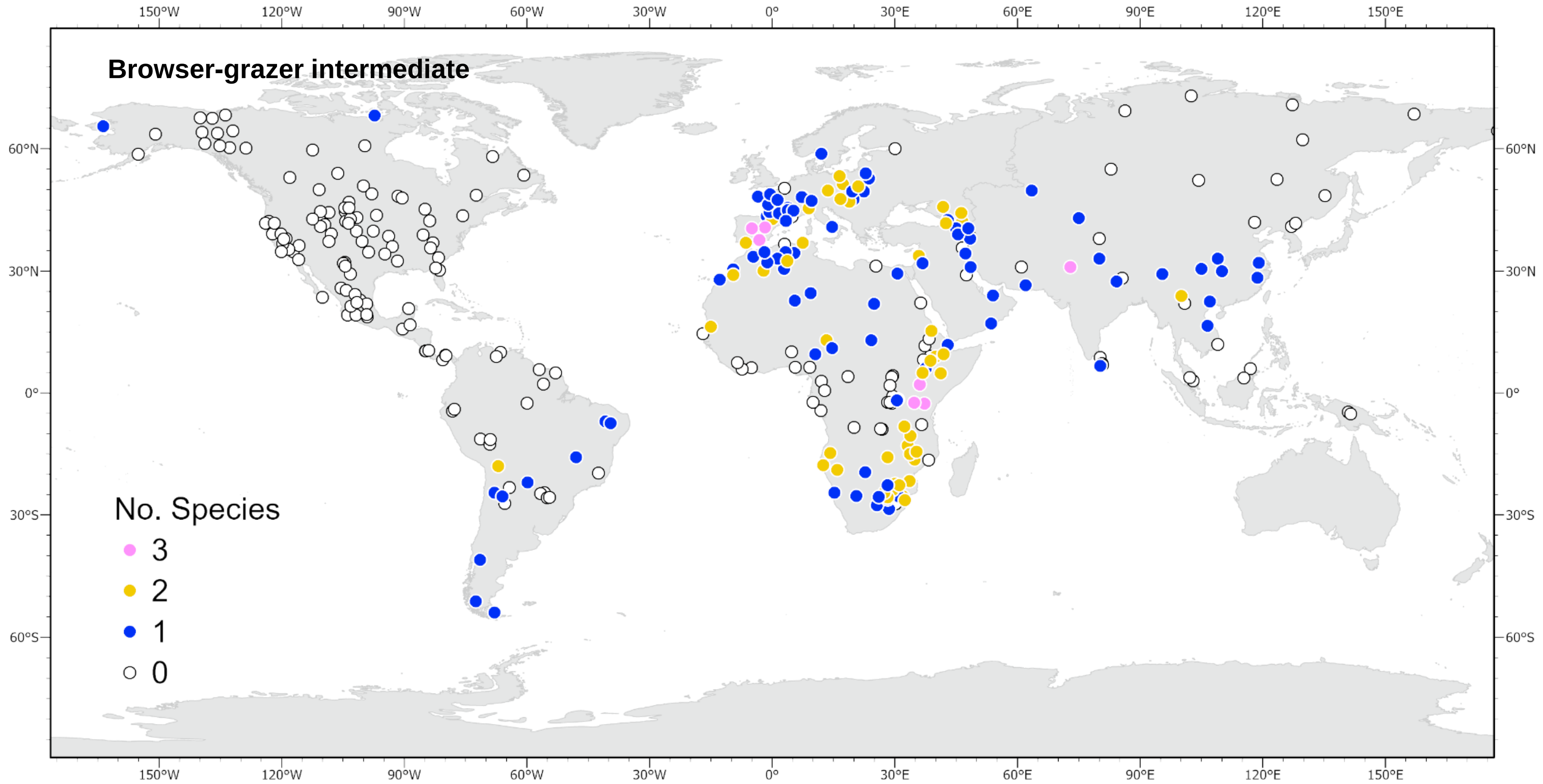


Figure 2.5 c Species richness pattern of browser-grazer intermediates.

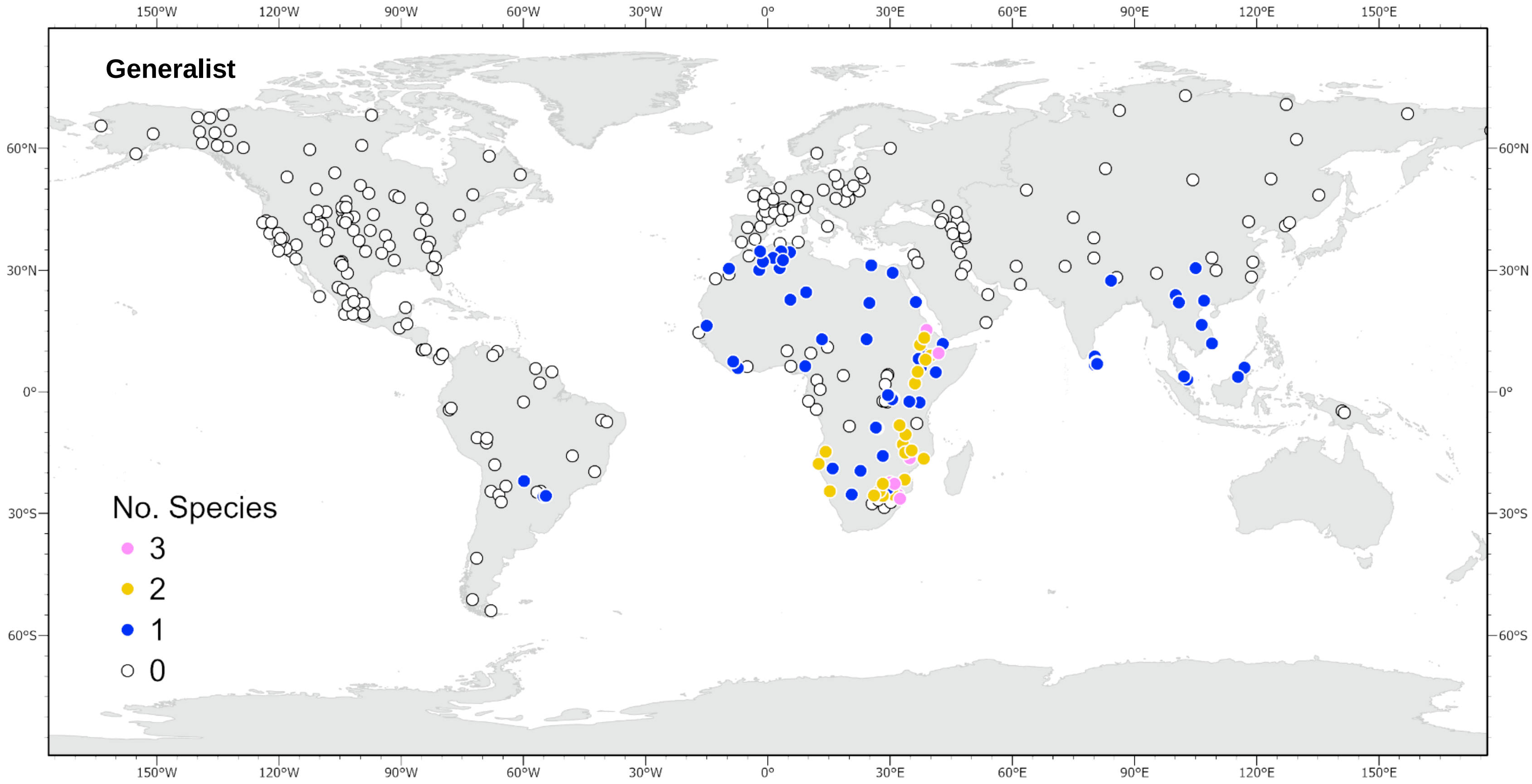


Figure 2.5 d Species richness pattern of generalists.

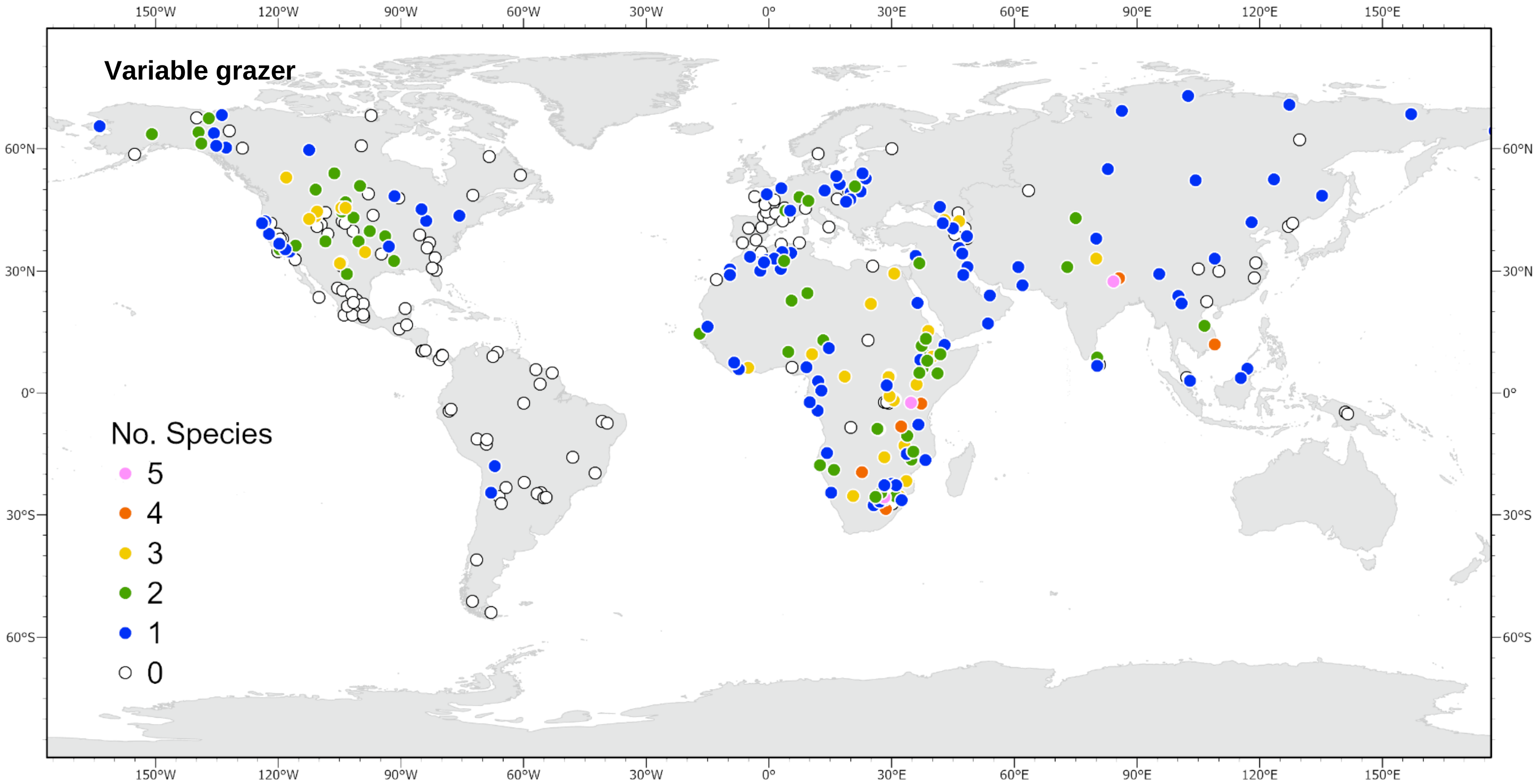


Figure 2.5 e Species richness pattern of variable grazers.

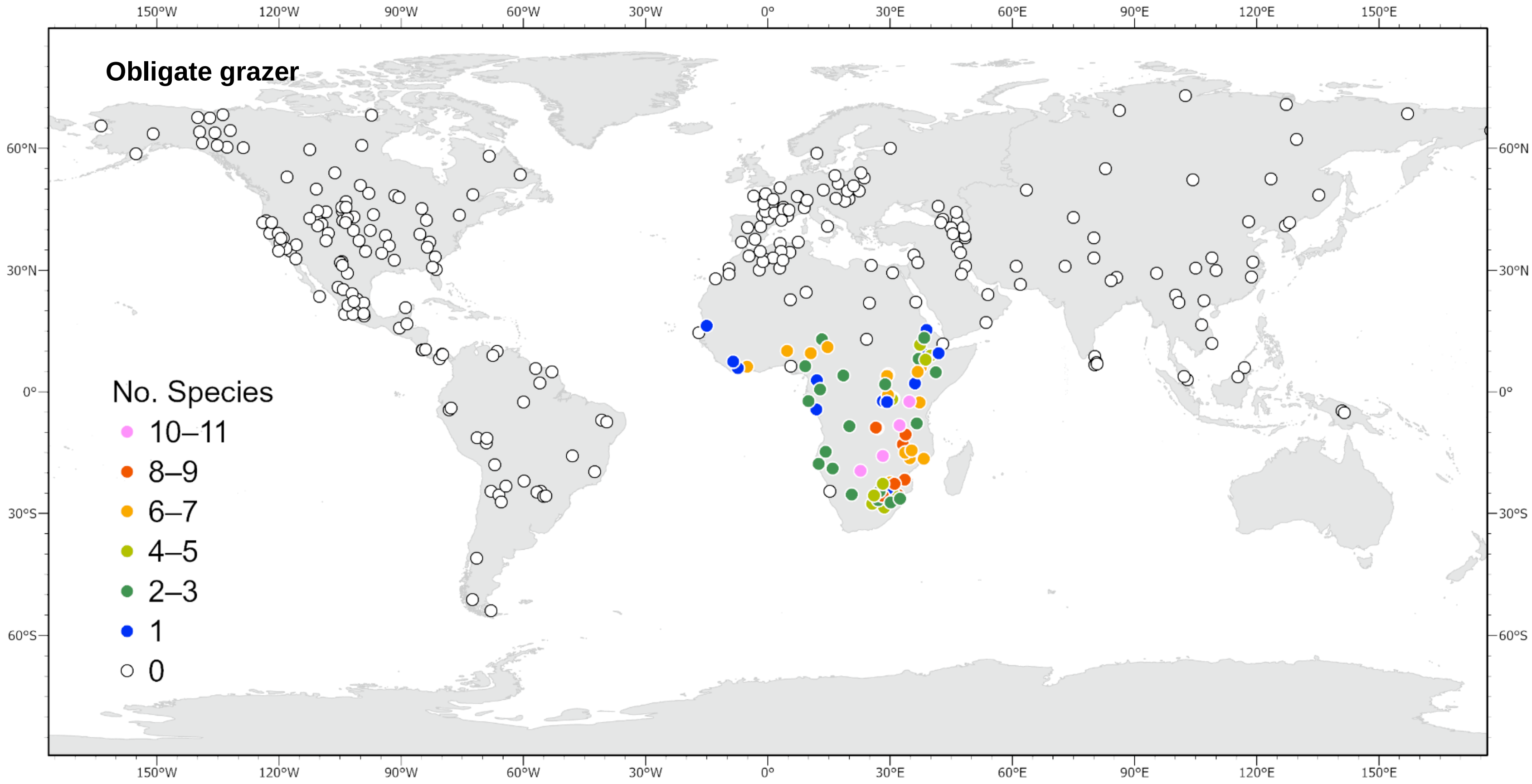


Figure 2.5 f Species richness pattern of obligate grazers.

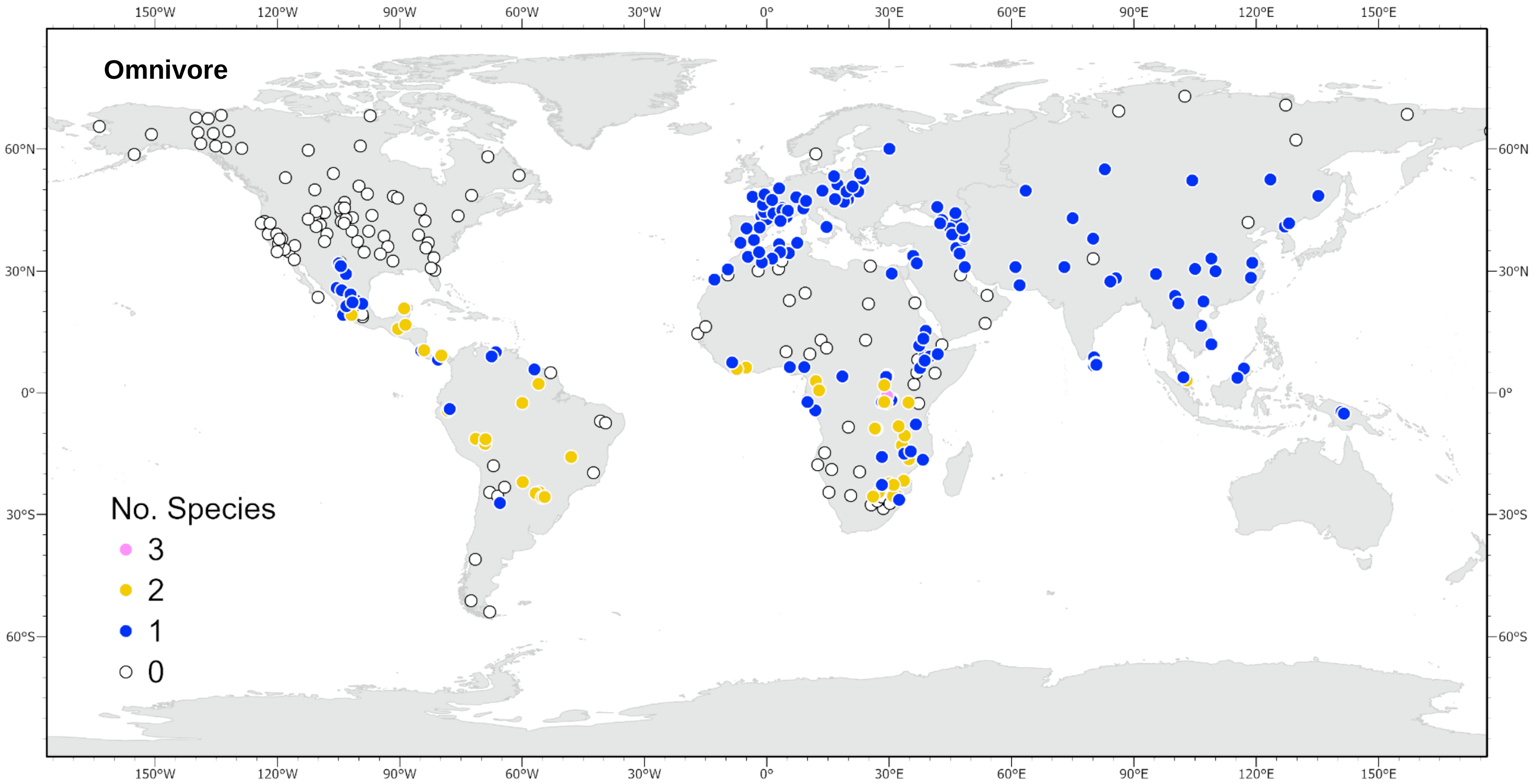


Figure 2.5 g Species richness pattern of omnivores.

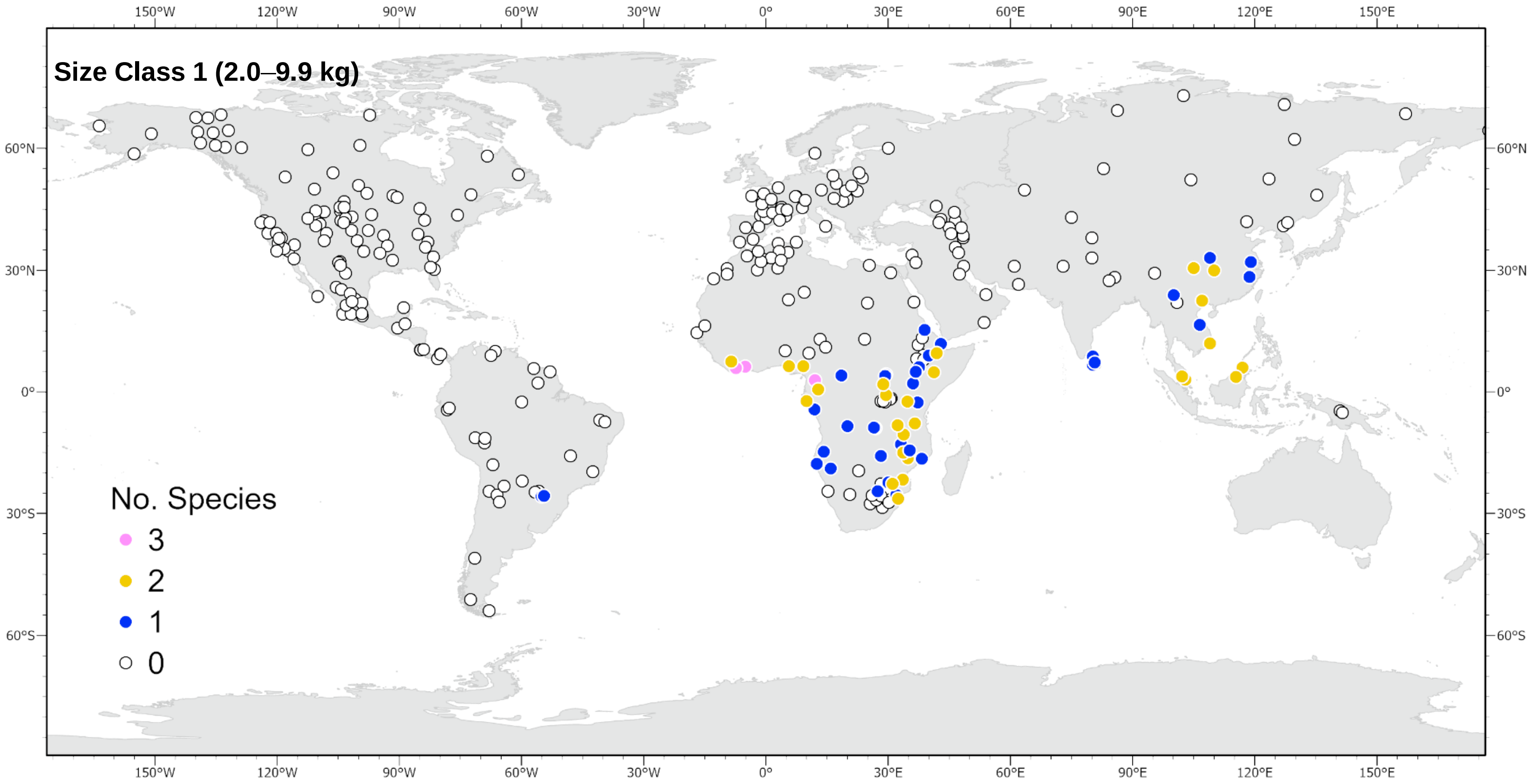


Figure 2.6 a Species richness pattern of size class 1.

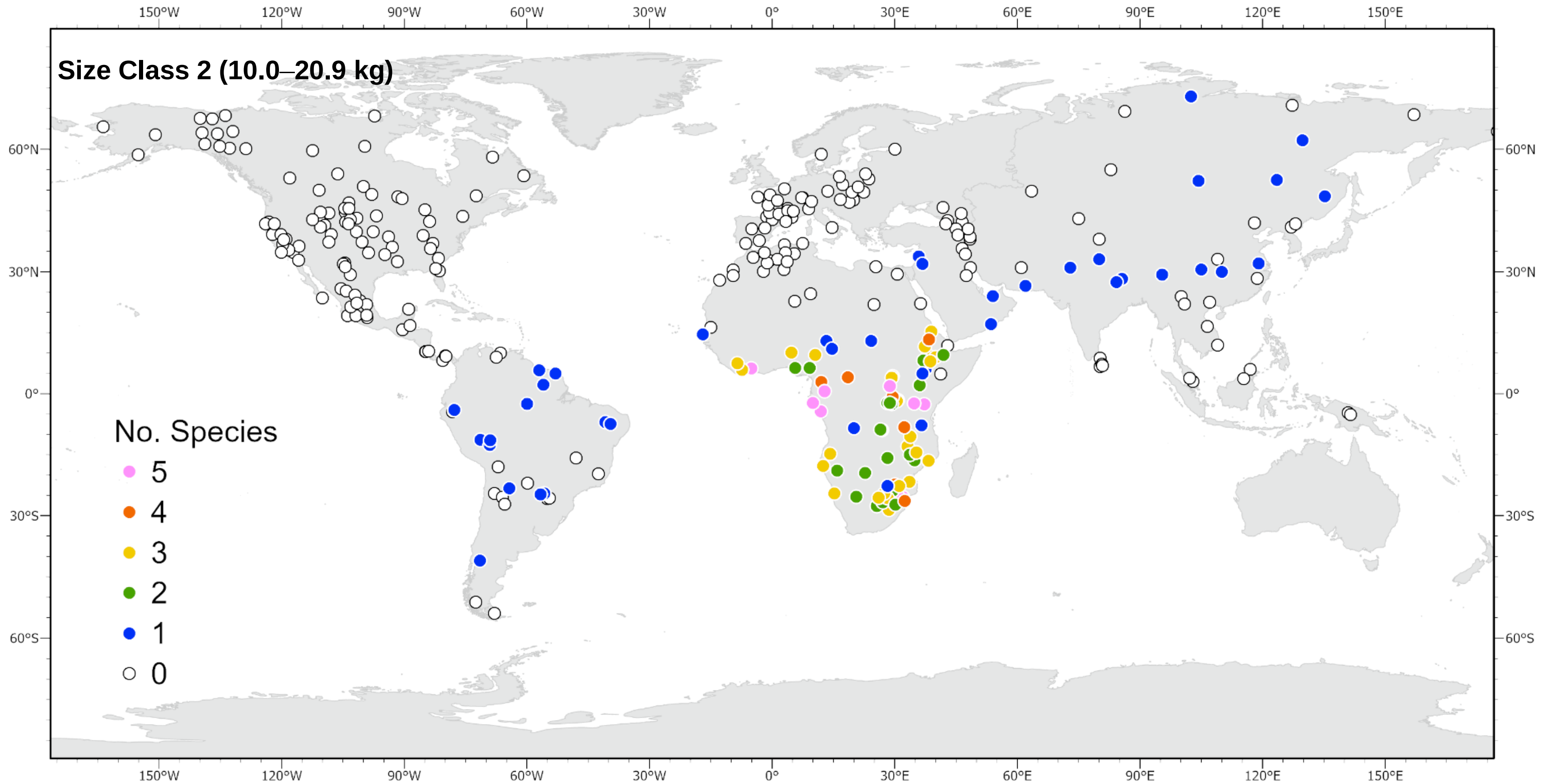


Figure 2.6 b Species richness pattern of size class 2.

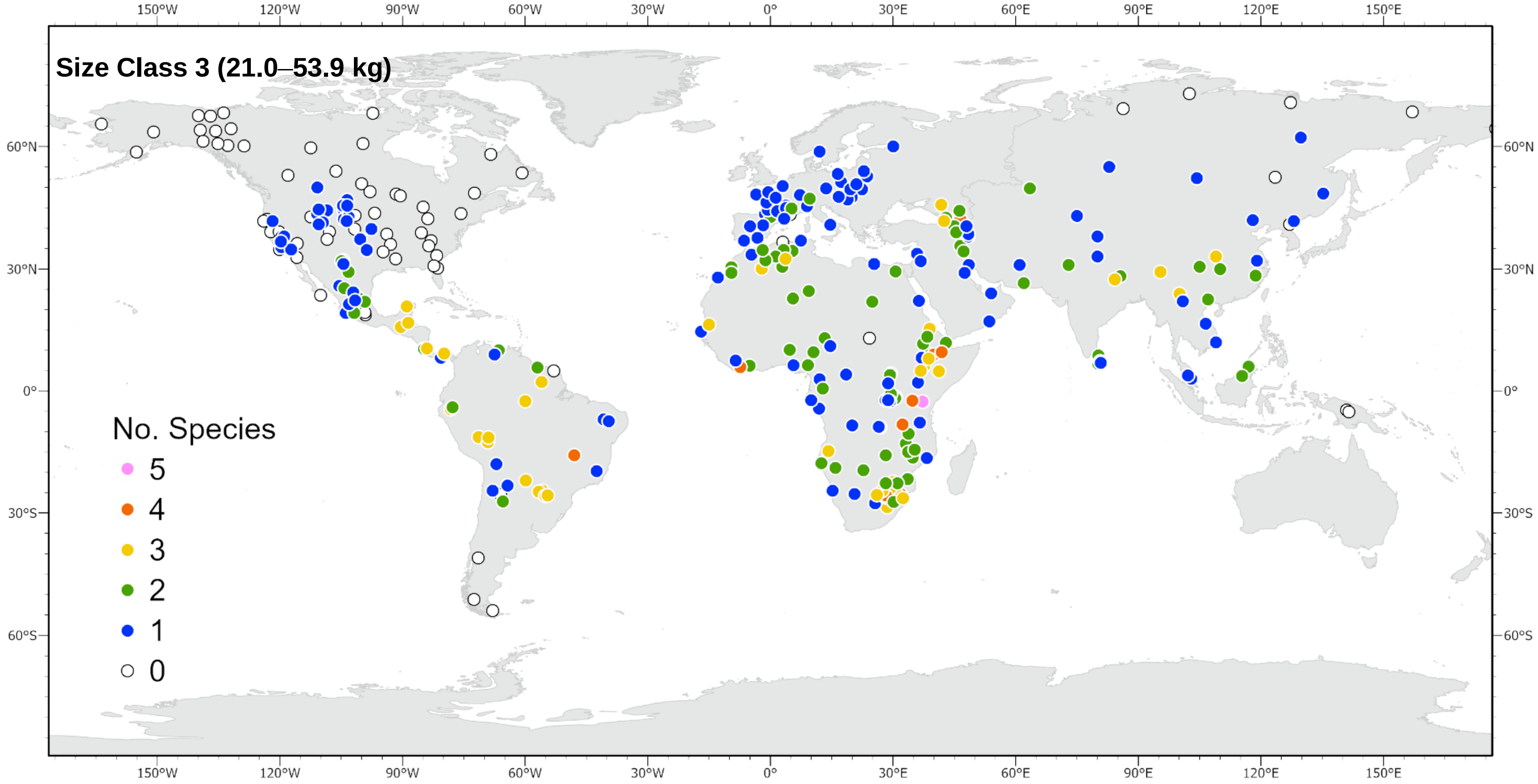


Figure 2.6 c Species richness pattern of size class 3.

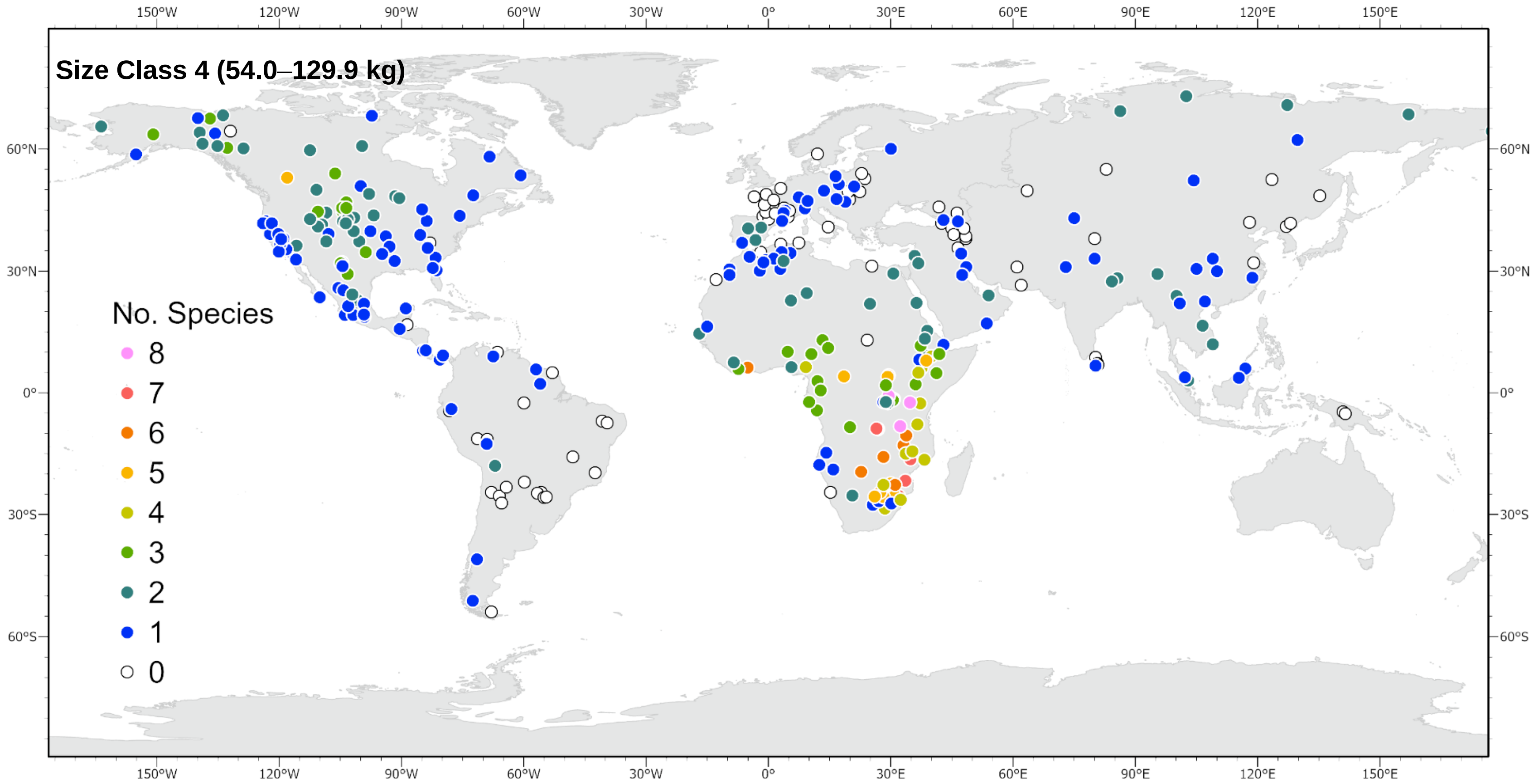


Figure 2.6 d Species richness pattern of size class 4.

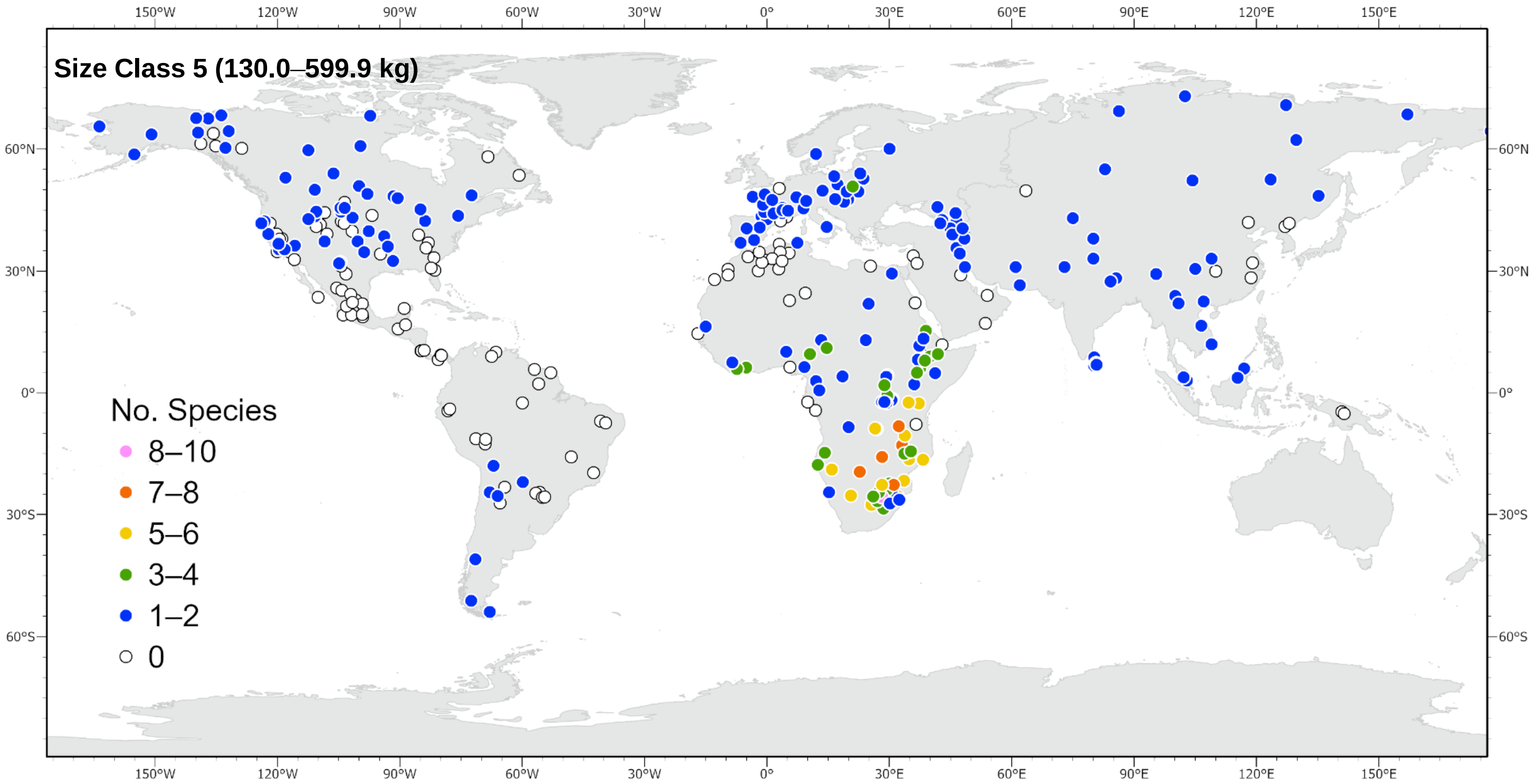


Figure 2.6 e Species richness pattern of size class 5.

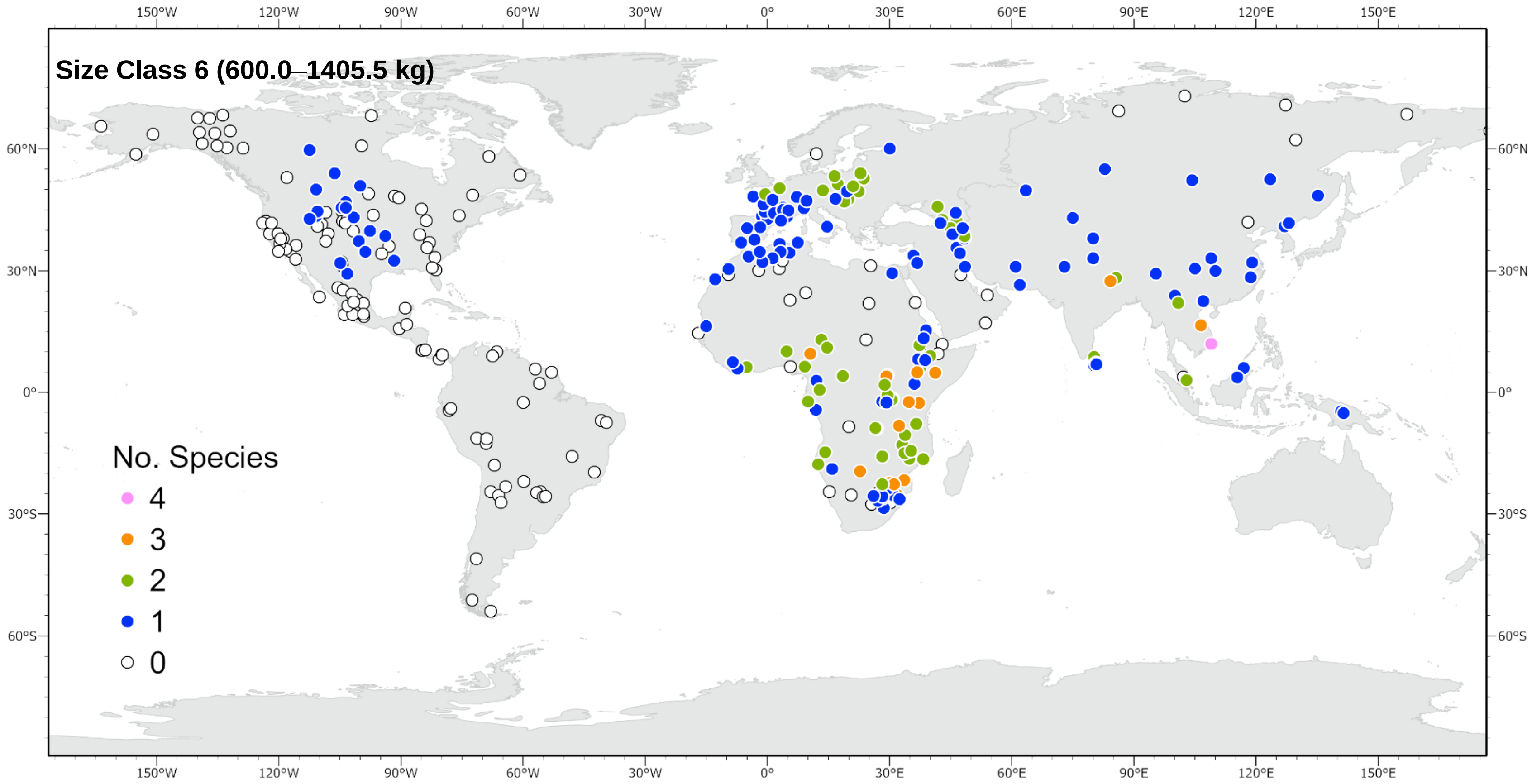


Figure 2.6 f Species richness pattern of size class 6.

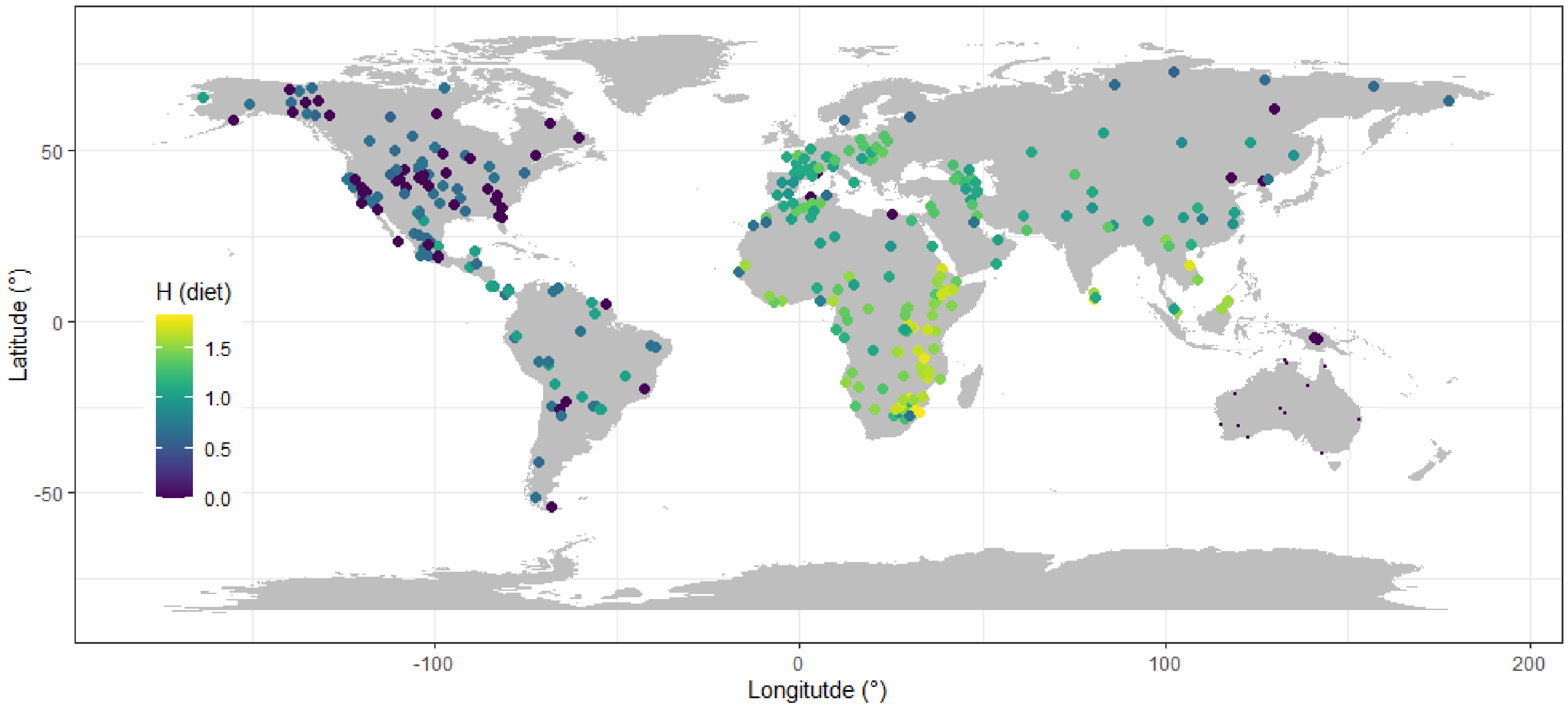


Figure 2.7 a Geographic pattern of Shannon diversity index (H) of diet.

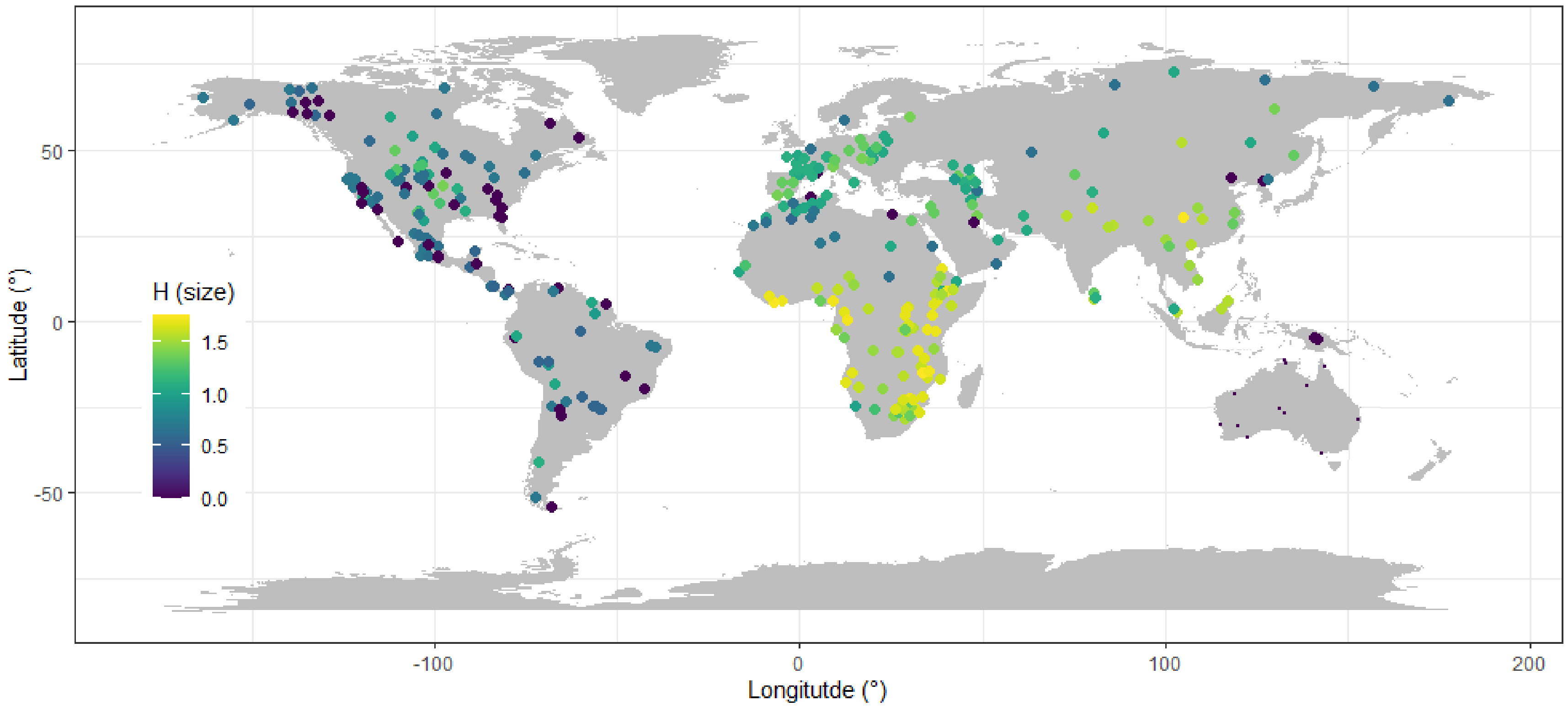


Figure 2.7 b Geographic pattern of Shannon diversity index (H) of size.

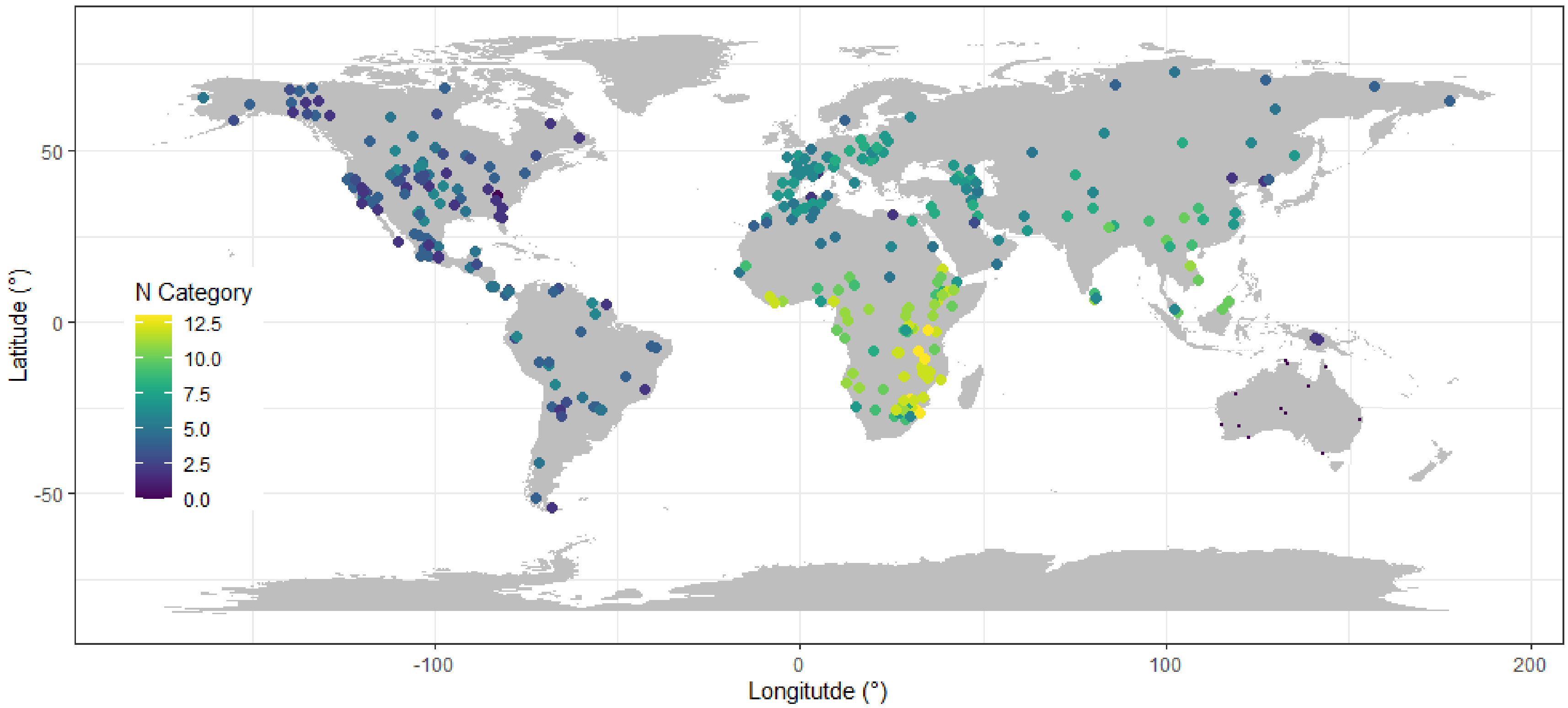


Figure 2.7 c Geographic pattern of the number of ecological categories occupied by artiodactyls.

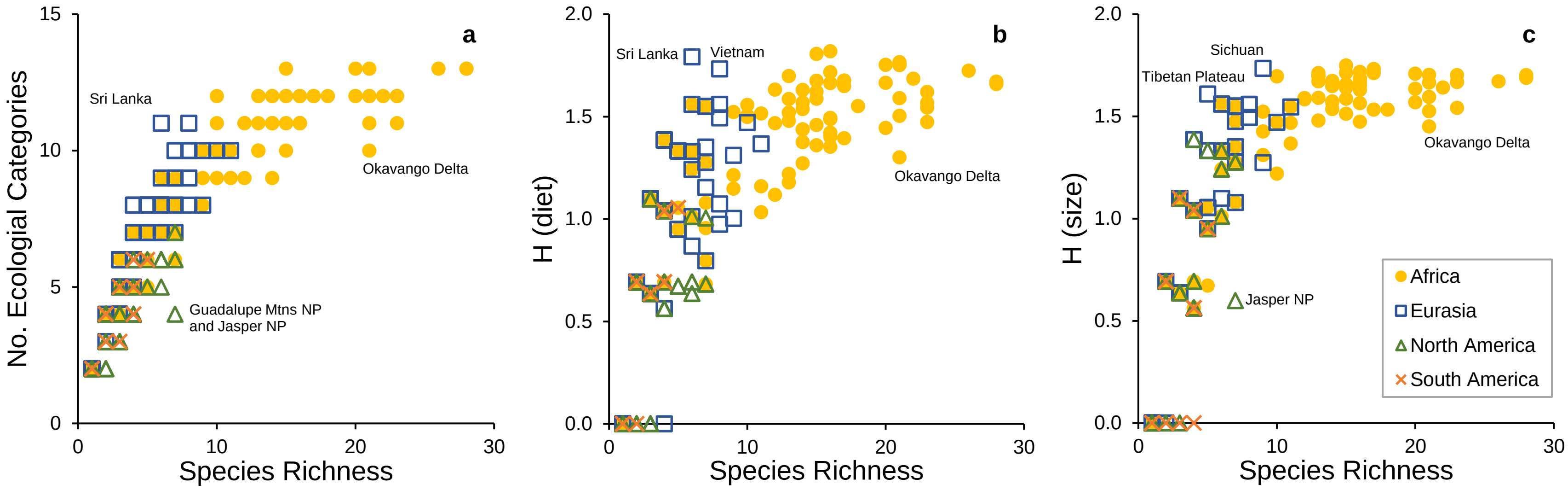


Figure 2.5 Artiodactyl species richness in relation to (a) number of ecological categories occupied, (b) Shannon diversity index (H) of diet, and (c) Shannon diversity index (H) of body size for 328 localities. High Shannon diversity indicates more coexisting species and more even distribution of species among ecological categories.

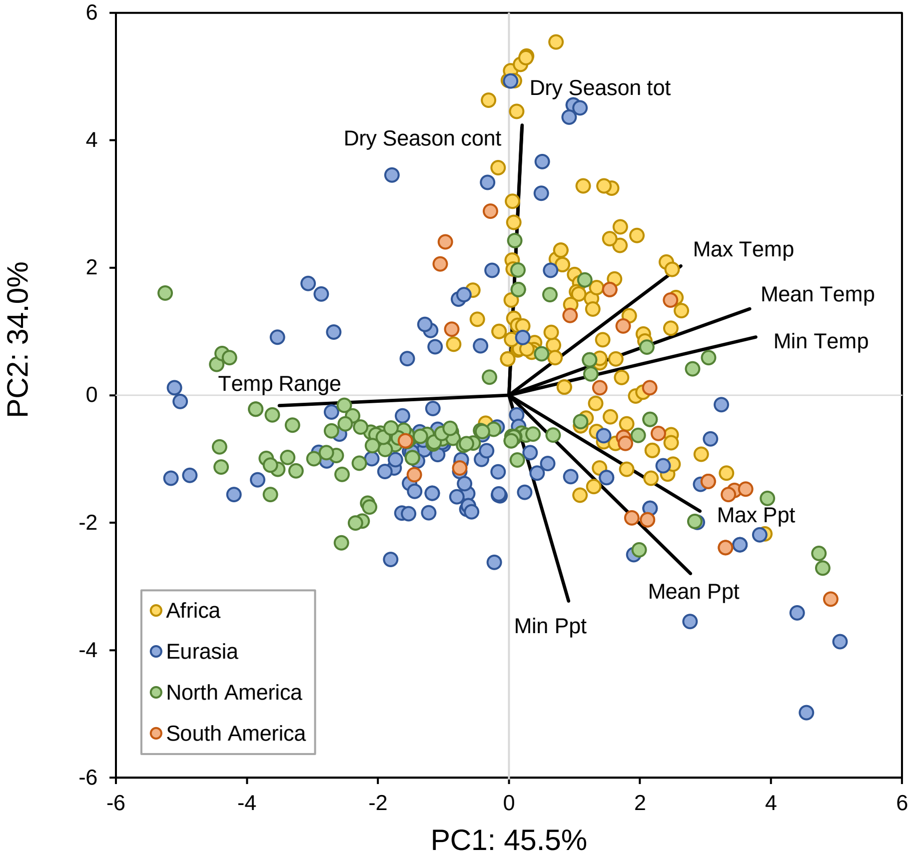


Figure 2.6 Biplot from principal component analysis of nine climatic variables. Data points are individual localities (N = 328). Abbreviated variables are explained in Table 2.2.

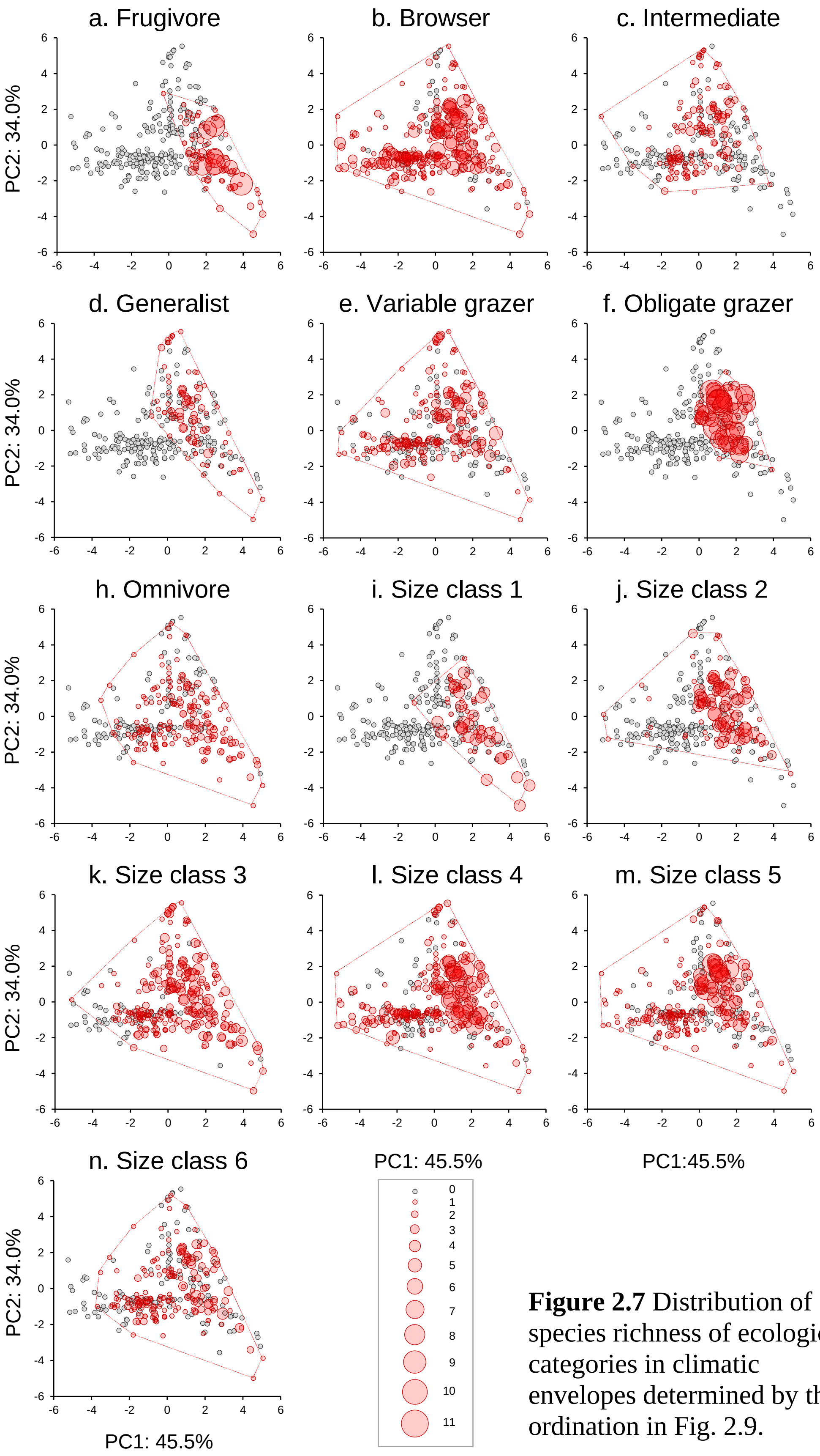


Figure 2.7 Distribution of species richness of ecological categories in climatic envelopes determined by the ordination in Fig. 2.9.

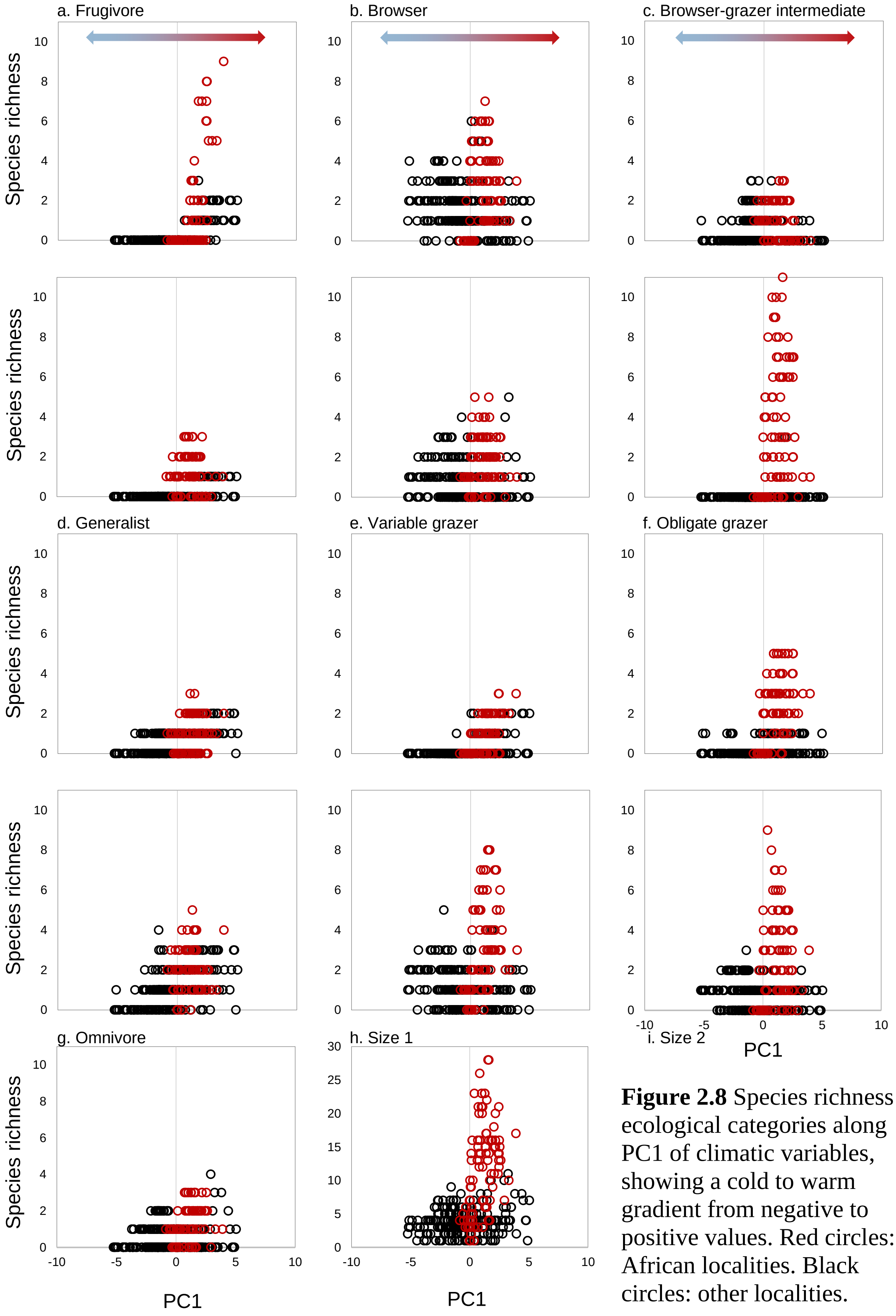


Figure 2.8 Species richness of ecological categories along PC1 of climatic variables, showing a cold to warm gradient from negative to positive values. Red circles: African localities. Black circles: other localities.

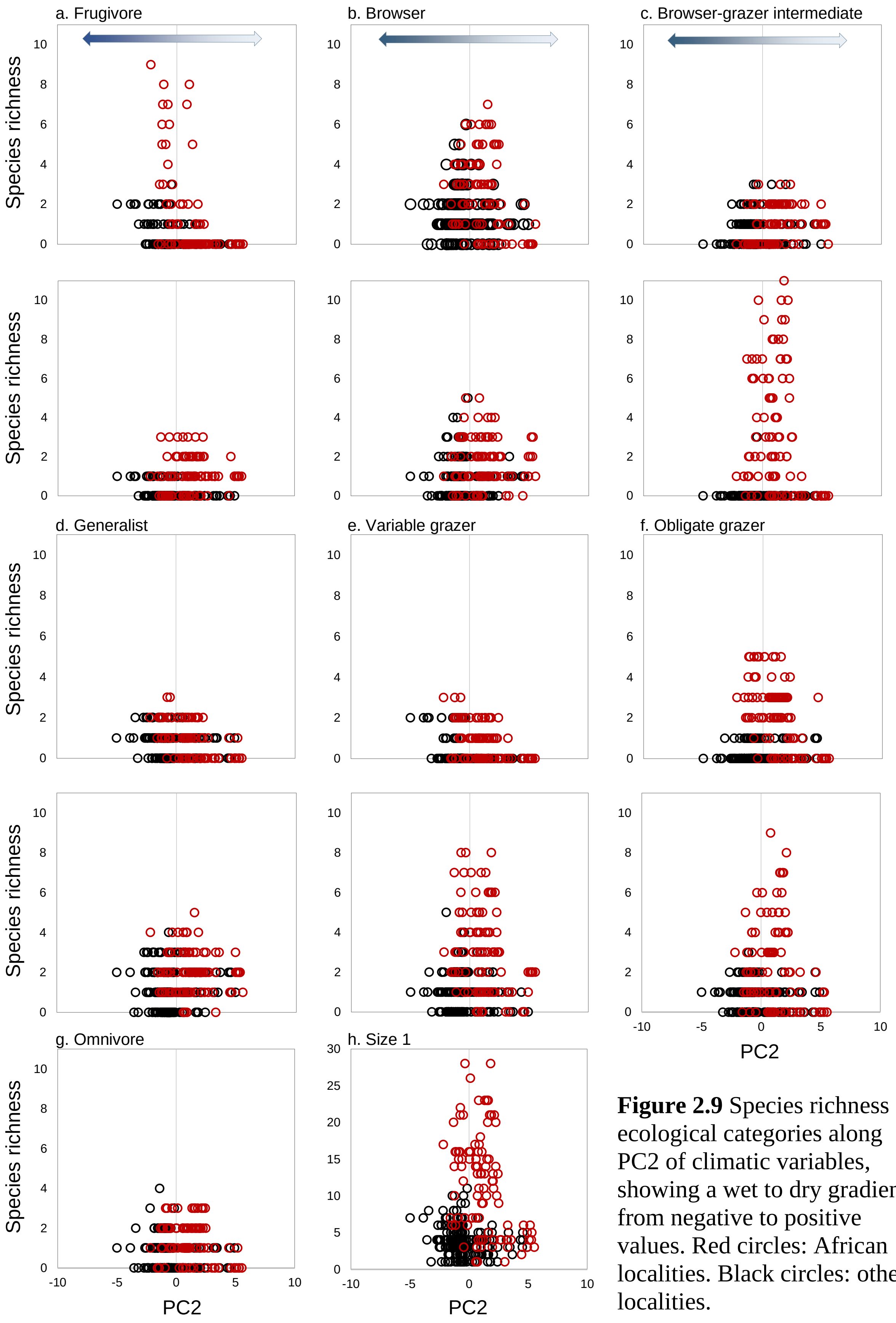


Figure 2.9 Species richness of ecological categories along PC2 of climatic variables, showing a wet to dry gradient from negative to positive values. Red circles: African localities. Black circles: other localities.

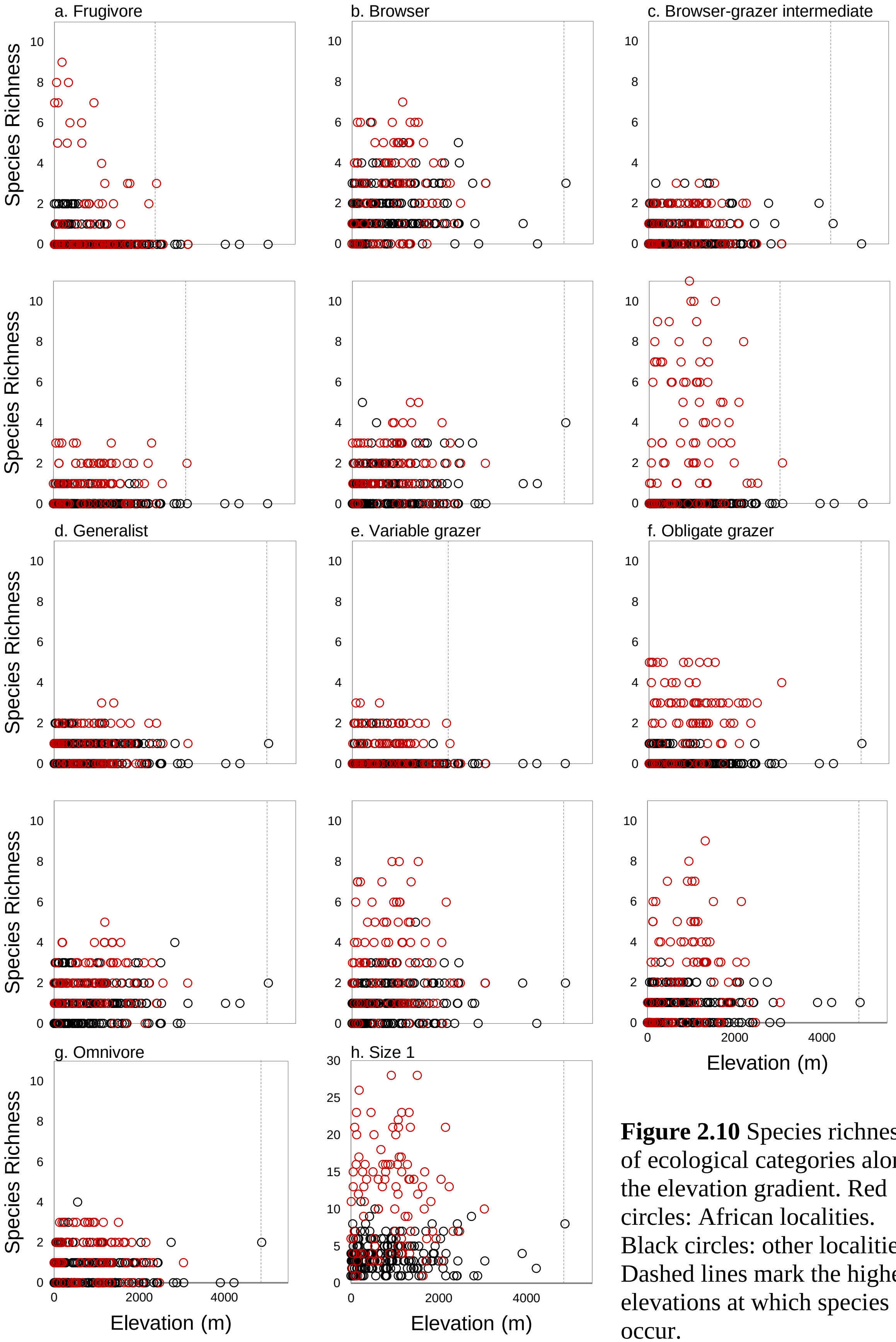


Figure 2.10 Species richness of ecological categories along the elevation gradient. Red circles: African localities. Black circles: other localities. Dashed lines mark the highest elevations at which species occur.

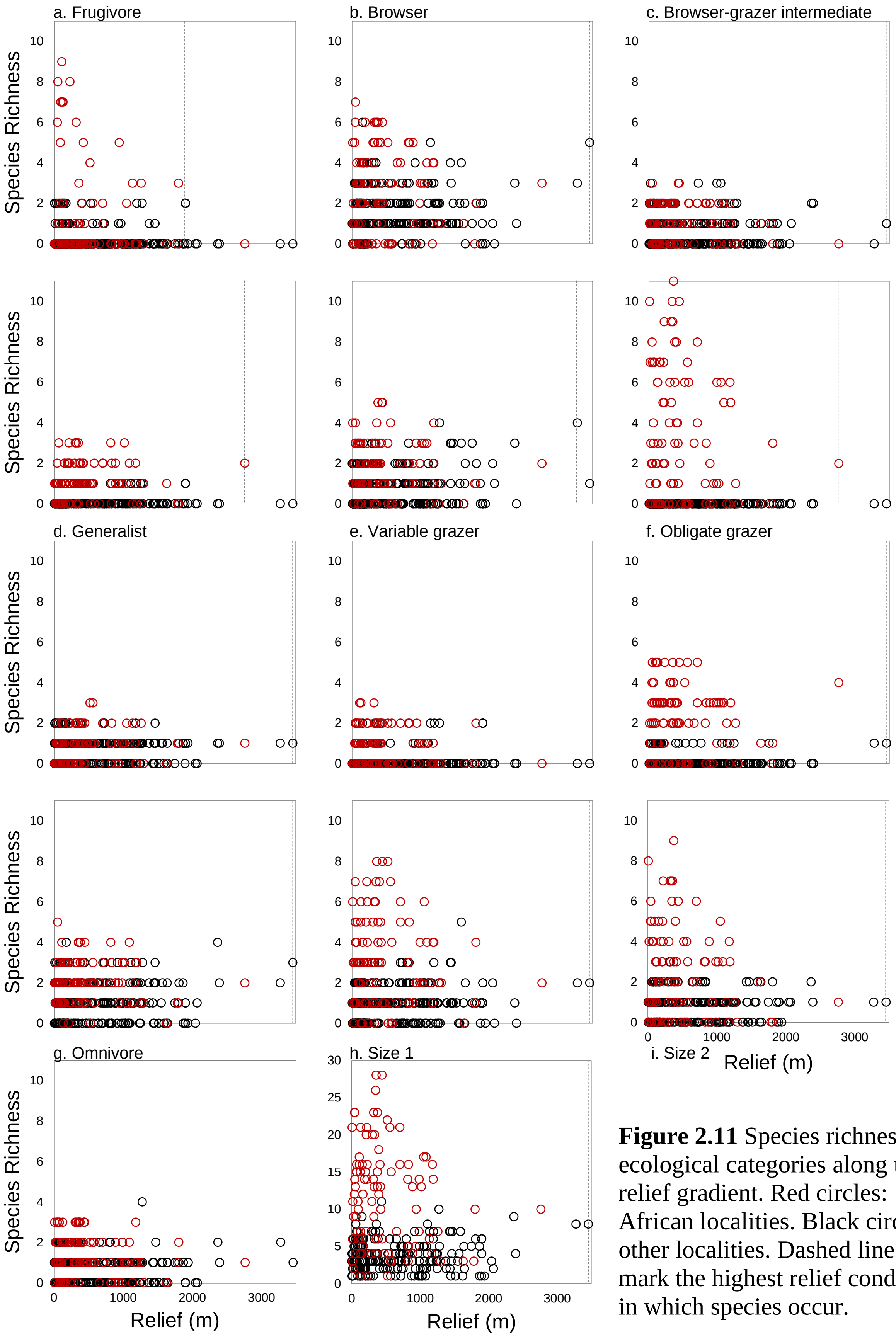


Figure 2.11 Species richness of ecological categories along the relief gradient. Red circles: African localities. Black circles: other localities. Dashed lines mark the highest relief condition in which species occur.

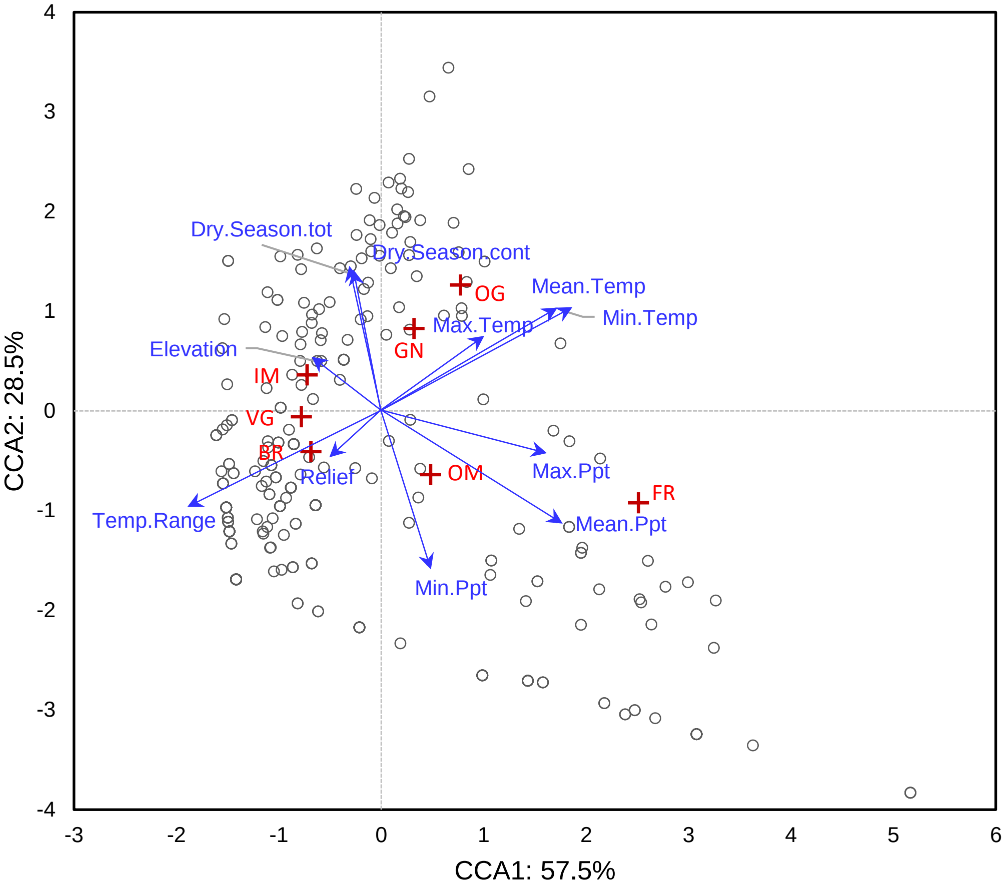


Figure 2.12 Canonical correspondence analysis of eleven environmental variables and seven faunal variables. FR, frugivore; BR, browser; IM, browser-grazer intermediate; GN, generalist; VG, variable grazer; OG, obligate grazer; OM, omnivore.

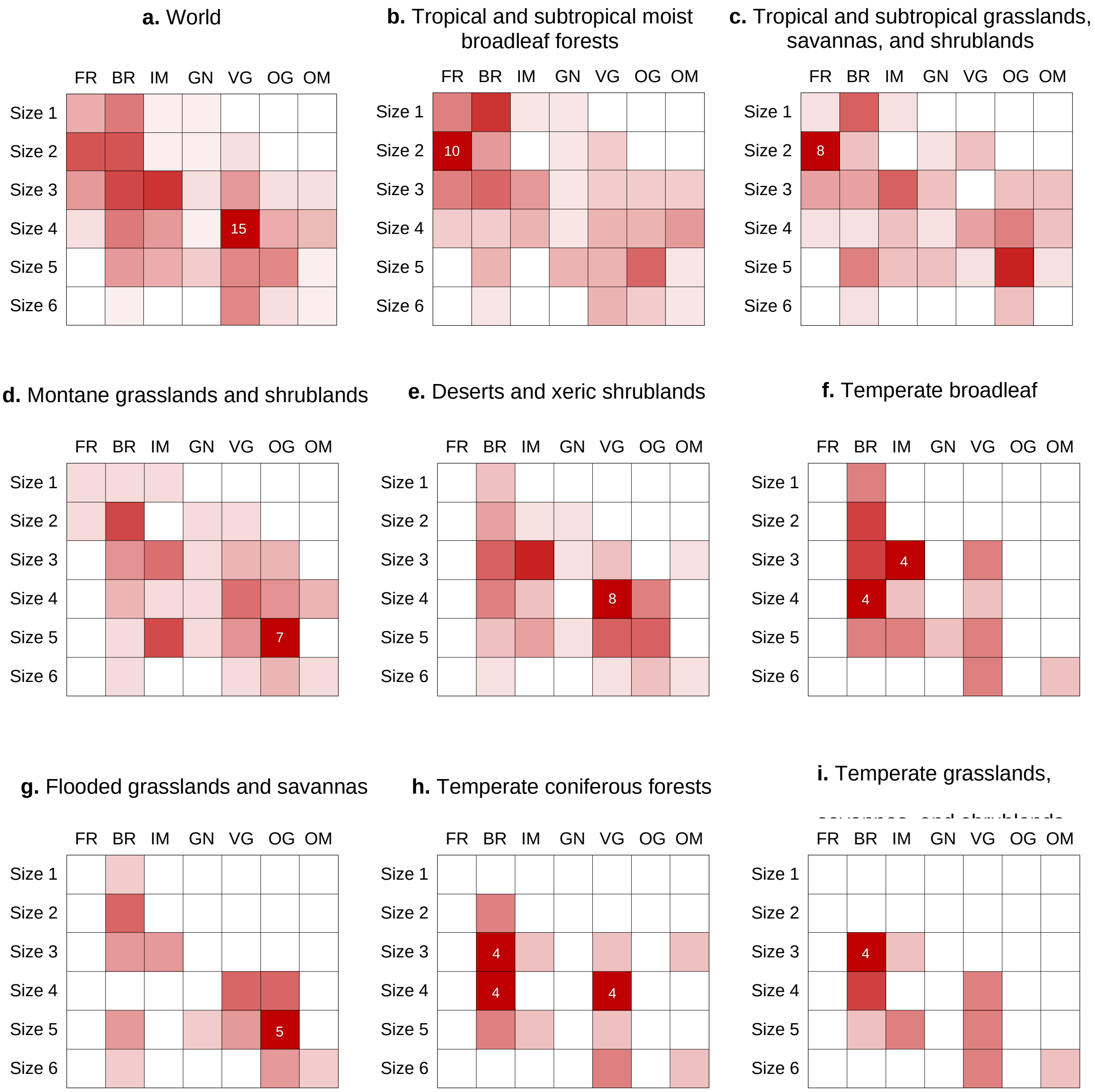
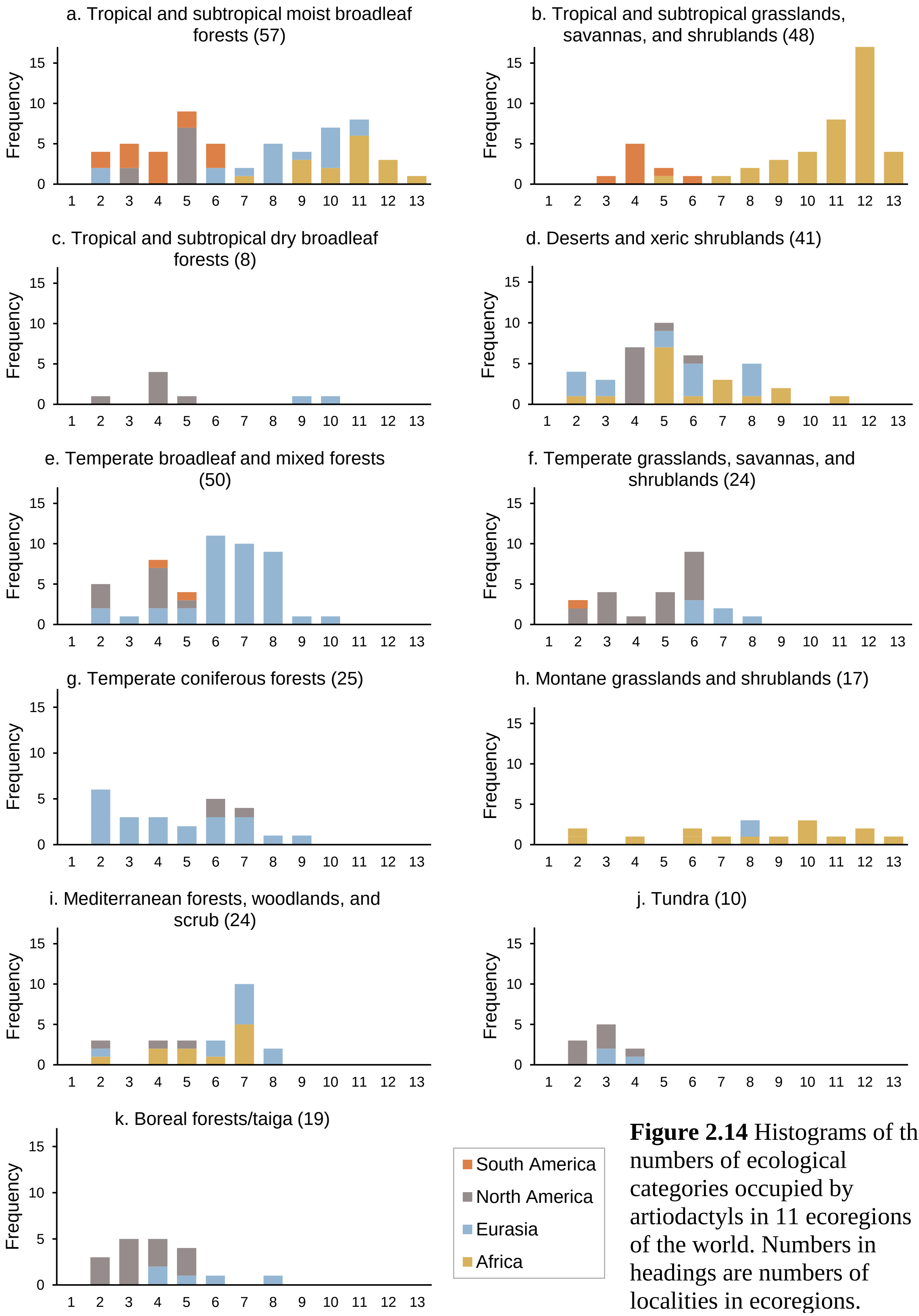


Figure 2.13 Proportional distribution of species in different combinations of feeding category and size class, illustrated for all localities and for the five most species-rich ecoregions. Shading in each panel is normalized to the grid with the highest count (dark red, number of species labeled). See Table 8 for full species counts in the grids. FR, frugivore; BR, browser; IM, browser-grazer intermediate; GN, generalist; VG, variable grazer; OG, obligate grazer; OM, omnivore.



a. Tropical and subtropical moist broadleaf forests (57)

b. Tropical and subtropical grasslands, savannas, and shrublands (48)

c. Tropical and subtropical dry broadleaf forests (8)

d. Deserts and xeric shrublands (41)

e. Temperate broadleaf and mixed forests (50)

f. Temperate grasslands, savannas, and shrublands (24)

g. Temperate coniferous forests (25)

h. Montane grasslands and shrublands (17)

i. Mediterranean forests, woodlands, and scrub (24)

j. Tundra (10)

k. Boreal forests/taiga (19)

Figure 2.14 Histograms of the numbers of ecological categories occupied by artiodactyls in 11 ecoregions of the world. Numbers in headings are numbers of localities in ecoregions.

Chapter 3

Geometric Morphometrics of Mandibles for Dietary Differentiation of Bovidae (Mammalia: Artiodactyla)[1]

3.1 Introduction

The Ruminantia is the largest suborder in the Cetartiodactyla today and consists of a diverse group of small, medium, and large herbivorous mammals with a rich fossil record. The dietary ecology of fossil ruminants has been widely studied and provides useful information about paleoenvironment (e.g., Ungar et al., 2007; DeMiguel et al., 2011). A large body of literature on ruminant ecomorphology focuses on the Bovidae, with important applications to reconstructing the paleohabitat of hominin sites in East Africa (e.g., Kappelman et al., 1997; Kovarovic and Andrews, 2007; Plummer et al., 2008). The Bovidae is one of six families of the Ruminantia, comprising 66% of extant species richness of the suborder (Burgin et al., 2018). Bovids encompass a wide range of body sizes, morphologies, and dietary behaviors; they are widely distributed across Africa, Eurasia, and North America, and occur in numerous habitats that differ in vegetation, climate, and topography (Groves and Leslie, 2011; Castelló, 2016). The ecological and morphological diversity of this group makes the bovids useful analogs for various extinct ungulates.

In the literature on ruminant feeding ecology, three dietary categories have been widely used. (1) Browsers, in a broad sense, primarily feed on leafy dicotyledonous material or fruits; (2) grass and roughage eaters (the grazers) primarily feed on monocotyledonous material which

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[1] Wang B, Zelditch M, Badgley C. Geometric morphometrics of mandibles for dietary differentiation of Bovidae (Mammalia: Artiodactyla). *Current Zoology*. In print.

is generally more abrasive; and (3) intermediate (mixed) feeders feed on a mixture of dicotyledonous and monocotyledonous materials across space and seasons (Hofmann and Stewart, 1972). Each category may be further divided into two to three subcategories based on detailed forage selectivity and preference. These categories and subcategories, with slight modifications in terminology and definition, have been widely used to classify the feeding habits of living as well as fossil ruminants (e.g., Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Langer, 1988; Solounias and Dawson-Saunders, 1988; Bodmer, 1990; Solounias and Moelleken, 1993b; Spencer, 1995; Dompierre and Churcher, 1996; Sponheimer et al,. 1999; Pérez-Barbería & Gordon, 2001; Clauss et al., 2008; Fraser and Theodor, 2011a; Forrest et al., 2018) (Table 3.S1). A number of studies have alternatively used the percentage of grass in species' diets to quantitatively (as opposed to categorically) place species along the browser-grazer spectrum (e.g., Clauss et al., 2003; Pérez-Barbería et al., 2004; Kaiser et al., 2011; Codron et al., 2019).

Comparative anatomical studies have shown that grazing and browsing ruminants differ in masticatory muscles, craniomandibular morphology, and dental features (Table 3.1), which can be attributed to differences in feeding habits and forage selection. Adaptations for browsing typically alter the anterior jaw and are primarily associated with the prehension of plant material. Because edible leaves tend to occur as spatially variable clusters (Demment and Van Soest, 1985; Sanson, 2006), browsers have muzzle characteristics adapted for selective cropping while foraging, such as a tall, narrow premaxilla on the cranium (Solounias and Moelleken, 1993a, 1993b; Spencer, 1995; MacFadden and Shockey, 1997; Mendoza and Palmqvist, 2006). In the anterior mandible, browsing adaptations include a relatively narrow symphysis, a relatively round incisor arcade, and central incisors that are large relative to lateral incisors (Owen-Smith, 1985; Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Solounias and Moelleken, 1993a; Janis, 1995; Fraser and Theodor, 2011a).

In contrast, the craniomandibular adaptations of grazers are primarily associated with processing food. Grasses occur in greater density than leaves and fruits and can be taken in larger amounts per bite (Solounias and Dawson-Saunders, 1988). Grazers generally have wider and flatter muzzles, with wider and more protruding incisors, than browsers (Janis and Ehrhardt, 1988; Pérez-Barbería and Gordon, 2001). Other dental as well as muscular adaptations to diet are also commonly recognized. Grasses are more abrasive than broad-leaf vegetation and are generally consumed in large quantities. Chewing tougher food material requires higher wear resistance of the teeth and a greater amount of occlusal pressure applied to the plant material during mastication. Grazing taxa have significantly higher dental wear rates than browsing taxa (Solounias et al., 1994). As a result, grazers generally have hypsodont (high-crowned) cheek teeth, whereas browsers have brachydont (low-crowned) cheek teeth (Janis, 1988). Hypsodonty is particularly associated with the second and third molars, resulting in a deeper mandibular body under those teeth. Taller teeth also bring occlusal surfaces closer to the condyle, which serves as the fulcrum of the chewing muscular apparatus (Solounias and Dawson-Saunders, 1988; Pérez-Barbería and Gordon, 1999). Hypsodonty, however, does not always signify increased grass consumption; high wear resistance is also an adaptation for consuming more dust and grit in the diet (Janis, 1988; MacFadden et al., 1999; Solounias and Semprebon, 2002; Strömberg, 2002; Damuth and Janis, 2011). Grazing ruminants generally have reduced premolar lengths compared to molar lengths and a more elongated diastema than browsing species (Solounias and Dawson-Saunders, 1988; Janis, 1990; Spencer, 1995; Lazagabaster et al., 2016). Grazers also have larger masseter muscles than browsers (Clauss et al., 2008). The larger area of attachment for the masseter profundus creates a fuller (less concave) outline on the posterior margin of the mandibular ramus, while the large masseter superficialis attachment fills out the ventral margin of the angular (Solounias and Dawson-Saunders, 1988).

It has been argued that the browser-grazer spectrum of ungulate diet should be, strictly speaking, a frugivore-browser-grazer spectrum, as intermediate forms can be found between fruit-eaters and leaf-eaters and between leaf-eaters and grass-eaters, but not between fruit-eaters and grass-eaters (Bodmer, 1990). Dietary data from Gagnon and Chew (2000) confirm this general pattern in African bovids. Enamel morphology and tooth-wear also distinguish patterns in frugivorous ruminants that differ from those in other feeding categories (Heywood, 2010; Louys et al., 2011; Scott, 2012; Gailer and Kaiser, 2014; DeSantis, 2016), suggesting that frugivores should be considered as a distinct dietary group in ecomorphological analyses. Indeed, fruits likely differ from leafy vegetation and grasses in terms of physical, chemical, and biological properties. Lumping frugivore and other browsers into one broad feeding category in ecomorphological studies may obscure patterns that are potentially important.

Much of the ecomorphological literature about bovid diets has used linear measurements of craniomandibular features (e.g., Mendoza and Palmqvist, 2006; Solounias et al., 1995; Spencer, 1995). More recently, several studies have utilized landmark-based, geometric-morphometric analyses to study ungulate jaw shape in relation to diet and function (Raia et al., 2010; Cassini, 2013; Cassini et al., 2017; Forrest et al., 2018; Cassini and Toledo, 2020). Results of these analyses show that mandibular shape is useful for reconstructing the ecology of extinct taxa. However, these studies cover limited taxonomic diversity of modern bovids.

The goal of this study is to identify mandibular morphological characteristics that are correlated with diets across the full spectrum of bovid taxonomic and functional diversity to increase the utility of bovid ecomorphology for reconstructing dietary habits and interpreting paleoenvironments in the fossil record. Using landmark-based geometric morphometrics, we address two questions: (1) Can browsers, mixed feeders, and grazers be distinguished in the morphospace of their mandibles? (2) Does a finer dietary classification scheme provide greater accuracy in differentiating diets? Our expectations are that browsers and grazers will be more readily differentiated from each other than from mixed feeders and that a finer classification will allow for certain groups, such as frugivores, to be better differentiated. We discuss the implications of our results for future ecological and paleoecological studies.

3.2 Data and methods

We obtained data on lower jaw morphology, dietary consumption, and phylogeny for 100 species of extant bovids, with representatives from all bovid tribes. Nearly two-thirds of these species have not been examined previously in ecomorphological studies of bovid diet. No domesticated species (e.g., *Bos frontalis*, *Bos grunniens*, *Bos taurus*, *Bubalus bubalis*, *Ovis aries*) were included. We analyzed the relationship between lower jaw shape and diet using multivariate analyses, taking phylogeny into account in most analyses.

3.2.1 Morphological data

We gathered geometric-morphometric data from standardized photographs of bovid mandibles in lateral view. Our sample includes 377 specimens from three museums: the Field Museum of Natural History (Chicago, IL), the University of Michigan Museum of Zoology (Ann Arbor, MI), and the Michigan State University Museum (East Lansing, MI). All mandibles have fully erupted dentition and no obvious deformation from dental pathology or preparation. Each mandible represents a unique individual animal. The sample size ranges from one to 13 specimens per species, and the average sample size per species is comparable among dietary groups (Appendix A). Whenever possible, we sampled an even number of males and females, although for many specimens this information was not available.

Fourteen landmarks and 53 semi-landmarks on the mandible were digitized with the program tpsDig (Rohlf, 2006) (Fig. 3.1; Table 3.S2). Landmarks represent analogous and morphologically distinct features; semi-landmarks are used to outline the curvature of the mandible between landmarks. Landmarks were superimposed by Generalized Procrustes Analysis (GPA) using the R package for geometric morphometrics, geomorph (Adams et al., 2020), sliding semi-landmarks using the minimum bending-energy criterion (Green, 1996; Bookstein, 1997). Mandible size was measured as the centroid size of the jaw, which is the square-root of the sum of squares of distances of all the landmarks and semi-landmarks from the specimen's centroid (Bookstein, 1989). Following Procrustes superimposition, the mean shape and mean size were computed for each species and used in subsequent analyses.

3.2.2 Dietary data

We used two feeding classification schemes in this study. The first scheme includes three feeding categories that are commonly used in the literature: browsers, mixed feeders, and grazers. The second includes six feeding categories identified by Gagnon and Chew (2000) based on proportional consumption of fruits, dicots, and monocots: frugivores, browsers, browser-grazer intermediates, generalists, variable grazers, and obligate grazers (Table 3.2). Browsers in the first classification correspond to browsers and frugivores in the second classification; mixed feeders correspond to browser-grazer intermediates and generalists; and grazers correspond to variable grazers and obligate grazers. Although other detailed dietary classifications have been useful in previous studies (e.g., Janis and Ehrhardt, 1988; Sponheimer et al., 1999) (Table 3.S1), we chose this classification because its quantitative criteria make it readily applicable to a wide range of species. Gagnon and Chew (2000) studied 78 African bovid species, 63 of which are included in our sample. Based on more recent dietary data in the literature, we reclassified eight of these species to a different feeding category. We also collated dietary information for 37 additional species and assigned each to a feeding category following the criteria derived from Gagnon and Chew's (2000) analysis (Table 3.2). These assignments were based on a combination of quantitative data from primary dietary studies, review papers that summarized primary data from various locations, and estimates of percent consumptions used in previous ecological or ecomorphological (Appendix A). When quantitative information was lacking for a species and estimates were also difficult from existing qualitative descriptions of dietary habits, we assigned species into feeding groups based on qualitative descriptions. Because most species exhibit seasonal and geographic dietary variation, tracking the availability of plant material in their environment, we calculated the average percentages of each food type consumed by each species. Therefore, we note that the spatiotemporally averaged data reflect the general position of species on the dietary spectrum but do not fully capture the breadth of their dietary niche or plasticity in their dietary habits.

3.2.3 Phylogenetic data

We obtained 1000 source trees of Artiodactyla from Upham et al. (2019). Then we used *TreeAnnotator* (Drummond et al., 2012) to generate a maximum clade credibility tree, which was pruned to the extant species in our sample for use in subsequent analyses. As evident from Fig. 3.2, molecular studies show that some of the traditionally recognized tribes are polyphyletic (e.g., Bibi, 2013; Bärmann and Schikora, 2014). For the purpose of this study (i.e., to differentiate among dietary groups), we employed the conventional taxonomic assignments of

Ammotragus clarkei to tribe Antilopini and *Neotragus pygmaeus* to tribe Neotragini, following Groves and Leslie (2011).

3.2.4 Multivariate analyses

We conducted a principal component analysis (PCA) to summarize the main dimensions of shape variation and projected phylogenetic branches and estimated ancestral states onto the resulting morphospace, using the gm.prcomp function in geomorph (Adams et al., 2020). This analysis allows for visualization of shape variation in phylogenetic context.

To determine whether shape is predicted by diet, we conducted a Phylogenetic Generalized Least Squares (Procrustes PGLS) analyses using the procD.pgls function in geomorph. Because our goal is to test the applicability of our results to paleontological studies of bovids, in which the exact phylogenetic placements of species are often not known *a priori* (and are often dependent, at least in part, on craniodental morphology, which would result in circular reasoning), we also conducted a Procrustes Analysis of Variance (Procrustes ANOVA), which does not account for phylogeny, using the procD.lm function in geomorph. We then conducted pairwise comparisons among the means of each feeding category to determine which categories can be distinguished statistically, using the pairwise function in the R package RRPP (Collyer and Adams, 2019). Because of the large number of pairwise comparisons, we used Holm's (1979) method to maintain a table-wide error rate of 5%. The magnitude of morphological differences was quantified by the Procrustes distance between group-mean shapes, also using the pairwise function in RRPP. All statistical analyses were performed using both dietary classifications. The shape variations between dietary groups are visualized as deformations. Since body size affects how morphology performs ecological functions, and ruminant body size correlates with digestive physiology and diet (e.g., Jarman, 1974), we tested for the effect of allometry using a PGLS analysis and generated box plots to compare ln-transformed centroid sizes (LCS) values among dietary groups.

In addition to comparison of the mean shapes, we used a between-group Principal Components Analysis (bgPCA) to determine whether dietary groups can be effectively discriminated by shape. This involves conducting a principal components analysis of the mean shapes of dietary groups, then projecting the data from all species onto those principal components. Unlike a Canonical Variates Analysis, this method does not assume a homogeneous covariance matrix or require inverting it, so a bgPCA can be computed even when the data are not full rank (Mitteroecker and Bookstein, 2011). Even bgPCA can result in spurious separation between groups when the sample size is small relative to the number of variables (Bookstein, 2019; Cardini et al., 2019), although covariances among the variables reduces that effect, and semilandmarks are highly correlated with each other (Cardini et al., 2019). However, cross-validation largely solves the issue of spurious separation, and the results will be largely consistent with distance-based permutation tests of statistical significance of the difference between means in the full data space (Cardini and Polly, 2020). To evaluate the performance of this classification function, we performed a jackknife (leave-one-out) cross-validation of the shape data, using the groupPCA function in the R package Morpho (Schlager, 2017), which provided estimates of classification accuracies and misclassification rates.

3.3 Results

Results are presented in three parts. First, the principal component analysis (PCA) presents a visual assessment of how well dietary groups are separated in two-dimensional morphospace, as well as the directions in which mandibular morphologies vary. We use Phylogenetic Generalized Least Square Analysis (PGLS) to test the hypothesis that evolutionary changes in shape are related to diet. Differences in mean mandibular shapes among dietary groups are also visualized as deformation plots. Lastly, we present results from Analysis of Variance (Procrustes ANOVA) and jackknife cross-validation to test the statistical significance of the between-group differentiation. We use these non-phylogenetic approaches to determine how well shapes could be classified to dietary groups in the absence of phylogenetic information, as would be the case for most fossil specimens.

3.3.1 Principal component analysis

PCA reveals moderate separation among dietary groups in a two-dimensional morphospace (Fig. 3.3A–B; Table 3.S3). PC1 and PC2 explain 45.59% and 14.70% of the shape variance, respectively. Browsers generally plot at the higher ends of PC1 and PC2 compared to grazers, with a relatively small overlap (Fig. 3.3A). Mixed feeders overlap extensively with both browsers and grazers in this plane, with little range of distinct morphospace. The total range of mixed feeders is stretched out considerably by *Bubalus depressicornis* and *B. mindorensis*, leaving much space unoccupied by mixed feeders in between. These two bovines are the only insular species in our dataset, occurring on islands of Southeast Asia.

Grouping species with the six-category classification reveals more about the relationship among dietary groups (Fig. 3.3B). Frugivores are well separated from other feeding categories along PC1 and occupy a distinct region of morphospace unoccupied by any other category. Obligate grazers, representing the opposite end of the dietary spectrum, overlap considerably with variable grazers but are separated from browsers and generalists along PC2. Browsers, browser-grazer intermediates, and variable grazers occupy the largest area of morphospace, in part due to the larger number of species in these groups (Table 3.2), with overlapping relationships similar to those in the first classification (Fig. 3.3A). Generalists are represented by only five species in our dataset and cluster near the center of the plot (Fig. 3.3B).

Comparing morphospace occupation across bovid tribes, the most distinctive pattern is the separation of Cephalophini (duikers) from other tribes along PC1 (Fig. 3.3C). This result is unsurprising since all frugivores sampled in our study belong to this tribe (Fig. 3.2). However, it is notable that the only browsing duiker, *Sylvicapra grimmia*, diverges markedly from its closest extant relatives and converges with other browsers. Other than frugivores, all dietary groups have common ancestors tracing back to the root of the tree (Fig. 3.2). Most obligate grazers belong in tribes Reduncini, Alcelaphini, and Hippotragini. *Syncerus caffer* is the only obligate grazer in tribe Bovini and, interestingly, its morphological convergence with other obligate grazers notably stretches the tribe's range of morphospace, which would otherwise not overlap with that of Reduncini (Fig. 3.3C). Variable grazers are common in the Caprini. The only grazer in Tragelaphini (*Tragelaphus spekii*) diverges markedly from its browsing sister taxa and converges with Bovini and Reduncini, which are grazers. These examples suggest that, although dietary habits exhibit a certain amount of phylogenetic clustering (Fig. 3.2), mandibular morphology reflects dietary adaptations.

Variation along the first principal component primarily concerns the length and height of the mandible (Fig. 3.3D). From the left to the right sides of the PC1 axis: (1) the mandible becomes more elongated, largely due to elongation of the diastema and the premolar row, (2) the coronoid process shortens and bends anteriorly, forming a right angle with the mandibular corpus, (3) the mandibular corpus becomes shallower, and (4) the curvature around the angular process increases. Variation along the PC2 axis primarily concerns the shape of the angular and coronoid processes (Fig. 3.3E). From lower to higher values along PC2: (1) the angular process becomes prominently reduced in size, (2) the coronoid process bends posteriorly and ventrally, accommodated by a more ventrally positioned mandibular condyle, (3) the cheek-tooth row lengthens despite no elongation of the mandible in general, accommodated by slight shortening of the diastema and the symphysis. Differences in shape of the coronoid and angular process, as well as in relative tooth lengths, are captured in both principal components. Changes in the relative length of the anterior mandible, however, occur primarily on PC1 (Fig. 3.3D), which separates frugivores from other feeding categories (Fig. 3.3B).

3.3.2 Relationship among diet, shape, and size

PGLS analysis shows that changes in dietary habits have a significant impact on evolutionary changes in shape ($p < 0.001$) (Table 3.3). The effect of the six-category classification of diet on shape has a greater standardized effect-size ($Z = 4.3$) than the three-category classification ($Z = 3.5$), which measures the strength of the relationship between variables. Deformation plots illustrate the differences in mean shapes among the feeding categories (Fig. 3.4). Using the first classification, grazers have a shorter cheek-tooth row, a deeper mandibular corpus, a shorter diastema and symphysis, a taller coronoid process, and a more dorsally- and posteriorly-positioned condyle than browsers (Fig. 3.4A). Comparing species using the second classification scheme reveals more details about shape variation among dietary groups. Differences found between browsers and grazers in the first classification are magnified in the second classification when comparing the mean shape of frugivores with that of variable grazers (Fig. 3.4B) and, to a lesser extent, with that of obligate grazers (Fig. 3.4C). Notable variations exist between frugivores and other browsers, which are often grouped as one category, with frugivores having a longer anterior mandible, a deeper mandibular corpus, a larger angular process, and a shorter coronoid process (Fig. 3.4D). Comparing the two grazers in the second classification scheme, obligate grazers have shorter a molar row, a longer diastema, a slightly larger angular, and a slightly anteriorly and dorsally oriented coronoid process than variable grazers (Fig. 3.4E). In addition to differences in tooth-crown height and coronoid process, obligate grazers also have a larger angular process than non-frugivorous browsers (Fig. 3.4F). No significant allometric effect was detected ($p = 0.091$) (Table 3.3). Although diet does not have a significant impact on size ($p > 0.16$), ln-centroid sizes (LCS) of mandibles do show differences among the dietary groups, with the smallest mean LCS value found in frugivores and the largest in obligate grazers (Fig. 3.5).

3.3.3 Differentiation of dietary groups

Most feeding categories can be statistically distinguished ($p < 0.05$) from each other in their mandibular shape using either classification scheme (Tables 3.4, 3.S4). Only three pairwise comparisons were statistically non-significant: generalists vs. browsers ($p = 0.50$), generalists vs. browser-grazer intermediates ($p = 0.47$), and variable grazers vs. browser-grazer intermediates ($p = 0.07$). After adjusting for p-values using Holm's (1979) method, all comparisons in the first classification are still significant ($p < 0.05$); in the second classification, significant comparisons include frugivores vs. each of the other feeding categories, obligate grazers vs. each of the other feeding categories except generalists, and browsers vs. variable grazers.

Using the first classification scheme, jackknife cross-validation of shape data yielded an average classification accuracy of 69.0%, which the highest accuracy in grazers (76.7%; Table 3.5). Browsers and grazers are both more frequently misclassified as mixed feeders (30.3% and 16.7% of the time, respectively) than with each other (< 7%). Mixed feeders are misclassified as browsers and grazers at equal rates (16.7%). For the more detailed classification scheme, the classification accuracy averaged across all six feeding categories is 67.4%, similar to that of the first classification scheme. However, the two dietary extremes, frugivores and obligate grazers, have higher classification accuracies than any feeding category does in the first classification scheme (100.0% and 93.3% classification accuracy, respectively) (Table 3.5). Notably, frugivores are never misclassified as another dietary group, and species in other groups were rarely misclassified as frugivores. Variable grazers have the next highest classification accuracy (67.9%) but can be misclassified as browser-grazer intermediates and generalists and, less frequently, as obligate grazers. Browsers, browser-grazer intermediates, and generalists are not as well differentiated from each other. It is worth noting that the sample size for generalists is relatively small (five species). Browsers have the lowest classification accuracy among all groups (40.9%).

3.4 Discussion

Mandibular morphology of bovids is moderately useful for differentiating the three feeding categories widely used in the ruminant literature: browsers, mixed feeders, and grazers (Fig. 3.3A, Tables 3.4a, 3.5a). Using a six-category dietary classification, our results show that frugivores and obligate grazers, which represent end members of the frugivore-browser-grazer spectrum proposed by Bodmer (1990), can be identified accurately with mandibular morphology alone (Fig. 3.3B, Tables 3.3–3.5). The finer classification also reveals subtle differences within browsing species (i.e., frugivore vs. browser; Fig. 3.4D) and within grazing species (i.e., variable grazer vs obligate grazer; Fig. 3.4E). Distinguishing mixed feeders from browsers and grazers has traditionally been difficult (Janis, 1995). Browser-grazer intermediates and generalists in our data are not well differentiated from each other or from most other dietary groups (Fig. 3.3B, Tables 3.4b, 3.5b). These groups by definition have broad, unspecialized dietary habits, and this is unsurprisingly reflected by their mandibular morphology. Although dietary extremes are more clustered in the bovid phylogeny than other feeding categories are (Fig. 3.2), which could have contributed to their distinctive shapes, the association of shape with dietary differentiation renders mandibular shape a potentially useful paleodietary proxy, regardless of the mechanism that creates the association. Our geometric morphometrics analysis identified variations in mandibular shape among dietary groups, including relative diastema length, relative cheek-tooth length and height, and relative size of muscle insertion areas (Figs. 3.3, 3.4). In the context of existing knowledge about ungulate ecology and functional morphology, our findings have implications for bovid ecology and raise questions that invite further research, discussed below.

3.4.1 Implications for frugivore ecology

Comparison between group-mean shapes shows that frugivorous bovids have a deeper mandibular corpus and a larger angular process than browsing bovids (Fig. 3.4D) and some grazing bovids (Fig. 3.4B) relative to mandible size. These differences suggest that consumption of fruits requires greater bite forces than of leafy material. Certain fruit tissues (e.g., large seed shells) have been considered as the most common hard-food objects eaten by mammals (Lucas et al., 2008). For example, tayassuid species that feed on palm fruits, which are tougher than other food materials they consume, have more biomechanically powerful skulls (Hendges et al., 2019). For bovids, studies have shown that frugivores are more similar to grazers than to browsers in the inter-tooth variation of enamel indentation, and they possess thickened enamel and large occlusal surface areas relative to body size (Heywood, 2010; Gailer and Kaiser, 2014). Higher biomechanical demands for hard-object feeding are considered to be a primary driver of occlusal dental morphology in bovids. Extant frugivorous bovids consume fruits from dozens of plant species but preferentially feed on those with small seeds (Gautier-Hion et al., 1985; Hofmann and Roth, 2003). However, little is known about the material properties of the specific fruits consumed by bovids or the biomechanical demand of frugivory in relation to body size. Our results call for more research on these topics.

Previous work on ruminant muzzle shape revealed that browsers have a longer diastema and a narrower symphysis than grazers, which is related to selectivity of feeding, the ability to discriminate and procure high-quality food from surrounding foliage (e.g., Fraser and Theodor, 2011a). Our shape data show that one notable difference between frugivores and other feeding groups (including browsers) is the elongation of the mandible anterior to the cheek teeth, including elongation of the symphysis, in frugivores. This difference implies even higher selectivity in the frugivore diet (i.e., fruits) than in the browser diet (i.e., leaves and stems).

In modern ecosystems, frugivorous bovids live in tropical forests of Africa, where temperature and precipitation conditions allow a year-round supply of fruits. Identifying frugivorous species in fossil faunas would be crucial for reconstructing paleo-ecosystems with dense vegetation. Although microwear and mesowear analyses of bovids have found distinctive tooth-wear patterns in frugivores (Solounias and Semprebon, 2002; Louys et al., 2011; Scott, 2012; DeSantis, 2016), existing ecomorphological studies of bovids (and ungulates in general) have given little attention to frugivores as a feeding group separate from browsers (Table 3.S1). Our results show that frugivorous bovids show the most distinctive mandibular morphology which is readily distinguished from any other groups using geometric morphometrics (Fig. 3.3B, Table 3.4b).

3.4.2 Implications for browser ecology

(Non-frugivorous) browsers in our data exhibit greater shape variation than we expected, and this is likely related to the nature of our classification criterion for this dietary group (> 70% dicots, Table 3.2). Browsing is the most common dietary guild among ungulate species, occurring in open grassland, arid habitats, and tropical rainforests. The wide distribution of browsers reflects the presence of dicotyledonous plants in a vast array of habitats. Resource partitioning among co-occurring species can occur in at least three ways: choice of primary food, habitat preference, and feeding-height preference (Jarman and Sinclair, 1979; Janis, 1995; Spencer, 1995; Mendoza et al., 2002). Our dietary classification reflects the first way, and further division of this dietary group may be possible. Our results highlight the high disparity and diversity within browsing bovids (and ungulates in general), which have likely been understudied in ecomorphological and ecometric analyses using broad-brush dietary classifications.

3.4.3 Implications for grazer ecology

Some dental and mandibular adaptions in grazers have been well studied. Specifically, hypsodont molars provide grazers with more materials for wear, and larger masseter muscles provide greater bite force for consuming monocotyledonous plants (e.g., Mendoza et al, 2002; Damuth and Janis, 2011). We were able to detect these features in our data with the depth of the mandibular corpus and the size of the angular process, respectively. Two other morphological characteristics of grazer mandibles evident in our results deserve further attention. The first characteristic is a taller, more posteriorly oriented coronoid process compared to browsers and frugivores (Figs. 3.3D, 3.4). The coronoid process serves as the effective moment arm of the temporalis muscle, and a longer coronoid process allows the muscle to generate greater bite force with the same torque (Kiltie, 1982; Pérez-Barbería and Gordon, 1999; Hendges et al., 2019). Omnivorous ungulates (pigs and peccaries) have a shorter coronoid process than herbivorous ungulates, reflecting their less tough diet (Pérez-Barbería and Gordon, 1999). These authors, however, found no difference in coronoid height between browsing and grazing species. Our results suggest that grazing bovids have temporalis muscles that generate greater bite force to meet the needs of a tougher diet. The second characteristic is a relatively short premolar row in grazers. Some extinct and living species (e.g., *Teleoceras* spp., *Connochaetes* spp.) have lost the second premolar (p2) over evolutionary time, and these species are generally considered grazers. Many other grazing species, while having maintained three premolars, have reduced premolar row lengths relative to mandible size (Fig. 3.3). Solounias and Dawson-Saunders (1988) speculated that reduced premolar lengths in grazing ruminants resulted from a more posterior chewing position, bringing the food closer to the fulcrum of the chewing musculature. Other authors have attributed reduced premolars to the facilitation of larger bite sizes (e.g., Codron et al., 2008). These explanations have not been rigorously tested or applied to inferring grazing adaptions in extinct species. A finite element analysis may be able to address this question (e.g., Fletcher et al., 2010; Zhou et al., 2019). It is worth noting that reduction of the premolar row is not always correlated with percent grass consumption in ungulate groups (Codron et al., 2019). In perissodactyls, there is in fact an opposite trend for a more pronounced premolar row (through molarization of the premolars) in grazing perissodactyls compared to browsing ones (Janis, 1990; Mendoza et al., 2002). Consequently, the total occlusal surface area (and the total occlusal volume) in grazing perissodactyls (e.g., horses) is larger than that of ruminants of similar diet (Janis, 1988).

3.4.4 Implications for paleontological studies

The study by Forrest et al. (2018) is the only one prior to ours that uses geometric morphometrics to study bovid mandibles in relation to diet. Based on three-dimensional shape data of 35 extant species, their analyses yielded cross-validated accuracy rates of 80%–97% (for individual specimens), higher than those in the present study (for species). Other than differences in sampled specimens and statistical methods, several factors may explain the difference in results. First, three-dimensional data capture variation in the transverse plane and frontal plane, including width of the symphysis (narrower in browsers) and lateral position of the coronoid process (more distally positioned in browsers). Second, different feeding categories can yield different results. Their classification scheme included grazing, fresh-grass grazing, mixed feeding-preferring grass, mixed feeding-preferring browse, and browsing (Table 3.S1), which may be more useful for differentiating diet, although it may not be readily applicable to species beyond their study due to its qualitative nature. Third, different taxonomic coverages capture different amounts of evolutionary and ecological information, which affects shape analysis. As shown by Solounias and Dawson-Saunders (1988), species classified in the same dietary group can have a mosaic of craniodental features. Asynchronous evolution of dietary habits and morphology, evolutionary reversal of feeding habits, independent evolution of morphology in the same environment could also result in similar but variable forms that perform the same ecological function (Solounias and Dawson-Saunders, 1988). Therefore, the wider taxonomic range covered in our study inherits more confounding factors that can complicate the significance of the functional signal. All these factors and associated uncertainties are important to consider in paleoecological reconstructions.

All but one species analyzed by Forrest et al. (2018) are also included in our data. Therefore, we re-ran a PCA and between-group PCA to compare the effect of dietary classification scheme. Our classification scheme performed better at the browsing end of the dietary spectrum, again highlighting the necessity of differentiating frugivores from other browsers, while their classification performed better on the grazing end of the spectrum (Fig. 3.S1). This difference suggests that qualitative and quantitative dietary data should be combined to better capture the variable vegetation that species consume, thereby improving the utility of the classification scheme used in ecomorphological research.

To fully evaluate the effectiveness of our morphometrics method for inferring the diet of extinct species, data from fossil bovid specimens and from more extant ruminant species should be incorporated into the model. Inferences made with mandibular morphology can be compared with those derived from other methods, such as hypsodonty index, microwear and mesowear analyses, and stable isotopes (e.g., Solounias and Moelleken, 1993b; MacFadden and Shockey, 1997; Sponheimer, 1999; Codron et al., 2008; Fraser and Theodor, 2011b; Louys et al., 2011; Lazagabaster et al., 2016) (Table 3.1). Combing results from multiple proxies should improve the dietary reconstruction of fossil taxa.

3.4.5 Implications for future studies

Overall, our study shows that a finer dietary classification has improvements over the traditional three categories (Fig. 3.3, Tables 3.3–3.5). How exactly to categorize diet should be, of course, tailored to the specific research goals of each ecomorphological study. However, based on findings of our comparative analyses, we recommend at least four dietary groups for ruminants: frugivores, browsers, mixed feeders, and grazers. Further divisions in browsers and in grazers could also reveal interesting patterns.

Combining evidence from this and previous studies, we here propose a conceptual model of the relative dietary mechanical demand and forage selectivity along the frugivore-browser-grazer spectrum (Fig. 3.5). In general, ruminants with small body sizes feed on higher-quality fruit and browse diets, which are often surrounded by lower-quality plant materials, while larger-bodied ruminants feed on browse and grass diets (Jarman, 1974; Langer, 1986). Comparison of mandible sizes and morphologies among dietary groups is consistent with this pattern (Figs. 3.4, 3.5). In frugivores, dental and angular morphologies indicate capability of consuming tough plants or plant parts, and anterior mandible morphologies and small body sizes suggest more selective cropping. In grazers, inferred hypsodonty (from mandibular depth), angular and coronoid morphologies, and potentially premolar length indicate capability of consuming tough plants, and their incisor morphology and large body size suggest low selectivity of forage. Details of this model require verification and refinement through further investigation. We note that "mechanical demand" here broadly summarizes all mechanical resistance that teeth and muscles experience during the acquisition and processing of forage, which can result from the hardness of the food material itself, shear from anterior-posterior movements of the jaw, and shear from lateral movements of the jaw. Specifically, we need better understanding of (a) the material property of the fruits that frugivorous bovids consume, especially in relation to body size, (b) the feeding behavior and evolutionary history regarding fallback foods in frugivores, (c) the mastication mechanisms of frugivores and grazers, and (d) the range of feeding habits of non-frugivorous browsers and mixed feeders.

3.5 Acknowledgements

We thank the following individuals for assistance with museum access: Adam Ferguson at the Field Museum of Natural History, Cody Thompson at the University of Michigan Museum of Zoology, and Laura Abraczinskas at the Michigan State University Museum. We thank our research assistant, Ethan VanValkenburg, for his contributions to collection of dietary data. We thank Donald Swiderski for helpful discussions at various stages of this research. Matthew Kolmann helped with phylogenetic data. Constructive comments by Marcus Clauss and three anonymous reviewers greatly improved the quality of the manuscript. Research grants were provided by Rackham Graduate School and the Paleontological Society to BW.

3.6 References

Adams DC, Collyer ML, Kaliontzopoulou A, 2020. *Geomorph: Software for geometric morphometric analyses.* R package version 3.3.1. Available from: https://CRAN.R-project.org/package=geomorph.

Bärmann EV, Schikora T, 2014. The polyphyly of *Neotragus* — Results from genetic and morphometric analyses. *Mamm Biol* **79**:283–286.

Bibi F, 2013. A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evol Biol* **13**:166.

Bodmer RE, 1990. Ungulate frugivores and the browser grazer continuum. *Oikos* **57**:319–325.

Bookstein FL, 1989. ‘‘Size and shape’’: A comment on semantics. *Syst Zool* **38**:173–180.

Bookstein FL, 1997. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. *Med Image Anal* **1**:225–243.

Bookstein FL, 2019. Pathologies of between-groups Principal Components Analysis in geometric morphometrics. *Evol Biol* **46**:271–302.

Burgin CJ, Colella JP, Kahn PL, Upham NS, 2018. How many species of mammals are there? *J Mammal* **99**:1–14.

Cardini A, O’Higgins P, Rohlf FJ, 2019. Seeing distinct groups where there are none: Spurious patterns from between-group PCA. *Evol Biol* **46**:303–316.

Cardini A, Polly PD, 2020. Cross-validated between group PCA scatterplots: A solution to spurious group separation? *Evol Biol* **47**:85–95.

Cassini GH, 2013. Skull geometric morphometrics and paleoecology of Santacrucian (Late Early Miocene; Patagonia) native ungulates (Astrapotheria, Litopterna, and Notoungulata). *Ameghiniana* **50**:193-216.

Cassini GH, Toledo N, 2020. An ecomorphological approach to craniomandibular integration in neotropical deer. *J Mamm Evol*. https://doi.org/10.1007/s10914-020-09499-5

Cassini GH, Muñoz NA, Vizcaino SF, 2017. Morphological integration of native South American ungulate mandibles. A tribute to D'arcy Thompson in the centennial of "On Growth and Form." *Palaeontol Electron* **17**:58–74.

Castelló JR, 2016. *Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and Relatives*. Princeton (NJ): Princeton University Press.

Clauss M, Lechner-Doll M, Streich WJ, 2003. Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. *Oikos* **102**:253–262.

Clauss M, Hofmann RR, Streich WJ, Fickel J, Hummel J, 2008. Higher masseter muscle mass in grazing than in browsing ruminants. *Oecologia* **157**:377–385.

Collyer ML, Adams DC, 2019. *RRPP: Linear Model Evaluation with Randomized Residuals in a Permutation Procedure.* R package version 0.4.0. Available from: https://CRAN.R-project.org/package=RRPP.

Codron D, Brink JS, Rossouw L, Clauss M, Codron J, Lee-Thorp JA, Sponheimer M, 2008. Functional differentiation of African grazing ruminants: An example of specialized adaptations to very small changes in diet. *Biol J Linn Soc* **94**:755–764.

Codron D, Hofmann RR, Clauss M, 2019. Morphological and physiological adaptations for browsing and grazing. In: Gordon IJ, Prins HHT, editors. *The ecology of browsing and grazing II*. Springer: Berlin, Germany. 81–125.

Damuth J, Janis CM, 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in paleoecology. *Biol Rev* **86**:733–758.

DeMiguel D, Azanza B, Morales J, 2011. Paleoenvironments and paleoclimate of the Middle Miocene of central Spain: A reconstruction from dental wear of ruminants. *Palaeogeogr Palaeoclimatol Palaeoecol* **302**:452–463.

Demment MW, van Soest PJ, 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am Nat* **125**:641–672.

DeSantis LRG, 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surf Topogr: Metrol Prop* **4**:023002.

Dompierre H, Churcher CS, 1996. Premaxillary shape as an indicator of the diet of seven extinct late Cenozoic new world camels. *J Vertebr Paleontol* **16**:141–148.

Drummond AJ, Suchard MA, Xie D, Rambaut A, 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol Biol Evol* **29**:1969–1973.

Fletcher TM, Janis CM, Rayfield EJ, 2010. Finite element analysis of ungulate jaws: Can mode of digestive physiology be determined? *Palaeontol Electron* **13**:21A.

Fraser D, Theodor JM, 2011a. Anterior dentary shape as an indicator of diet in ruminant artiodactyls. *J Vertebr Paleontol* **31**:1366–1375.

Fraser D, Theodor JM, 2011b. Comparing ungulate dietary proxies using discriminant function analysis. *J Morphol* **272**:1513–1526.

Forrest F, Plummer T, Raaum R, 2018. Ecomorphological analysis of bovid mandibles from Laetoli Tanzania using 3D geometric morphometrics: Implications for hominin paleoenvironmental reconstruction. *J Hum Evol* **114**:20–34.

Gagnon M, Chew AE, 2000. Dietary preferences in extant African Bovidae. *J Mammal* **81**:490–511.

Gailer JP, Kaiser TM, 2014. Common solutions to resolve different dietary challenges in the ruminant dentition: The functionality of bovid postcanine teeth as a masticatory unit. *J Morphol* **275**:328–341.

Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Moungazi A, Roussilhon C, Thiollay JM, 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**:324–337.

Green WDK, 1996. The thin-plate spline and images with curving features. In: Mardia KV, Gilland CA, Dryden L, editors. *Image fusion and shape variability*. Leeds: University of Leeds Press. 79–87.

Groves CP, Leslie DM Jr, 2011. Family Bovidae (hollow-horned ruminants). In: Wilson DE, Mittermeier RA, editors. *Handbook of the Mammals of the World. Vol. 2. Hoofed Mammals.* Barcelona: Lynx Edicions. 444–575.

Gordon IJ, Illius AW, 1988. Incisor arcade structure and diet selection in ruminants. *Funct Ecol* **2**: 15–22.

Hendges CD, Patterson BD, Cáceres NC, Gasparini GM, Ross CF, 2019. Skull shape and the demands of feeding: a biomechanical study of peccaries (Mammalia, Cetartiodactyla). *J Mammal* **100**: 475–486.

Heywood JJN, 2010. Functional anatomy of bovid upper molar occlusal surfaces with respect to diet. *J Zool* **281**:1–11.

Hofmann T, Roth H, 2003. Feeding preferences of duiker (*Cephalophus maxwelli, C. rufilatus,* and *C. niger*) in Ivory Coast and Ghana. *Mamm Biol* **68**:65–77.

Hofmann RR, Stewart DRM, 1972. Grazer or browser: A classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* **36**:226–240.

Holm S, 1979. A simple sequentially rejective multiple test procedure. *Scand J Stat* **6**:65–70.

Janis CM, 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. *Mém Mus natl hist nat* **53**:367–387.

Janis CM, 1990. Correlation of cranial and dental variables with dietary preferences in mammals: A comparison of macropidoids and ungulates. *Mem Queensl Mus* **28**:349–366.

Janis CM, 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason JJ, editor. *Functional Morphology in Vertebrate Paleontology*. Cambridge: Cambridge University Press. 76–98.

Janis CM, Ehrhardt D, 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool J Linn Soc* **92**:267–284.

Jarman PJ, Sinclair ARE, 1979. Feeding strategy and the pattern of resource-partitioning in ungulates. In: Sinclair ARE, Norton-Griffiths M, editors. *Serengeti, dynamics of an ecosystem*. Chicago: University of Chicago Press, Chicago. 130–163.

Kaiser TM, Müller DWH, Fortelius M, Schulz E, Codron D, Clauss M, 2011. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Rev* **43**:34–46.

Kappelman J, Plummer T, Bishop L, Duncan A, Appleton S, 1997. Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *J Hum Evol* **32**:229–256.

Kiltie RA, 1982. Bite force as a basis for niche differentiation between rain forest peccaries (*Tayassu tajacu* and *T. pecari*). *Biotropica* **14**:188–195.

Kovarovic K, Andrews P, 2007. Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *J Hum Evol* **52**:663–680.

Langer P, 1986. Large mammalian herbivores in tropical forests with either hindgut- or forestomach-fermentation. *Z. Säugetierkd* **51**:173–187.

Langer P, 1988. *The Mammalian Herbivore Stomach: Comparative Anatomy, Function, and Evolution*. Stuttgart: G. Fischer.

Lazagabaster IA, Rowan J, Kamilar JM, Reed KE, 2016. Evolution of craniodental correlates of diet in African Bovidae. *J Mamm Evol* **23**:385–396.

Louys J, Meloro C, Elton S, Ditchfield P, Bishop LC, 2011. Mesowear as a means of determining diets in African antelopes. *J Archaeol Sci* **38**:1485–1495.

Lucas P, Constantino P, Wood B, Lawn B, 2008. Dental enamel as a dietary indicator in mammals. *BioEssays* **30**:374–385.

MacFadden, BJ, Shockey BJ, 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: Morphological and isotopic evidence. *Paleobiology* **23**:77–100.

MacFadden BJ, Solounias N, Cerling TE, 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science* **283**:824–827.

Mendoza M, Palmqvist P, 2006. Characterizing adaptive morphological patterns related to diet in Bovidae (Mammalia: Artiodactyla). *Acta Zool Sin* **52**:988–1008.

Mendoza M, Janis CM, Palmqvist P, 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: A multivariate approach. *J Zool* **258**:223–246.

Mitteroecker P, Bookstein F, 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evol Biol* **38**:100–114.

Owen-Smith N, 1985. Niche separation among African ungulates. In: Vrba ES, editor. *Species and Speciation, Vol. 4*. Pretoria: Transvaal Museum. 167–171.

Pérez-Barbería FJ, Gordon IJ, 1999. The functional relationship between feeding type and jaw and cranial morphology in ungulates. *Oecologia* **118**:157–165.

Pérez-Barbería FJ, Gordon IJ, 2001. Relationships between oral morphology and feeding style in the Ungulata: A phylogenetically controlled evaluation. *Proc B Soc Lond B* **268**:1023–1032.

Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius AW, 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proc R Soc Lond B Biol Sci* **271**:1081–1090.

Plummer TW, Bishop LC, Hertel F, 2008. Habitat preference of extant African bovids based on astragalus morphology: Operationalizing ecomorphology for palaeoenvironmental reconstruction. *J Archaeol Sci* **35**:3016–3027.

Raia P, Carotenuto P, Meloro C, Piras O, Pushkina D, 2010. The shape of contention: adaptation, history, and contingency in ungulate mandibles. *Evolution* **64**:1489–1503.

Rohlf FJ, 2006. *tpsDig, Digitize Landmarks and Outlines.* Version 2.05. Stony Brook (NY): Department of Ecology and Evolution, State University of New York.

Sanson G, 2006. The biomechanics of browsing and grazing. *Am J Bot* **93**:1531–1545.

Schlager S, 2017. Morpho and Rvcg – Shape Analysis in R. In: Zheng G, Li S, Szekely G, editors. *Statistical Shape and Deformation Analysis*. Academic Press. 217–256.

Scott JR, 2012. Dental microwear texture analysis of extant African Bovidae. *Mammalia* **76**:157–174.

Solounias N, Dawson-Saunders B, 1988. Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeogr Palaeoclimatol Palaeoecol* **65**:149–172.

Solounias N, Moelleken SMC, 1993a. Dietary adaptation of some extinct ruminants determined by premaxillary shape. *J Mamm* **74**:1059–1071.

Solounias N, Moelleken SMC, 1993b. Tooth microwear and premaxillary shape of an archaic antelope. *Lethaia* **26**:261–268.

Solounias N, Semprebon G, 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am Mus Novit* **3366**:1–49.

Solounias N, Fortelius M, Freeman P, 1994. Molar wear rates in ruminants: a new approach. *Ann Zool Fenn* **31**: 219–227.

Solounias N, Moelleken S, Plavcan J, 1995. Predicting the diet of extinct bovids using masseteric morphology. *J Vertebr Paleontol* **15**:795–805.

Strömberg CAE, 2002. The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: Preliminary results concerning the evolution of hypsodonty. *Palaeogeogr Palaeoclimatol Palaeoecol* **177**: 59–75.

Spencer LM, 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. *J Mammal* **76**:448–471.

Sponheimer M, Reed KE, Lee-Thorp JA, 1999. Combining isotopic and ecomorphological data to refine bovid dietary reconstruction: A case study from the Makapansgat Limeworks hominin locality. *J Hum Evol* **36**: 705–718.

Ungar PS, Merceron G, Scott RS, 2007. Dental microwear texture analysis of Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, western Cape Province, South Africa. *J Mammal Evol* **14**:163–181.

Upham NS, Esselstyn JA, Jetz W, 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol* **17**: e3000494.

Zhou Z, Winkler DE, Fortuny J, Kaiser TM, Marcé-Nogué J, 2019. Why ruminating ungulates chew sloppily: Biomechanics discern a phylogenetic pattern. *PLoS ONE* **14**:e0214510.

Table 3.1 Differences in craniodental characteristics between browsing and grazing ruminants. Sources: Solounias and Dawson-Saunders (1988), Mendoza et al. (2002) and references therein, Sponheimer et al. (2003); Scott (2012).

	Browser	Grazer
Morphological features		
Shape of the incisor arcade	Curved	Straight
Size of incisors	I_1 and I_3 of similar size	I_1 larger than I_3
Muzzle width	Narrow	Broad
Premaxilla width	Narrow	Broad
Depth of mandibular corpus	Shallow	Deep
Hypsodonty index (M_3 height/width)	Low	High
Mandible size	Small	Large
Mandible diastema	Long	Short
Relative length of premolar row to molar row	High	Low
Masseter size	Small	Large
Posterior and ventral borders of angular	Concave	Full
Tooth-wear patterns		
Mesowear score (sharpness of cusps)	Low (sharp)	High (flat)
Microwear (microscopic abrasion)	More complex	Less complex
Stable isotope composition		
Stable carbon-isotope value of tooth enamel	Depleted	Enriched

Table 3.2 Two dietary classification schemes of 100 species of extant bovids used in this study.

Dietary Classification 1	**Dietary Classification 2 (after Gagnon and Chew, 2000)**	**Dietary Composition (after Gagnon and Chew, 2000)**	**No. Sampled Species**
Browser	Frugivore	>70% fruits, little or no monocots	11
	Browser	>70% dicots	22
Mixed feeder	Browser-grazer intermediate	<70% dicots, <60% monocots, <20% fruits [a]	19
	Generalist	>20% of all food types	5
Grazer	Variable grazer	60–90% monocots, variable	28
	Obligate grazer	>90% monocots, not variable	15

[a] Classification criterion for browser-grazer intermediates in the original paper has been modified for a more accurate description

Table 3.3 Effects of size on shape, diet on shape, and diet on size analyzed by Phylogenetic Generalized Least Squares (PGLS) for 100 species of extant bovids. A three-part classification (browser, mixed feeder, grazer) and a six-part classification (frugivore, browser, browser-grazer intermediate, generalist, variable grazer, obligate grazer) of diet are used. Note that the six-category classification yields a greater effect size of diet on shape.

Effect	Df	SS	MS	R^2	F	Z	P
Size on shape	1	0.0011	0.0011	0.018	1.800	1.375	0.091
Residuals	98	0.0613	0.0006				
Total	99	0.0625					
3 diets on shape	2	0.0050	0.0025	0.080	4.214	3.660	0.001
Residuals	97	0.0575	0.0006				
Total	99	0.0625					
3 diets on size	2	0.0083	0.0041	0.008	0.375	-0.426	0.663
Residuals	97	1.0699	0.0110				
Total	99	1.0782					
6 diets on shape	5	0.0105	0.0021	0.168	3.805	4.952	0.001
Residuals	94	0.0520	0.0006				
Total	99	0.0625					
6 diets on size	5	0.0852	0.0170	0.079	1.613	1.006	0.167
Residuals	94	0.9930	0.0106				
Total	99	1.0782					

Table 3.4 Procrustes distances (above diagonal line) and p-values (below diagonal line) of pairwise comparisons between feeding categories of 100 bovid species. Asterisks (*) denote adjusted p-values < 0.05.

(a) The three-category classification scheme

	Browser	Mixed feeder	Grazer
Browser		0.052	0.071
Mixed feeder	0.001*		0.037
Grazer	0.001*	0.003*	

(b) The six-category classification scheme

	Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer
Frugivore		0.086	0.107	0.085	0.124	0.108
Browser	0.001*		0.039	0.031	0.057	0.071
Browser-grazer intermediate	0.001*	0.016		0.032	0.030	0.059
Generalist	0.003*	0.501	0.467		0.055	0.067
Variable grazer	0.001*	0.001*	0.067	0.029		0.052
Obligate grazer	0.001*	0.001*	0.001*	0.009	0.001*	

Table 3.5 Cross-validated classification rate (%) of feeding categories of 100 bovid species.

(a) The three-category classification scheme (average classification accuracy = 69.0%)

		Inferred Diet		
		Browser	Mixed feeder	Grazer
Observed Diet	Browser	63.6	30.3	6.1
	Mixed feeder	16.7	66.7	16.7
	Grazer	4.7	16.7	76.7

(b) The six-category classification scheme (average classification accuracy = 67.4%)

		Inferred Diet					
		Frugivore	Browser	Browser-grazer intermediate	Generalist	Variable grazer	Obligate grazer
Observed Diet	Frugivore	100.0	0	0	0	0	0
	Browser	9.1	40.9	27.3	13.6	9.1	0
	Browser-grazer intermediate	0	10.5	42.1	21.1	26.3	0
	Generalist	0	20.0	20.0	60.0	0	0
	Variable grazer	0	0	14.3	14.3	67.9	3.6
	Obligate grazer	0	0	0	0	6.7	93.3

Table 3.S 1 Dietary classifications of bovid species in selected previous studies of craniomandibular ecomorphology.

Species	Gordon and Illius (1988)	Janis and Ehrhardt (1988)	Solounias and Dawson-Saunders (1988)	Solounias and Moelleken (1993)	Spencer (1995)	Dompierre and Churcher (1996)	Sponheimer et al. (1999)	Pérez-Barbería and Gordon (2001)	Mendoza et al. (2002)	Fraser and Theodor (2011)	Forrest et al. (2018)
Addax nasomaculatus								Mixed feeder	Mixed feeder (open habitat)		Mixed feeder preferring grass
Aepyceros melampus	Intermediate feeder	Mixed feeder (open habitat)	Intermediate	Mixed feeder	Mixed-grass feeder (all levels)	Mixed feeder	Mixed feeder preferring grass	Mixed feeder	Mixed feeder (open habitat)		Mixed feeder preferring grass
Alcelaphus buselaphus	Grazer	Dry grass grazer			Grass feeder (tall plants)	Grazer	Grass feeder	Grazer	General grazer	Grazer	Grass feeder
Alcelaphus lichtensteinii	Grazer							Grazer			
Ammodorcas clarkei	Browser	High level browser						Mixed feeder	High-level browser		
Ammotragus lervia	Intermediate feeder							Mixed feeder	Mixed feeder (open habitat)		
Antidorcas marsupialis	Intermediate feeder	Mixed feeder (open habitat)		Mixed feeder	Mixed-dicot feeder (ground level)	Mixed feeder		Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	Mixed feeder preferring grass
Antilope cervicapra				Mixed feeder		Mixed feeder		Grazer	General grazer	Mixed feeder	
Beatragus hunteri	Grazer	Mixed feeder (open habitat)			Grass feeder (all levels)			Grazer	General grazer		
Bison bison	Grazer	Dry grass grazer		Grazer	Grass feeder (ground level)	Grazer		Grazer	General grazer	Grazer	
Bison bonasus	Grazer	Mixed feeder (closed habitat)						Mixed feeder	Mixed feeder (open habitat)		
Bos gaurus	Grazer	Mixed feeder (open habitat)						Grazer	General grazer		
Bos grunniens	Grazer							Grazer			
Bos indicus	Grazer								General grazer		
Bos javanicus	Grazer							Mixed feeder	Mixed feeder (open habitat)		
Bos taurus	Grazer		Grazer	Grazer		Grazer		Mixed feeder			
Boselaphus tragocamelus		Mixed feeder (closed habitat)	Intermediate	Mixed feeder		Mixed feeder		Mixed feeder	Mixed feeder (closed habitat)		
Bubalus bubalis	Grazer							Grazer	Fress-grass grazer		
Bubalus depressicornis								Mixed feeder	Mixed feeder (closed habitat)		
Budorcas taxicolor	Intermediate feeder	Mixed feeder (open habitat)	Intermediate					Mixed feeder	Mixed feeder (open habitat)		
Capra aegagrus	Intermediate feeder							Mixed feeder			
Capra caucasica	Intermediate feeder							Mixed feeder			
Capra falconeri								Mixed feeder			

Capra ibex		Mixed feeder (open habitat)				Mixed feeder		Mixed feeder	Mixed feeder (open habitat)		
Capra nubiana						Mixed feeder					
Capra pyrenaica								Mixed feeder			
Capricornis sumatraensis		Mixed feeder (open habitat)	Intermediate					Mixed feeder	Mixed feeder (closed habitat)		
Cephalophus callipygus								Browser			
Cephalophus dorsalis	Frugivore					Browser		Browser	Frugivore		Browser
Cephalophus harveyi			Browser								
Cephalophus jentinki								Browser			
Cephalophus leucogaster	Frugivore							Browser			Browser
Cephalophus natalensis	Frugivore						Browser	Browser			Browser
Cephalophus niger				Browser				Browser			
Cephalophus nigrifrons								Browser			Browser
Cephalophus ogilbyi								Browser			
Cephalophus rufilatus								Browser			
Cephalophus silvicultor	Frugivore	Unspecialized browser			Dicot feeder (ground level)			Browser	Frugivore		
Cephalophus spadix								Browser	Frugivore		
Cephalophus weynsi											Browser
Cephalophus zebra								Browser			
Connochaetes gnou		Dry grass grazer						Grazer	General grazer	Grazer	
Connochaetes taurinus	Grazer	Dry grass grazer		Grazer	Grass feeder (ground level)	Grazer		Grazer	General grazer	Grazer	Grass feeder
Damaliscus lunatus	Grazer	Dry grass grazer	Grazer	Grazer	Grass feeder (medium level)	Grazer	Grass feeder	Grazer	General grazer		Grass feeder
Damaliscus pygargus	Grazer	Dry grass grazer			Grass feeder (medium level)			Grazer	General grazer	Grazer	Grass feeder
Dorcatragus megalotis		Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)		
Eudorcas rufifrons								Mixed feeder			
Eudorcas thomsonii		Mixed feeder (open habitat)	Intermediate	Grazer	Mixed-grass feeder (ground level)	Mixed feeder	Mixed feeder preferring grass	Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	Mixed feeder preferring grass
Gazella cuvieri								Mixed feeder			
Gazella dorcas								Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	

Gazella gazella								Mixed feeder			
Gazella leptoceros								Mixed feeder			
Gazella spekei								Mixed feeder			
Gazella subgutturosa								Mixed feeder			
Hemitragus jayakari								Mixed feeder			
Hemitragus jemlahicus	Intermediate feeder							Mixed feeder	Mixed feeder (open habitat)		
Hippotragus equinus	Grazer	Dry grass grazer			Grass feeder (medium level)	Grazer		Grazer	General grazer		Mixed feeder preferring grass
Hippotragus niger	Grazer	Dry grass grazer	Grazer		Grass feeder (medium level)	Grazer		Grazer	General grazer		Mixed feeder preferring grass
Kobus ellipsiprymnus	Grazer	Fresh grass grazer	Grazer		Grass feeder (ground level)	Grazer	Fresh grass feeder	Grazer	Fresh-grass browser		Fresh grass feeder
Kobus kob		Fresh grass grazer			Grass feeder (ground level)		Fresh grass feeder	Grazer	Fresh-grass browser	Grazer	Fresh grass feeder
Kobus leche		Fresh grass grazer			Grass feeder (medium level)		Fresh grass feeder	Grazer	Fresh-grass browser		
Kobus megaceros								Mixed feeder			Fresh grass feeder
Kobus vardonii	Grazer				Grass feeder (ground level)			Grazer	Fresh-grass browser		
Litocranius walleri	Browser	High level browser	Browser	Browser	Dicot feeder (tall plants)	Browser	Browser	Browser	High-level browser	Browser	
Madoqua guentheri	Browser								General browser		
Madoqua kirkii	Browser	Selective browser						Browser	General browser	Browser	Browser
Madoqua piacentinii								Browser			
Madoqua saltiana	Browser							Browser			Browser
Naemorhedus baileyi											
Naemorhedus goral	Browser	Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)		
Nanger dama								Mixed feeder			
Nanger granti	Intermediate feeder	Mixed feeder (open habitat)	Intermediate	Mixed feeder	Mixed-dicot feeder (ground level)	Mixed feeder	Mixed feeder preferring browse	Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	Mixed feeder preferring browse
Nanger soemmerringii					Mixed-dicot feeder (ground level)		Mixed feeder preferring browse	Mixed feeder			
Neotragus batesi										Browser	
Nesotragus moschatus	Browser	Selective browser						Browser	General browser	Browser	Browser
Neotragus pygmaeus								Browser	General browser		
Nilgiritragus hylocrius								Mixed feeder			

Oreamnos americanus	Intermediate feeder	Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)		
Oreotragus oreotragus	Intermediate feeder				Dicot feeder (ground level)			Browser	General browser	Mixed feeder	
Oryx beisa	Grazer										
Oryx dammah								Mixed feeder			
Oryx gazella		Mixed feeder (open habitat)			Grass feeder (all levels)	Mixed feeder	Mixed feeder preferring grass	Mixed feeder	Mixed feeder (open habitat)		Mixed feeder preferring grass
Oryx leucoryx	Grazer							Mixed feeder			
Ourebia ourebi	Grazer	Mixed feeder (open habitat)	Grazer	Grazer	Mixed-grass feeder (ground level)	Mixed feeder		Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	Mixed feeder preferring grass
Ovibos moschatus	Intermediate feeder	Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)		
Ovis ammon	Grazer							Mixed feeder			
Ovis aries			Grazer								
Ovis canadensis	Intermediate feeder	Mixed feeder (open habitat)				Mixed feeder		Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	
Ovis dalli								Mixed feeder	Mixed feeder (open habitat)		
Ovis nivicola								Mixed feeder			
Ovis orientalis								Mixed feeder			
Pantholops hodgsonii	Grazer							Mixed feeder	Mixed feeder (open habitat)		
Pelea capreolus		Mixed feeder (open habitat)						Browser	General browser		
Philantomba maxwellii								Browser			
Philantomba monticola	Frugivore	Selective browser						Browser	Frugivore		Browser
Procapra gutturosa								Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	
Procapra picticaudata											
Pseudois nayaur	Grazer	Mixed feeder (open habitat)		Mixed feeder		Mixed feeder		Mixed feeder	Mixed feeder (open habitat)		
Raphicerus campestris	Intermediate feeder	Mixed feeder (open habitat)	Intermediate				Mixed feeder preferring browse	Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	Mixed feeder preferring browse
Raphicerus melanotis		Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	
Raphicerus sharpei	Browser							Mixed feeder			
Redunca arundinum	Grazer	Fresh grass grazer			Grass feeder (tall plants)		Fresh grass feeder	Grazer	Fresh-grass grazer		Fresh grass feeder
Redunca fulvorufula	Grazer	Mixed feeder (open habitat)	Grazer		Grass feeder (ground level)		Grass feeder	Grazer	Fresh-grass grazer		Grass feeder
Redunca redunca					Grass feeder (ground level)		Fresh grass feeder	Grazer			Fresh grass feeder

Rupicapra rupicapra	Browser	Mixed feeder (open habitat)						Mixed feeder	Mixed feeder (open habitat)		
Saiga tatarica	Grazer							Mixed feeder	Mixed feeder (open habitat)	Mixed feeder	
Sylvicapra grimmia	Browser	Unspecialized browser	Browser		Dicot feeder (ground level)	Browser	Browser	Browser	General browser	Browser	Browser
Syncerus caffer	Grazer	Mixed feeder (open habitat)		Grazer	Grass feeder (tall plants)	Grazer	Fresh grass feeder	Grazer	General grazer		
Taurotragus derbianus								Mixed feeder			
Taurotragus oryx	Intermediate feeder	Mixed feeder (open habitat)		Mixed feeder	Mixed-dicot feeder (all levels)	Mixed feeder	Mixed feeder preferring browse	Mixed feeder	Mixed feeder (open habitat)		Mixed feeder preferring browse
Tetracerus quadricornis		Mixed feeder (closed habitat)	Browser			Mixed feeder		Grazer	Mixed feeder (closed habitat)		
Tragelaphus angasii	Intermediate feeder	Mixed feeder (closed habitat)						Mixed feeder	Mixed feeder (closed habitat)		
Tragelaphus buxtoni		Unspecialized browser						Browser	General browser		
Tragelaphus eurycerus	Browser	Unspecialized browser		Browser	Dicot feeder (ground level)	Browser	Browser	Mixed feeder	General browser		Mixed feeder
Tragelaphus imberbis		Unspecialized browser	Browser		Dicot feeder (tall plants)	Browser	Browser	Browser	Mixed feeder (closed habitat)		
Tragelaphus scriptus	Browser	Unspecialized browser	Browser	Mixed feeder	Dicot feeder (medium level)	Browser	Browser	Browser	Mixed feeder (closed habitat)		Mixed feeder
Tragelaphus spekii	Intermediate feeder			Browser	Dicot feeder (tall plants)	Mixed feeder	Mixed feeder preferring browse	Mixed feeder	Mixed feeder (closed habitat)		Mixed feeder preferring browse
Tragelaphus strepsiceros	Browser	Unspecialized browser			Dicot feeder (tall plants)		Browser	Browser	General browser		Mixed feeder

Table 3.S 2 Mandibular landmarks used in this study.

Landmark	Description
1	Posterior end of the last incisor on the mandibular margin
2	Anterior end of the premolars on the mandibular margin
3	Midpoint between premolars and molars on the mandibular margin
4	Posterior end of the third molar on the mandibular margin
5	Most dorsal point of the coronoid process
6	Most posterior point of the coronoid process
7	Point of maximum concavity between the condyle and the coronoid process
8	Most dorsoposterior point of the condyle
9	Most dorsocaudal rugosity from masseter insertion on the posterior margin of the angular
10	Point of maximum convexity on the posterior margin of the angular
11	Point of maximum concavity on the ventral margin of the angular
12	Posterior end of the symphysis on the ventral mandibular margin
13	Anterior end of the first incisor on the mandible
14	Center of the mental foramen

Table 3.S 3 Scores of 100 bovids species from principal component analysis. Numbers in column headings denote variance explained by each principal component (PC).

Species	PC1 (45.6%)	PC2 (14.7%)	PC3 (13.5%)	PC4 (8.8%)	PC5 (3.8%)	PC6 (3.1%)
Bos gaurus	0.0420	-0.0368	0.0041	0.0265	0.0113	0.0137
Bos javanicus	0.0147	-0.0129	0.0176	0.0411	0.0149	0.0104
Bison bonasus	0.0060	-0.0060	-0.0029	0.0637	-0.0111	-0.0100
Bison bison	0.0147	0.0001	0.0033	0.0449	-0.0119	0.0051
Bubalus mindorensis	0.0226	-0.0321	0.0311	0.0491	0.0090	-0.0125
Bubalus depressicornis	0.0437	-0.0435	0.0198	0.0043	0.0199	-0.0126
Syncerus caffer	-0.0122	-0.0444	0.0114	0.0301	0.0015	0.0069
Tragelaphus angasii	-0.0012	0.0133	-0.0148	0.0028	-0.0066	0.0039
Tragelaphus strepsiceros	0.0343	-0.0150	-0.0196	-0.0085	-0.0120	0.0154
Tragelaphus scriptus	0.0379	0.0465	-0.0257	0.0052	0.0123	-0.0016
Tragelaphus buxtoni	0.0212	0.0407	0.0040	0.0123	0.0010	0.0089
Tragelaphus eurycerus	0.0509	0.0149	0.0015	0.0241	0.0032	0.0035
Tragelaphus spekii	0.0235	-0.0318	0.0068	-0.0106	0.0019	-0.0128
Taurotragus oryx	0.0096	0.0447	-0.0272	0.0224	-0.0094	0.0160
Taurotragus derbianus	0.0076	0.0169	0.0122	0.0193	-0.0095	0.0063
Tragelaphus imberbis	0.0447	0.0319	-0.0155	0.0018	-0.0073	-0.0015
Ammodorcas clarkei	-0.0338	0.0091	-0.0318	-0.0500	-0.0087	-0.0173
Tetracerus quadricornis	0.0461	0.0389	0.0131	-0.0056	0.0069	-0.0025
Boselaphus tragocamelus	0.0452	0.0028	-0.0079	-0.0027	0.0050	-0.0052
Nesotragus moschatus	0.0398	0.0329	0.0125	-0.0113	-0.0099	-0.0164
Neotragus batesi	0.0764	0.0229	0.0061	0.0029	-0.0038	-0.0082
Aepyceros melampus	-0.0289	0.0145	-0.0155	0.0018	0.0009	-0.0004
Redunca fulvorufula	-0.0026	-0.0258	-0.0472	-0.0255	0.0187	0.0046
Redunca redunca	0.0090	-0.0333	-0.0374	-0.0168	0.0105	-0.0085
Redunca arundinum	0.0129	-0.0294	-0.0459	-0.0276	0.0025	-0.0173
Kobus megaceros	0.0275	-0.0482	0.0002	0.0110	0.0152	-0.0006
Kobus leche	0.0120	-0.0629	-0.0120	-0.0200	0.0172	-0.0025
Kobus vardonii	-0.0003	-0.0456	-0.0157	-0.0180	0.0169	-0.0049
Kobus kob	0.0183	-0.0448	0.0124	0.0036	0.0031	-0.0022
Kobus ellipsiprymnus	-0.0161	-0.0260	-0.0269	-0.0029	-0.0216	-0.0021
Procapra gutturosa	-0.0661	-0.0078	0.0144	0.0056	0.0009	0.0050
Ourebia ourebi	0.0087	-0.0086	0.0130	-0.0121	-0.0028	0.0136
Raphicerus sharpei	-0.0051	0.0197	0.0338	0.0009	-0.0194	0.0034
Raphicerus campestris	-0.0023	0.0130	0.0238	-0.0193	-0.0226	0.0058
Madoqua saltiana	-0.0072	0.0311	0.0235	-0.0478	-0.0022	0.0094
Madoqua kirkii	-0.0247	0.0185	0.0193	-0.0433	-0.0117	0.0177
Madoqua guentheri	-0.0183	0.0254	0.0233	-0.0444	-0.0117	0.0052
Dorcatragus megalotis	-0.0308	-0.0068	0.0069	-0.0352	-0.0196	0.0440
Saiga tatarica	-0.0919	-0.0066	0.0336	-0.0044	0.0206	0.0082
Nanger granti	-0.0240	-0.0001	0.0282	-0.0198	0.0002	-0.0119
Nanger soemmerringii	-0.0136	0.0160	0.0241	0.0008	0.0014	-0.0140
Nanger dama	-0.0128	0.0163	0.0206	-0.0086	-0.0104	-0.0103
Eudorcas thomsonii	-0.0504	-0.0175	0.0445	-0.0223	-0.0047	-0.0240
Eudorcas rufifrons	-0.0266	0.0152	0.0043	-0.0137	-0.0115	-0.0040

Gazella leptoceros	-0.0202	0.0116	0.0419	-0.0085	0.0062	-0.0016
Gazella subgutturosa	-0.0045	0.0183	0.0501	0.0062	0.0124	-0.0055
Gazella dorcas	-0.0080	0.0245	0.0319	-0.0146	0.0000	-0.0072
Gazella gazella	-0.0021	0.0289	0.0283	-0.0084	-0.0007	-0.0070
Gazella arabica	0.0134	0.0051	0.0586	-0.0122	0.0062	0.0044
Gazella spekei	-0.0280	0.0066	0.0242	-0.0453	0.0087	0.0025
Antilope cervicapra	-0.0297	-0.0360	0.0421	-0.0068	0.0219	-0.0156
Litocranius walleri	0.0241	0.0501	-0.0639	-0.0291	0.0132	-0.0343
Antidorcas marsupialis	-0.0562	-0.0070	0.0243	0.0111	0.0045	-0.0152
Neotragus pygmaeus	0.0478	0.0047	0.0020	0.0005	-0.0141	0.0208
Oreotragus oreotragus	0.0250	0.0052	0.0492	0.0155	-0.0244	0.0010
Philantomba monticola	0.0835	0.0212	-0.0287	-0.0176	-0.0045	-0.0036
Philantomba maxwellii	0.1208	0.0000	-0.0077	0.0164	-0.0125	-0.0075
Cephalophus zebra	0.0726	-0.0062	-0.0013	0.0071	0.0017	0.0032
Sylvicapra grimmia	0.0669	0.0198	-0.0172	0.0082	0.0037	0.0185
Cephalophus spadix	0.1011	-0.0174	-0.0022	-0.0111	0.0047	-0.0102
Cephalophus silvicultor	0.0954	-0.0229	0.0093	0.0011	-0.0033	0.0097
Cephalophus dorsalis	0.0623	-0.0187	0.0203	0.0033	-0.0066	0.0085
Cephalophus leucogaster	0.0807	-0.0275	0.0156	-0.0050	0.0033	0.0166
Cephalophus nigrifrons	0.0847	0.0079	-0.0178	-0.0010	-0.0039	-0.0072
Cephalophus natalensis	0.0986	-0.0131	0.0001	-0.0110	0.0219	0.0134
Cephalophus harveyi	0.0767	0.0090	-0.0175	-0.0213	-0.0045	0.0083
Cephalophus callipygus	0.1104	0.0101	-0.0246	0.0015	0.0003	-0.0105
Pantholops hodgsonii	-0.0734	-0.0308	0.0087	0.0044	0.0169	-0.0188
Ovibos moschatus	-0.0048	0.0180	-0.0071	0.0262	-0.0409	-0.0280
Naemorhedus goral	-0.0136	-0.0074	0.0310	-0.0116	-0.0049	-0.0080
Capricornis sumatraensis	0.0039	0.0017	-0.0074	-0.0099	-0.0105	-0.0019
Ovis nivicola	-0.0450	0.0118	-0.0105	0.0171	0.0040	0.0115
Ovis dalli	-0.0472	0.0371	-0.0070	0.0347	0.0008	0.0105
Ovis canadensis	-0.0681	0.0230	-0.0219	0.0065	0.0026	0.0197
Ovis orientalis	-0.0425	0.0206	-0.0141	0.0082	0.0041	0.0036
Ovis ammon	-0.0350	0.0102	-0.0290	0.0108	0.0108	0.0002
Nilgiritragus hylocrius	-0.0628	-0.0053	-0.0553	0.0089	-0.0045	-0.0183
Hemitragus jemlahicus	-0.0555	0.0220	0.0007	0.0218	0.0088	0.0011
Capra sibirica	-0.0498	0.0150	0.0003	0.0051	0.0265	0.0022
Capra pyrenaica	-0.0166	0.0169	0.0091	0.0133	0.0184	0.0078
Capra ibex	-0.0153	0.0190	0.0061	0.0253	0.0213	0.0064
Capra walie	-0.0115	0.0428	0.0053	-0.0151	0.0267	-0.0065
Capra nubiana	-0.0195	0.0467	-0.0035	0.0256	0.0070	-0.0239
Capra falconeri	-0.0144	0.0283	0.0094	-0.0071	0.0300	0.0184
Pseudois nayaur	-0.0904	0.0254	-0.0096	0.0067	0.0105	0.0057
Budorcas taxicolor	-0.0023	0.0110	-0.0100	0.0123	0.0104	-0.0069
Oreamnos americanus	-0.0393	0.0162	-0.0020	0.0123	0.0089	0.0169
Rupicapra rupicapra	-0.0398	0.0045	-0.0213	-0.0012	-0.0060	0.0050
Ammotragus lervia	-0.0543	0.0258	-0.0190	0.0041	-0.0079	-0.0049
Connochaetes taurinus	-0.0375	-0.0342	-0.0260	-0.0044	-0.0131	0.0003
Connochaetes gnou	-0.0668	-0.0065	-0.0223	0.0197	-0.0109	-0.0154
Damaliscus pygargus	-0.0493	-0.0389	-0.0348	0.0218	0.0084	0.0166

Damaliscus lunatus	-0.0317	-0.0241	-0.0449	-0.0155	0.0108	0.0061
Alcelaphus buselaphus	-0.0413	-0.0088	-0.0840	-0.0077	-0.0020	0.0161
Hippotragus niger	-0.0272	-0.0486	0.0004	0.0040	-0.0149	-0.0002
Hippotragus equinus	-0.0099	-0.0574	0.0203	-0.0293	-0.0064	0.0011
Oryx dammah	-0.0221	-0.0221	-0.0074	0.0179	-0.0194	-0.0077
Oryx gazella	-0.0427	-0.0262	-0.0149	0.0083	-0.0313	0.0083
Oryx beisa	-0.0654	-0.0325	-0.0001	-0.0085	-0.0301	0.0031
Addax nasomaculatus	-0.0245	-0.0270	0.0196	0.0124	-0.0249	-0.0052

Table 3.S 4 Non-phylogenetic ANOVA for 100 species of extant bovids, using a three-part (browser, mixed feeder, grazer) and a six-part (frugivore, browser, browser-grazer intermediate, generalist, variable grazer, obligate grazer) dietary classification.

Effect	Df	SS	MS	R^2	F	Z	Pr (>F)
3 diets on shape	2	0.107	0.054	0.228	14.320	5.685	0.001
Residuals	97	0.363	0.004				
Total	99	0.470					
6 diets on shape	5	0.192	0.038	0.409	12.994	7.737	0.001
Residuals	94	0.278	0.003				
Total	99	0.470					

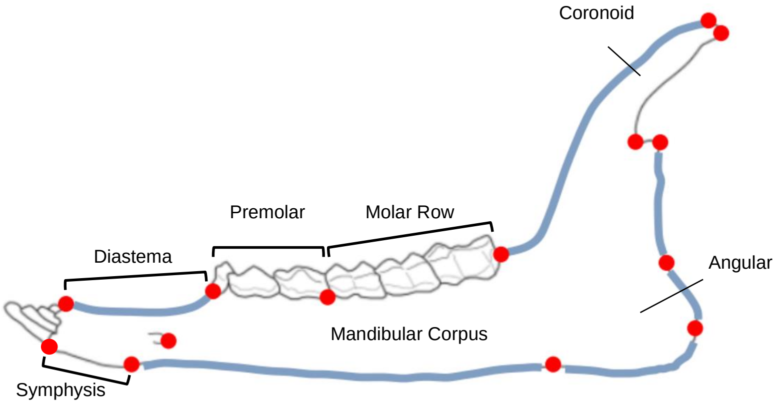
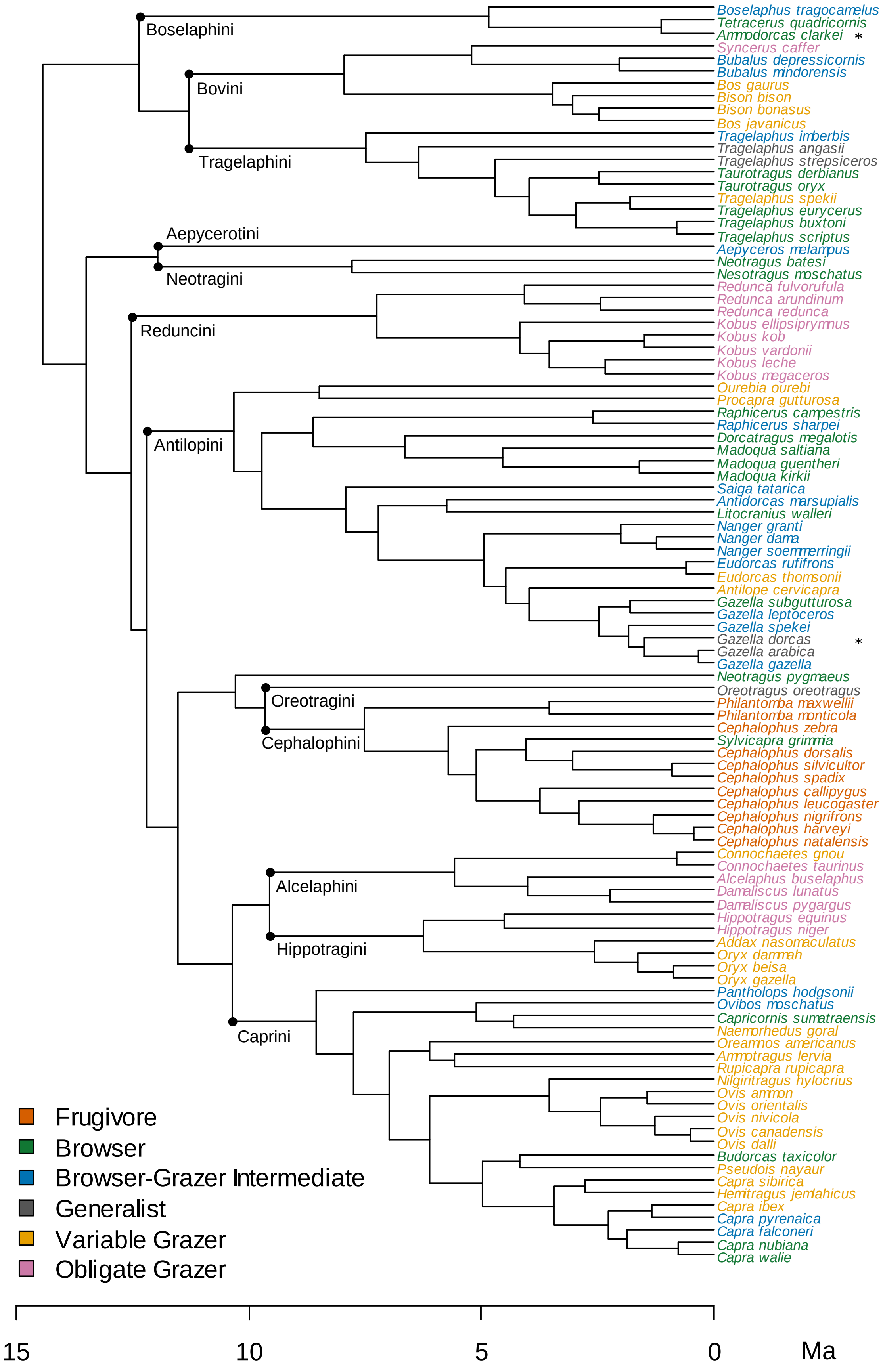


Figure 3.1 Landmarks (red circles) and semilandmarks (along blue curves) on a representative mandible of *Madoqua kirkii*.

Figure 3.2 Distribution of six feeding categories in the bovid phylogenetic tree. Phylogeny from Upham et al. (2019). Species with polyphyletic tribe assignments are noted with an asterisk (see section 3.2).


Boselaphus tragocamelus
Tetracerus quadricornis
Ammodorcas clarkei *
Syncerus caffer
Bubalus depressicornis
Bubalus mindorensis
Bos gaurus
Bison bison
Bison bonasus
Bos javanicus
Tragelaphus imberbis
Tragelaphus angasii
Tragelaphus strepsiceros
Taurotragus derbianus
Taurotragus oryx
Tragelaphus spekii
Tragelaphus eurycerus
Tragelaphus buxtoni
Tragelaphus scriptus
Aepyceros melampus
Neotragus batesi
Nesotragus moschatus
Redunca fulvorufula
Redunca arundinum
Redunca redunca
Kobus ellipsiprymnus
Kobus kob
Kobus vardonii
Kobus leche
Kobus megaceros
Ourebia ourebi
Procapra gutturosa
Raphicerus campestris
Raphicerus sharpei
Dorcatragus megalotis
Madoqua saltiana
Madoqua guentheri
Madoqua kirkii
Saiga tatarica
Antidorcas marsupialis
Litocranius walleri
Nanger granti
Nanger dama
Nanger soemmerringii
Eudorcas rufifrons
Eudorcas thomsonii
Antilope cervicapra
Gazella subgutturosa
Gazella leptoceros
Gazella spekei
Gazella dorcas *
Gazella arabica
Gazella gazella
Neotragus pygmaeus
Oreotragus oreotragus
Philantomba maxwellii
Philantomba monticola
Cephalophus zebra
Sylvicapra grimmia
Cephalophus dorsalis
Cephalophus silvicultor
Cephalophus spadix
Cephalophus callipygus
Cephalophus leucogaster
Cephalophus nigrifrons
Cephalophus harveyi
Cephalophus natalensis
Connochaetes gnou
Connochaetes taurinus
Alcelaphus buselaphus
Damaliscus lunatus
Damaliscus pygargus
Hippotragus equinus
Hippotragus niger
Addax nasomaculatus
Oryx dammah
Oryx beisa
Oryx gazella
Pantholops hodgsonii
Ovibos moschatus
Capricornis sumatraensis
Naemorhedus goral
Oreamnos americanus
Ammotragus lervia
Rupicapra rupicapra
Nilgiritragus hylocrius
Ovis ammon
Ovis orientalis
Ovis nivicola
Ovis canadensis
Ovis dalli
Budorcas taxicolor
Pseudois nayaur
Capra sibirica
Hemitragus jemlahicus
Capra ibex
Capra pyrenaica
Capra falconeri
Capra nubiana
Capra walie
Boselaphini
Bovini
Tragelaphini
Aepycerotini
Neotragini
Reduncini
Antilopini
Oreotragini
Cephalophini
Alcelaphini
Hippotragini
Caprini
Frugivore
Browser
Browser-Grazer Intermediate
Generalist
Variable Grazer
Obligate Grazer
15
10
5
0
Ma

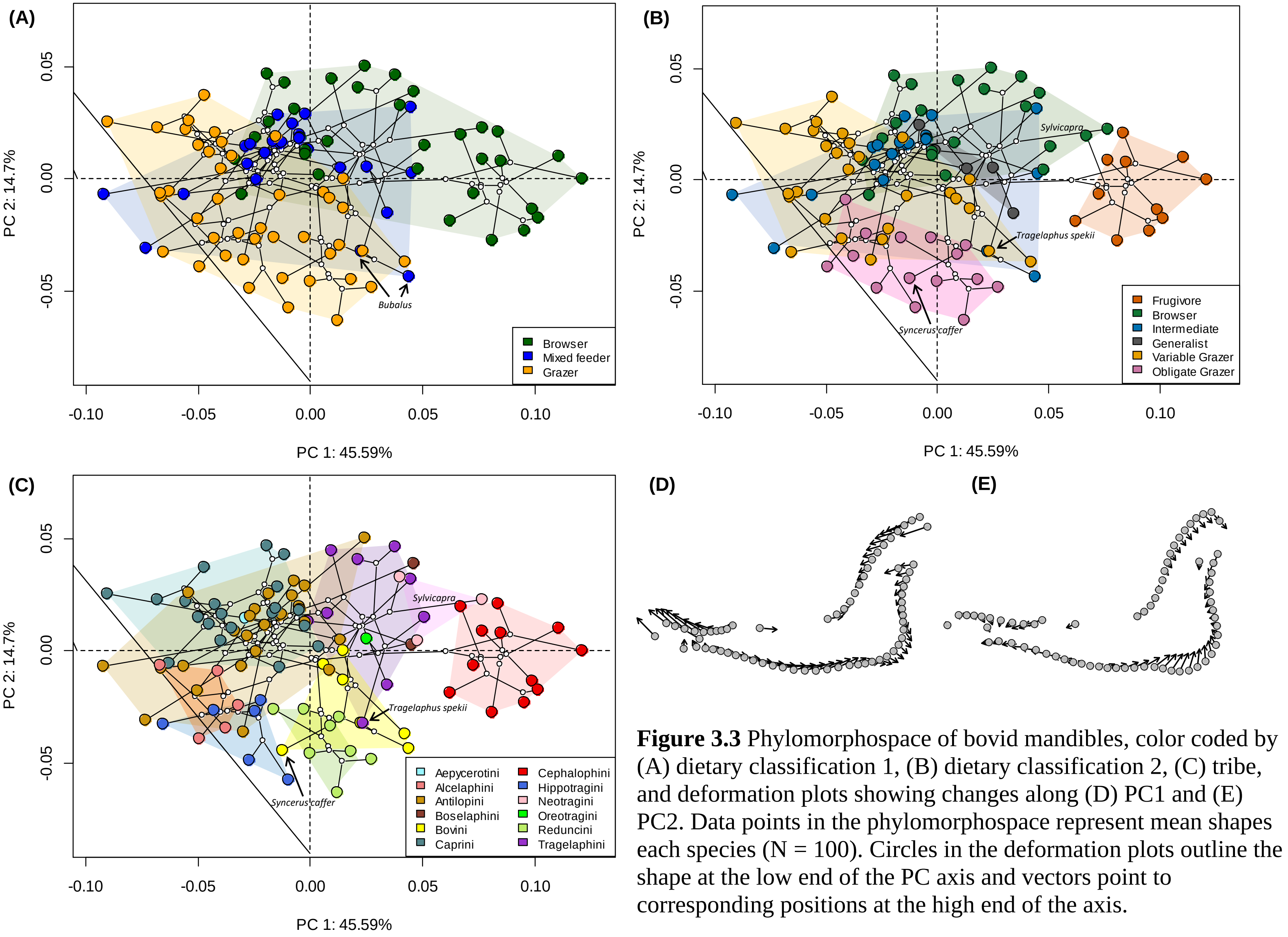


Figure 3.3 Phylomorphospace of bovid mandibles, color coded by (A) dietary classification 1, (B) dietary classification 2, (C) tribe, and deformation plots showing changes along (D) PC1 and (E) PC2. Data points in the phylomorphospace represent mean shapes each species (N = 100). Circles in the deformation plots outline the shape at the low end of the PC axis and vectors point to corresponding positions at the high end of the axis.

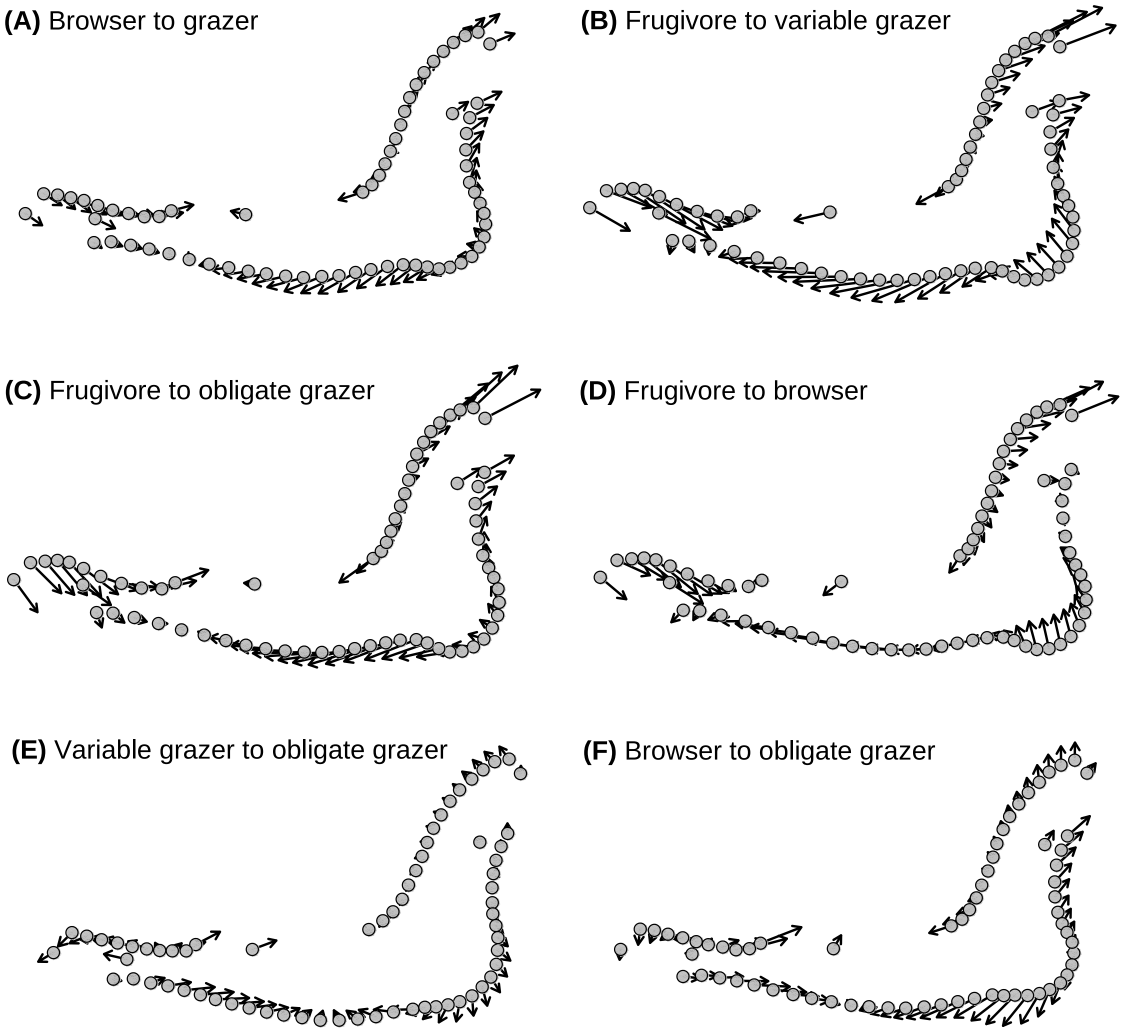


Figure 3.4 Deformation plots showing differences between feeding categories. Circles in the deformation plot outline the mean shape of the reference dietary group and vectors point to corresponding positions in the mean shape of the target dietary group.

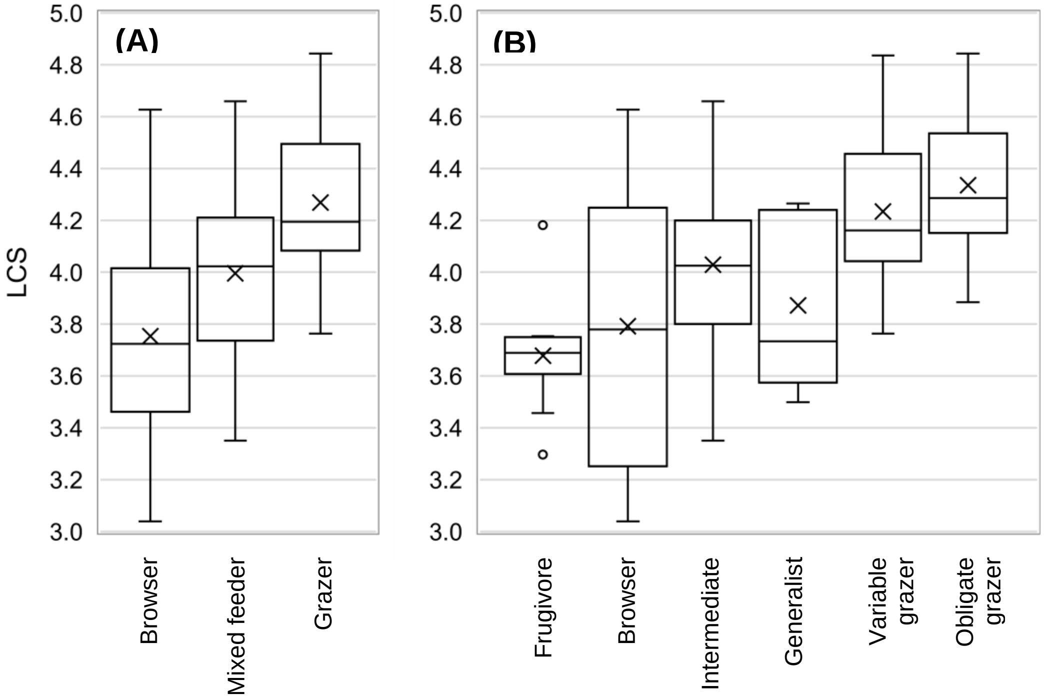


Figure 3.5 Box plots of ln-transformed centroid sizes (LCS) of dietary groups for the first (A) and second (B) classification schemes. Crosses (×) are mean values. Horizontal lines of boxes mark the 1st quartile, mean, and 3rd quartile values. Whiskers represent the range of values (excluding outliers). Circles are outliers.

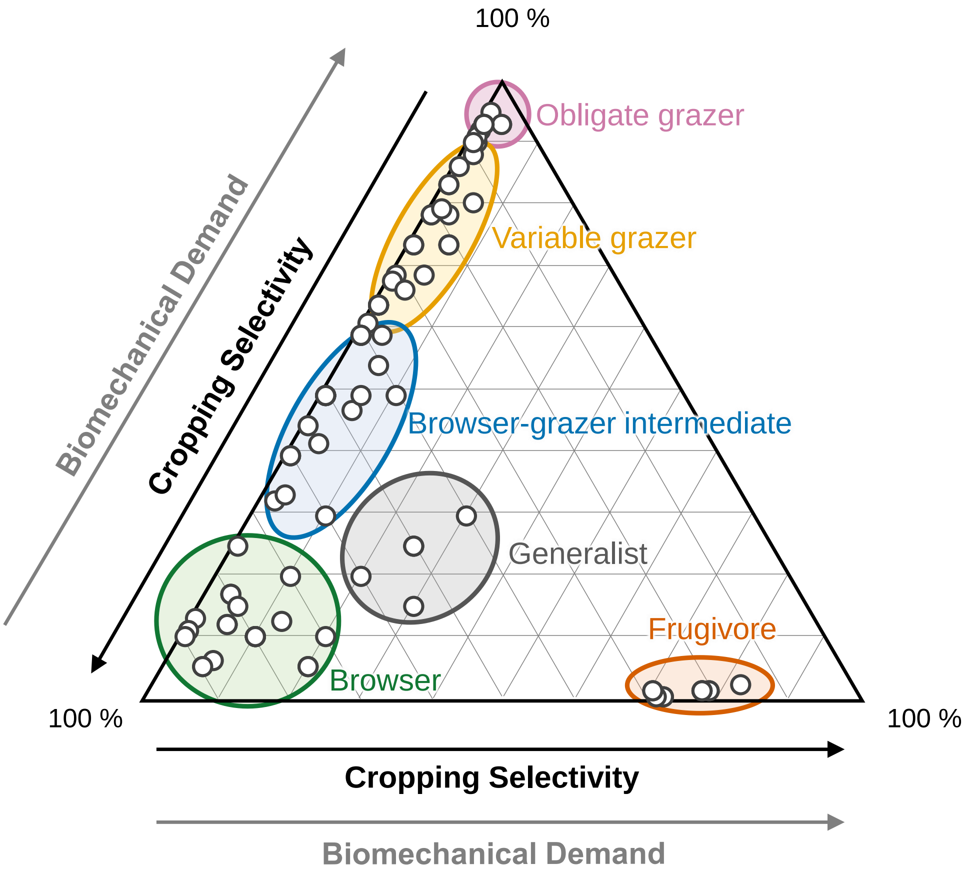


Figure 3.6 Proposed conceptual ruminant dietary spectrum and its properties. Ternary diagram shows the average diets of 100 species of bovids. Black arrows point to higher cropping selectivity during foraging. Gray arrows point to higher mechanical demand of food-processing.

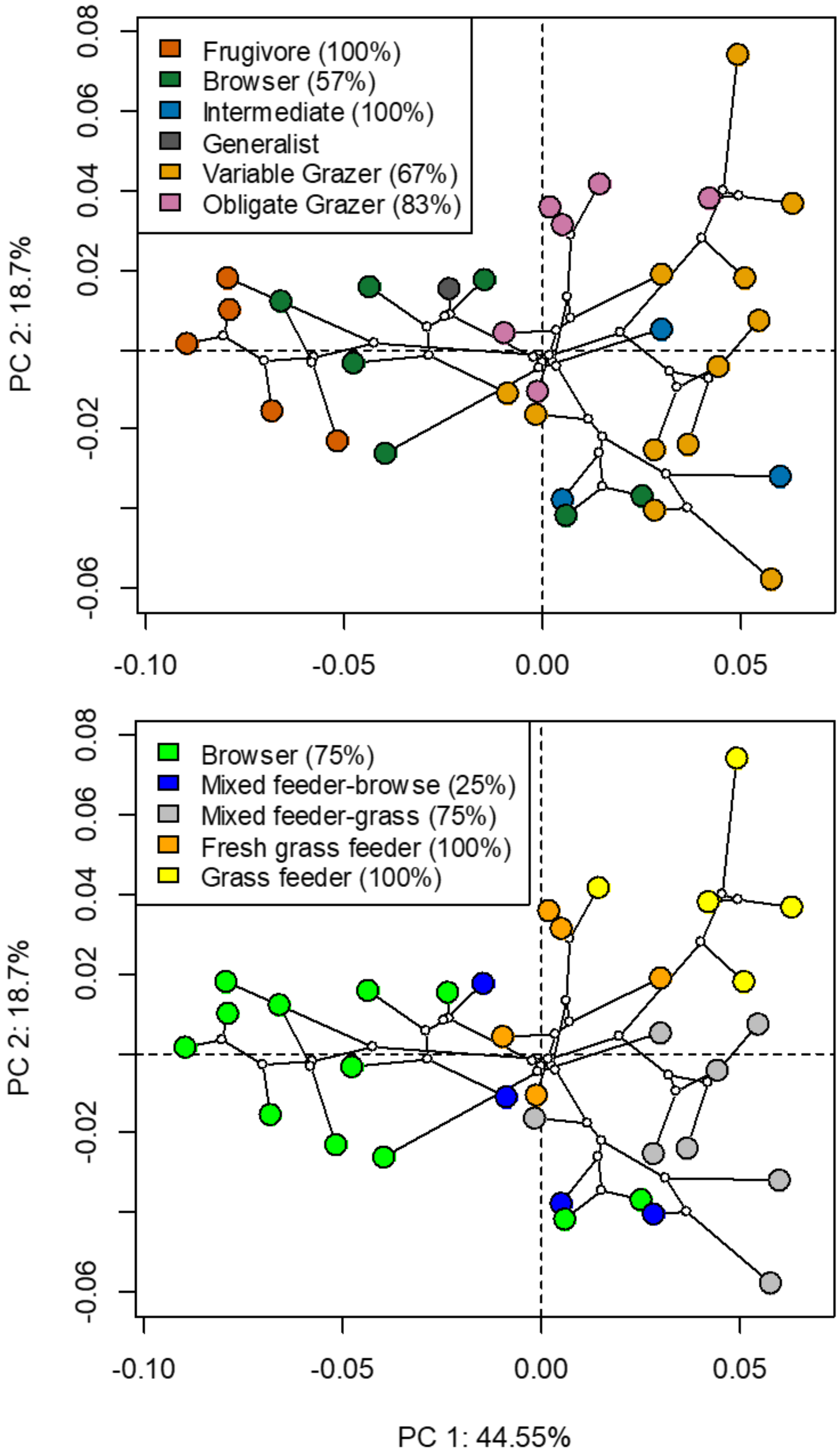


Figure 3.S 1 Phylomorphospace of bovid mandibles color coded by the dietary classification used in our study (top panel) and in Forrest et al. (2018) (bottom panel). Data points represent mean shapes of species (N = 34). Percentages in legend are classification accuracies from jackknife cross-validation, performed for groups with more than one sampled species.

Chapter 4

Ecological Diversity of Extant Artiodactyls in Relation to Climate and Topography

4.1 Introduction

Stable isotopes are one of nature's great ecological recorders and have been widely used to study organisms and ecosystems across time and space (West et al., 2006). Among the animal tissues that are commonly sampled for stable isotope analyses of mammals (tooth enamel, dentin, bone collagen, hair, blood), only tooth enamel is resistant to long-term fossilization processes and diagenesis (e.g., Lee-Thorp, 2002). Therefore, data generated from modern mammal teeth can be readily applied to the interpretation of deep-time records. Isotope data from African ungulates, for example, have contributed substantial insights to our understanding of ungulate dietary ecology and have laid the foundations for a large body of literature on inferring paleodiet and paleoenvironment from fossil herbivore teeth (e.g., Koch et al., 1991; Bocherens and Geraads, 1996; Cerling and Harris, 1999; Passey and Cerling, 2002; Cerling et al., 2003; Sponheimer et al., 2003).

The stable isotope composition of carbon ($\delta^{13}C$) in the enamel of mammalian herbivores provides information about animals' feeding ecology and vegetation present in the habitat. Plants that use different photosynthetic pathways differ in their fractionation of atmospheric CO_2 during photosynthesis. The resulting $\delta^{13}C$ values in plant tissues are lowest in plants using the C_3 pathway, intermediate in plants using the crassulacean acid metabolism (CAM) pathway, and highest in plants using the C_4 pathway (O'Leary, 1988; Cerling et al., 1997). Mammalian herbivore enamel bioapatites are systematically enriched in $\delta^{13}C$ relative to bulk plant diet with measurable enrichment factors (Lee-Thorp and van der Merwe, 1987; Cerling and Harris, 1999; Passey et al., 2005). Thus, the carbon isotope composition of tooth enamel reliably reflects the values in the ingested plants, and mammals feeding on isotopically different vegetation are readily distinguishable from each other. Pure C_3 and C_4 consumers have non-overlapping $\delta^{13}C$ values, while mammals with mixed C_3/C_4 diets have intermediate $\delta^{13}C$ values (MacFadden and Cerling, 1996; Cerling et al., 1997, 1998; Koch, 1998; Cerling et al., 2015). CAM plants commonly grow in xeric habitats and (Ehleringer et al., 1991). Although some extant rhinos eat CAM plants, possibly to avoid competition with elephants (Landman et al., 2013), CAM plants are not typically consumed by ungulates. Therefore, they are not usually considered when interpreting the carbon isotopic values of modern or fossil ungulates.

Isotopic variability among C_3 plants is generally greater than that in C_4 plants (e.g., Cerling et al., 1997). In general, higher (more enriched) values of the carbon isotope composition of tooth enamel of herbivorous mammals are representative of open-canopy, drier habitats (such as shrubland and grassland), while low values represent closed-canopy habitats (such as woodlands and forests) (O'Leary et al., 1992; Koch, 1998; Cerling and Harris, 1999; Feranec, 2003, 2007; Feranec and MacFadden, 2006; Secord et al., 2008). Resource partitioning in diet and habitat use may be revealed through stable isotope analysis (Koch et al., 1998; Feranec and MacFadden, 2006), and has been documented for medium-to large-bodied herbivores in both modern and ancient environments in which a mixture of C_3 and C_4 plants is present (e.g., Wang et al., 1994; MacFadden and Cerling, 1996; Koch, 1998; Feranec and MacFadden, 2006).

Although this study focuses on the diets of artiodactyls and does not evaluate oxygen isotope composition ($\delta^{18}O$), it is worth mentioning that the $\delta^{18}O$ values of mammalian tooth enamel are often analyzed in association with $\delta^{13}C$ values, and can provide useful information about animal drinking behavior and habitat preference, as well as local climatic conditions (Kohn, 1996; Kohn et al., 1996; Levin et al., 2006; Secord et al., 2008, 2010; Wang and Secord, 2020).

Recent research has identified gaps in our knowledge of the stable isotope ecology of large mammals and its application in the fossil record, such as what factors influence enrichment processes and how much variability in resource partitioning exists among different faunas (Tejada-Lara et al., 2018, 2020; DeSantis et al., 2020). These findings highlight the need for more data from a range of modern ecosystems for better understanding of processes and factors that affect the isotopic signatures in mammal tissues. In addition, stable-isotope ratios of ungulate tooth enamel can be compared to morphological and use-wear variables, including the hypsodonty index, dental mesowear (sharpness of tooth cusps), dental microwear (microscopic abrasion patterns on the occlusal surface), as well as stomach- and fecal contents and other types of data that are commonly used to document ungulate dietary ecology. Such cross-method comparisons capture dietary behaviors and adaptations recorded through different processes and over different time scales, thus providing more reliable and detailed dietary information for extant and fossil species (e.g., Sponheimer et al., 2003; Boisserie et al., 2005; Merceron et al., 2006; Louys et al., 2012; Bradham et al., 2018; Uno et al., 2018; Gong et al., 2020).

In this study, I compile and compare the carbon-isotope data that have been published to date from the tooth enamel of extant artiodactyls. To build on existing data and better understand the range and distribution of isotopic values across taxa and regions, I additionally sampled and analyzed 80 tooth specimens from 23 species of artiodactyls. Each species was chosen either because it had not been previously analyzed for stable isotope of enamel or because existing isotope data for the species included small sample sizes from restricted locations. The resulting dataset includes published and new isotope data for 80 artiodactyl species, covering a range of habitats and dietary ecology. Combining the isotope data from artiodactyl enamel, dietary data derived from other studies, and the environmental setting of localities, I address the following research questions: (1) How do species with different dietary habits compare in the mean and range of $\delta^{13}C$ values of their diet? (2) How do artiodactyl diets in different ecoregions of the world compare in the mean and range of $\delta^{13}C$ values? (3) How do phylogenetic groups of artiodactyls compare in the mean and range of $\delta^{13}C$ values? (4) What is the nature of geographic variation in the $\delta^{13}C$ values of forage in wide-ranging species?

4.2 Data and Methods

I compiled a global dataset of the carbon-isotope values of artiodactyl tooth enamel ($\delta^{13}C_E$) from the literature, supplemented by 80 newly analyzed samples to expand the taxonomic and geographic coverage for extant species (Fig. 4.1). After correcting for differences in atmospheric carbon-isotope composition ($\delta^{13}C_{atm}$), body mass, and digestive physiology among sampled individuals, the inferred carbon-isotope values of the vegetation that each species fed on ($\delta^{13}C_{diet}$) were compared among seven herbivore feeding categories, eleven terrestrial ecoregions, phylogenetic groups (species and families), and geographic regions.

4.2.1 Published $\delta^{13}C_E$ data

Published $\delta^{13}C_E$ values of extant artiodactyls were assembled from 23 primary sources (see Table 4.1). Data from paleontological or archaeological sites or from other body tissues were not included. In most instances, only samples from wild animals are included. The exception was one study of free-range yak and goat on the Tibetan Plataeu to increase the sample size from Asia. Along with published $\delta^{13}C_E$ data, I collected the following information from the literature whenever available: taxonomic identification, sample identification number (field number or museum catalogue number), provenance (locality name, geographic coordinates, elevation), year of collection, sampled element (tooth position), method of sampling (serial or bulk), and whether or not samples were pretreated before analysis. If multiple samples were taken from the same tooth or duplicates were run for the same bulk sample, then average values for the tooth were used. If multiple teeth were sampled from an individual animal, then samples taken from teeth that erupted late in the sequence (more posteriorly positioned in the premolar or molar row) were used in my analysis. Some data have appeared in multiple studies or review papers since they were published, in which case I traced them back to the original publication. Only studies that reported original $\delta^{13}C_E$ data of extant artiodactyls were cited as primary sources.

4.2.2 New $\delta^{13}C_E$ data

Eighty enamel samples from 23 species of artiodactyls were gathered from specimens housed in the University of Michigan Museum of Zoology (UMMZ). Samples were chosen with consideration for their prior taxonomic representation and geographic coverage in the literature, as well as the availability and abundance of specimens in the collection.

The general method for sampling and pretreating tooth enamel followed Koch et al. (1997). Bulk samples were gathered by drilling approximately 5 mg of pristine enamel powder on the lateral surface of the tooth parallel to the growth axis. Sampling was done using a portable dental drill with a 1-mm diamond burr. Preference was given to sampling third molars or fourth premolars to avoid a weaning signal, as these teeth are among the last ones to develop (Hillson, 2005). Samples were treated with 3% reagent grade NaOCl for 24 h to remove organic matter and with 1M buffered acetic acid for 24 h to remove nonstructural carbonate. Each treatment was followed by centrifuging and rinsing five times with deionized water. Samples were dried by lyophilization. At the University of Michigan Stable Isotope Laboratory, samples were reacted at 77°±1 °C with anhydrous phosphoric acid for 8 min in a Thermo Scientific Kiel IV preparation device coupled directly to the inlet of a Thermo Delta V triple collector isotope ratio mass spectrometer, which measured the resultant CO_2. Analytical precision was better than ±0.1‰ (1 S.D.), based on international standards for carbonate (NBS-18, NBS-19). Isotope values are expressed in standard δ-notation: $\delta^{13}C_E = [(R_{sample}/R_{standard}) - 1] \times 1000$, where $R={}^{13}C/{}^{12}C$. The $\delta^{13}C_E$ values are reported relative to the Vienna PeeDee Belemnite (VPDB) standard.

4.2.3 Correcting for the Suess effect and calculating $\delta^{13}C$ of dietary sources

Tooth-enamel samples in the compiled dataset were from specimens collected from the field as long ago as 1891 to as recently as 2017. During this time interval, $\delta^{13}C_{atm}$ has decreased by almost 1.8 ‰ due to anthropogenic activities (Suess effect). To account for this effect, all $\delta^{13}C_E$ data were corrected to the preindustrial $\delta^{13}C_{atm}$ level of the year 1750 ($\delta^{13}C_{1750}$, taken to be −6.3‰). Correction values were based on $\delta^{13}C_{atm}$ data from Antarctic ice cores and fern samples in Francey et al. (1999) and direct $\delta^{13}C_{atm}$ measurements from NOAA's CarbonTracker (Jacobson et al., 2020). For some specimens, the exact year of collection was unknown or not reported, so the correction value could not be accurately determined. In these cases, I estimated the year of collection based on year of publication or other information provided by the authors. These samples constitute a small proportion (5%) of the dataset and should not affect the overall analytical results.

The $\delta^{13}C$ values of the consumed vegetation ($\delta^{13}C_{diet}$) were calculated from $\delta^{13}C_{1750}$ to allow for cross-species comparison of forage selection. An enrichment factor between diet and enamel ($\varepsilon^*_{diet\text{-}bioapatite}$) was determined for each artiodactyl species, accounting for its body mass and digestive physiology (foregut vs. hindgut fermentation), using equations derived by Tejada-Lara et al. (2018). Resulting $\varepsilon^*_{diet\text{-}bioapatite}$ values range from 11.0‰ (*Neotragus batesi*) to 15.0‰ (*Hippopotamus amphibius*).

4.2.4 Comparing $\delta^{13}C_{diet}$ values among feeding categories and among ecoregions

Species were assigned to one of seven feeding categories based on forage preference and selectivity, using dietary information compiled from the literature. The feeding categories include one omnivorous category (omnivore) and six herbivorous categories (frugivore, browser, browser-grazer intermediate, variable grazer, and obligate grazer). Detailed methods and dietary assignments follow those in Chapter 2. Based on geographic coordinates, each sampled locality was assigned to one of the Global 200 terrestrial ecoregions, which were established on the bases of biodiversity dynamics and environmental conditions (Olson and Dinerstein, 2002). Different ecoregions provide different habitats for artiodactyls and different plants that they feed on. Therefore, $\delta^{13}C_{diet}$ values are expected to vary among ecoregions.

Box and whisker plots were used to illustrate the summary statistics for feeding categories (Fig. 4.2) and for ecoregions (Fig. 4.3). Histograms of $\delta^{13}C_{diet}$ values illustrate the total dataset, for each feeding category, and for each ecoregion with sufficiently large sample size (>100 samples, Figs. 4.2–4.5). These diagrams allow for an assessment of the differences and similarities in the range and frequency of $\delta^{13}C_{diet}$ values that each feeding category or ecoregion represents. Parametric (ANOVA) and non-parametric statistical tests (Kruskal-Wallis) were used to compare the difference between group-means.

4.2.5 Comparing $\delta^{13}C_{diet}$ values among taxa

Since sampling is highly uneven among geographic regions (Fig. 4.1) and among taxa (Table 4.1), the $\delta^{13}C_{diet}$ values of well-sampled species from certain locations could have an oversize impact on the overall distribution of $\delta^{13}C_{diet}$ values. Therefore, I also evaluated the distribution of mean $\delta^{13}C_{diet}$ values of species (Fig. 4.6). In addition, to examine the $\delta^{13}C_{diet}$ values among phylogenetic groups, I generated a maximum clade credibility tree of artiodactyls using *TreeAnnotator* (Drummond et al., 2012), which summarizes mammalian phylogenies from Upham et al. (2019). The phylogeny and the isotope dataset share 72 species. Box and whisker plots were generated for each and aligned with their position in the phylogenetic tree (Fig. 4.7).

4.2.6 Comparing $\delta^{13}C_{diet}$ values among geographic region

I evaluated the geographic variation in $\delta^{13}C_{diet}$ values in two ways, first at the faunal level and then at the species level. First, for an ecoregion that occurs in more than one continent and has sufficient sample size from each continent, I compared the faunal $\delta^{13}C_{diet}$ values between the same environmental setting on different continents. Only one ecoregion met these criteria: tropical and subtropical moist broadleaf forests. I compared the range and distribution of $\delta^{13}C_{diet}$ values from four areas where this ecoregion occurs: 1) tropical and subtropical Latin America, including localities in Guatemala, Ecuador, Peru, Bolivia, and Paraguay; 2) localities in central Africa, specifically the Democratic Republic of Congo; 3) localities in West Africa, including Gabon and Cameroon; and 4) localities in the East African Rift Zone, specifically those in Kenya, Uganda, and Tanzania (Fig. 4.8).

At the species level, published data for the Cape buffalo (*Syncerus caffer*) and the hippopotamus (*Hippopotamus amphibius*) cover wide enough geographic ranges to enable an evaluation of geographic variation (Fig. 4.9). Additionally, the new data from specimens in the

UMMZ enabled a comparison of white-tailed deer (*Odocoileus virginianus*) $\delta^{13}C_{diet}$ values from two areas: Michigan, United States, and Petén, Guatemala (Fig. 4.10). These areas are close to the northern and southern borders of the species' range. A third set of data was compiled from Rivera-Araya and Birch's (2018) study of the same species from Georgia, United States, which represents a latitudinally intermediate location.

4.3 Results

Including the new samples from this study, the $\delta^{13}C_{diet}$ compilation resulted in a dataset with 1492 data values from 24 primary sources (Table 4.1). The samples come from 80 taxa of artiodactyls (78 identified to the species level and 2 to the genus level; Table 4.1) collected from Africa, Asia, North America, and South America, with the highest number of samples from Africa (Fig. 4.1). Thirteen of the 23 species sampled from UMMZ (Table 4.2) were not covered in previously published $\delta^{13}C_E$ data. Other specimens were chosen to expand the geographic range of sampled species. The total dataset included representatives from nine out of ten families of terrestrial artiodactyls, missing only the Moschidae (Table 4.1).

4.3.1 $\delta^{13}C_{diet}$ among feeding categories

The $\delta^{13}C_{diet}$ values of the seven artiodactyl feeding categories differ significantly from each other, using both parametric and non-parametric tests ($p < 0.001$). Post-hoc tests show that group-means are differ significantly for most pairwise comparisons ($p < 0.05$), except for that between frugivores and browsers and some that involve omnivores or generalists (Table 4.3).

Among the six herbivorous feeding categories, mean $\delta^{13}C_{diet}$ values increase along the dietary continuum from frugivores, through browsers, the mixed feeders (browser-grazer intermediates and generalists, for which the relative position on the continuum is arbitrary), variable grazers, to obligate grazers (Fig. 4.2a). Generalists and omnivores have smaller sample sizes, although omnivores still exhibit a wide range of $\delta^{13}C_{diet}$ values, reflecting their wide dietary niche breadth (Table 4.3a).

The entire dataset exhibits a generally bimodal distribution in $\delta^{13}C_{diet}$ values, with a saddle around −20‰ (Fig. 4.2b). Grazers dominate the C_4 (enriched) mode of the distribution but extend considerably into the C_3 realm. The mixed feeders occupy the intermediate range of values. Frugivores, browsers, and omnivores are prevalent in the C_3 range and are only represented by a few samples with $\delta^{13}C_{diet}$ higher than the separation value.

The bimodal distribution of $\delta^{13}C_{diet}$ values in the total dataset is comprised of several different patterns among artiodactyl feeding groups (Fig. 4.3). Most feeding categories exhibit a unimodal distribution but vary in mean, median, mode, and peak frequency (Table 4.3, Fig. 4.3). The mode in browser-grazer intermediates (Fig. 4.3c), although present, is more right-skewed than in some other categories. The taxonomic composition differs among feeding categories. Obligate grazers and variable grazers exhibit interesting patterns that differ from other feeding categories. Obligate grazers exhibit a left-skewed bimodal distribution, with the higher peak driven primarily by the high frequency of enriched $\delta^{13}C_{diet}$ values in bovids (Fig. 4.3f). All but one sample of Hippopotamidae are from *Hippopotamus amphibius;* this species makes up roughly an-eighth of the total sample size (Table 4.1), and their $\delta^{13}C_{diet}$ values contribute to a second, lower mode in the obligate-grazer data. Variable grazers exhibit a bimodal distribution of $\delta^{13}C_{diet}$ values, with comparable frequencies of the modes (35–40 samples) separated around ~10‰ (Fig. 4.3e). Within this group, bovids are the most abundant (as is the case for all herbivorous feeding categories) and are the main contributor to the bimodal pattern. Other families in this feeding category are well separated between C_3-feeders (camelids and cervids) and C_4-feeders (suids—pigs and warthogs). Associated with taxonomic differentiation, it is worth noting that the C_3-C_4 separation in variable grazers is strongly influenced by geography, with samples from North America being mostly in the C_3 range while samples from Africa are mostly in the C_4 range (Fig. 4.3h).

4.3.2 $\delta^{13}C_{diet}$ among ecoregions

Sample localities in the dataset are distributed among 11 terrestrial ecoregions of the world (Table 4.4a, Fig. 4.4a). The $\delta^{13}C_{diet}$ values of species in different ecoregions differ significantly from each other, using both parametric and non-parametric tests ($p < 0.001$). Pairwise comparisons yielded significant differences ($p < 0.05$) between grassland ecoregions (tropical and subtropical, temperate, flooded, and montane) and forest ecoregions, as well as between desert and xeric shrublands and most other ecoregions (Table 4.4b). Mesic environments (forests and woodlands from a range of temperature conditions) occupy the lower range of the $\delta^{13}C_{diet}$ spectrum while intermediate to semiarid environments (grasslands) occupy the middle and higher ranges (Fig. 4.4b).

Because sample size is highly variable among the ecoregions (Table 4.3a), histograms were generated for four ecoregions with the largest sample sizes. Tropical and subtropical moist broadleaf forests, mostly occurring in Africa, exhibit a weakly bimodal distribution of $\delta^{13}C_{diet}$ values (Fig. 4.5a). The peak in the C_3 range is well-established and consists mostly of frugivores and omnivores, although other feeding categories are also present. The low peak in the C_4 range is primarily from obligate grazers. Similar to the pattern for obligate grazers in general (Fig. 4.3f), the large sample of hippopotamuses is mainly responsible for the pattern in this range of $\delta^{13}C_{diet}$ values. Desert and xeric shrublands also have a weakly bimodal distribution of $\delta^{13}C_{diet}$ values, with more enriched values overall (Fig. 4.5b). There is a clear division between browsers and browser-grazer intermediates, which contribute to $\delta^{13}C_{diet}$ values in the C_3 range, and the grazers, which contribute to $\delta^{13}C_{diet}$ values in the C_4 range. Tropical and subtropical grasslands, savannas, and shrublands are represented isotopically almost exclusively by samples from Africa (Fig. 4.5c), showing a grazer-dominated (especially obligate grazers) distribution of $\delta^{13}C_{diet}$ values. Some browsers and mixed feeders are also present, forming a small mode of $\delta^{13}C_{diet}$ values in the C_3 range. Samples from temperate coniferous forests are all from North America (Fig. 4.5d). There, variable grazers and browsers form a unimodal distribution of $\delta^{13}C_{diet}$ values in the C_3 range.

4.3.3 $\delta^{13}C_{diet}$ among taxonomic groups

Of the 80 species covered in this dataset, more species have mean $\delta^{13}C_{diet}$ values in the C_3 than in the C_4 range (Fig. 4.6). Frugivore species mostly have mean $\delta^{13}C_{diet}$ values between −26‰ and −25‰, with a range from −26.4‰ (*Cephalophus nigrifrons*) to −21.7 ‰ (*Mazama gouazoubira*). The most depleted $\delta^{13}C_{diet}$ values occur in two browsers, the okapi (*Okapia johnstoni*) and the dwarf antelope (*Neotragus batesi*) (Table 4.1), both living in closed-canopy forests of western equatorial Africa. The intermediate feeders have variable mean $\delta^{13}C_{diet}$ values in the C_3 and C_3-C_4 transitional ranges. Variable grazers have the widest range of mean $\delta^{13}C_{diet}$ values, ranging from −28.06‰ (*Tragelaphus spekei*) to −9.84‰ (*Connochaetes gnou*). As expected, high mean $\delta^{13}C_{diet}$ values are found in obligate grazers.

The mean and range of $\delta^{13}C_{diet}$ values are more constrained in some artiodactyl clades than in others. Within the suborder Ruminantia, lineages with the oldest node ages (Giraffidae, Cervidae, Tragulidae,) are exclusively C_3 feeders, while C_4 feeders appear in relatively young lineages (<13 million years old; Fig. 4.7). Species with a pure C_4 diet, corresponding to their assignment in the obligate grazer category, belong to two bovid tribes, the Reduncini and the Hippotragini. Other clades have a mixture of C_3 feeders, C_4 feeders, and mixed C_3-C_4 feeders.

4.3.4 $\delta^{13}C_{diet}$ values among geographic regions

Four regions from the tropical and subtropical moist forests of Africa and Latin America show three patterns in the distribution of $\delta^{13}C_{diet}$ values (Fig. 4.8). Samples from the Congo Basin and from various localities in low latitudes of Latin America have a generally unimodal distribution well within the C_3 realm, with similar modal values (data from Boisserie et al., 2005; Cerling et al., 2004, 2008, 2015; Tejada-Lara et al., 2020; this study). Samples from western equatorial Africa (Gabon and Cameroon) have a generally bimodal distribution of $\delta^{13}C_{diet}$ values. The higher, more enriched peak primarily results from hippopotamus samples (data from Boisserie et al., 2005), while the lower, more depleted peak includes various bovid species (data from Marin et al., 2015, and this study). Lastly, samples from equatorial East Africa (Kenya, Tanzania, Uganda) exhibit a multimodal distribution of $\delta^{13}C_{diet}$ values.

The dataset also contains notable examples of intraspecific geographic variation. The Cape buffalo (*Syncerus caffer*) and the hippopotamus (*Hippopotamus amphibius*) have the largest sample sizes in this dataset, and both species exhibit a wide range of $\delta^{13}C_{diet}$ values (>15‰), primarily in the C_4 range (Fig. 4.9). The Cape buffalo is characterized as an obligate grazer based on spatiotemperally averaged bulk diet of the species; however, samples of this species exhibit a nearly 20‰ range over a relatively small geographic area. The hippopotamus has a more widely sampled geographic range, but notably the greatest difference in $\delta^{13}C_{diet}$ values also occurs between the Congo Basin and East Africa, reflecting both the variability in their diet and the transition between ecoregions. In contrast with the Cape buffalo and the hippopotanus, the white-tailed deer from North America is a C_3 feeder and exhibits relatively low variation in $\delta^{13}C_{diet}$ values across its large latitudinal span of geographic range (Fig. 4.10). The three geographic samples are not significantly different ($p = 0.17$, Kruskal−Wallis). Sampled individuals from northern Georgia, however, have a notably wider range than those from Michigan and Guatemala, as well as a lower mean $\delta^{13}C_{diet}$ value. These samples likely reflect the mosaic vegetation and complex topography in northern Georgia, which lies at the transitional zone between the southern Appalachian Mountains and the Southeastern Piedmont.

4.4 Discussion

This isotopic dataset documents variation in $\delta^{13}C_{diet}$ values among feeding categories, taxonomic groups, ecoregions, and geographic locations of extant artiodactyls. Most of the observed patterns correspond broadly with existing knowledge about stable isotope ecology, but deviations from the general trend can be identified in well-sampled taxa and regions. It is important to note, however, that ecology, taxonomy, biogeography, and environmental settings are often correlated and interactive. The combination of available vegetation, ecological interactions, and physiological processes affects the $\delta^{13}C$ values recorded in artiodactyl tooth enamel.

4.4.1 The herbivore dietary spectrum

The frugivore-browser-grazer dietary spectrum corresponds to an increase in group-mean $\delta^{13}C_{diet}$ values over a range of 20‰ from frugivores (–34.75‰) to obligate grazers (–13.42‰) (Table 4.3, Fig. 4.2). Feeding groups have different dietary preferences as well as niche breadth. The two herbivore dietary extremes have the narrowest range of species mean $\delta^{13}C_{diet}$ values. The intermediate feeding categories (i.e., generalist and browser-grazer intermediate), by their defining criteria, have inherently wider dietary variation than the dietary extremes.

Considerable variation also exists in browsers and variable grazers. The lowest $\delta^{13}C_{diet}$ values occur in two subcanopy browsers, the dwarf antelope (*Neotragus batesi*) and the okapi (*Okapia johnstoni*) (Table 4.1; Fig. 4.7). Both species inhabit closed-canopy forests in equatorial Africa. Okapis are endemic to the forests in northeastern Congo Basin. The dwarf antelope has discontinuous ranges in central and western equatorial Africa. The two specimens of *N. batesi* that I sampled from Cameroon have more variable $\delta^{13}C_{diet}$ values (–29.6‰ and –34.8‰) than do the two specimens from the Ituri Forest reported by Cerling et al. (2004) (–34.3‰ and –35.1‰), and more variation may be present in this group across its geographic range than previously recognized. Variable grazers exhibit an unambiguous bimodal distribution of $\delta^{13}C_{diet}$ values that is distinct from the other feeding categories, and the pattern can be best explained by a distinction between the North American species feeding primarily on C_3 vegetation and the African species feeding primarily on C_4 vegetation (Fig. 4.3h). In North America, variable grazers include the bison (*Bison bison*), elk (*Cervus canadensis*), muskox (*Oreamnos americanus*), Bighorn sheep (*Ovis canadensis*), and the Dall sheep (*Ovis dalli*). Bison are sampled from a range of latitudes in the western United States; their $\delta^{13}C_E$ values vary considerably and are correlated with mean annual temperature (Hoppe et al., 2006). In Africa, warthog (*Phacochoerus africanus*) makes up most of the variable-grazer sample; the rest are from oryx (*Oryx beisa*), oribi (*Ourebia ourebia*), and the marshbuck (*Tragelaphus spekii*). Species in both continental faunas consume over 60% monocots in their average diets. Their contrasting $\delta^{13}C_{diet}$ signatures likely reflect variation in the amount of C_4 biomass in the vegetation, which is affected by temperature and seasonality of precipitation (Boutton et al., 1980; Winslow et al., 2003; Kohn, 2010). Differentiating C_3 graze from C_3 browse in the fossil record would require incorporation of other types of data, such as morphological and use-wear traits.

4.4.2 Dietary breadth

While sampled individuals may be categorized as a browser, a mixed feeder, or a grazer solely by their $\delta^{13}C_{diet}$ values (Cerling et al., 2015), it is evident from Fig. 4.2b that there are no clear-cut boundaries among the three broad feeding types. Individuals belonging to the same taxonomic group or feeding category can have a range of $\delta^{13}C_{diet}$ values. Consequently, the C_3-C_4 cutoff is frequently crossed by clades and feeding groups (Figs. 4.2, 4.7).

Grazing taxa have wider dietary niche breadths than browsing taxa do, as represented by their $\delta^{13}C_{diet}$ values (Table 4.3, Fig. 4.2). The difference between maximum and minimum $\delta^{13}C_{diet}$ values in browsing taxa (including frugivores and browsers) is ~18‰ (~12‰ if excluding the outliers from understory browsers), and few browsing taxa plot in the C_4 range. Grazing taxa (including variable grazers and obligate grazers) have a total range of over 22‰, with many samples extending well into the C_3 range. Corresponding to this difference in extant artiodactyls, recent findings in the North American fossil record show that species with grazing-adapted morphology have broader diets than browsing-adapted ones and consume more browse than previously anticipated (Pardi and DeSantis, 2021). Herbivores with grazing adaptations, such as hypsodont teeth, are able to consume grass but can also eat other foods if they are available. This would have implications for species duration over evolutionary time scales, especially during times of climate change. For example, in the Miocene Siwalik record, species that were able to alter their diet (from browsing to grazing) in response to vegetation change persisted substantially longer than those that were not (Badgley et al., 2008).

The greatest variation in $\delta^{13}C_{diet}$ values within individual species occurs in those inhabiting transitional zones between ecoregions, where vegetation and topographic complexity are high. Such examples can be found in both C_3 and C_4 feeders (Figs. 4.9, 4.10). Such behavioral flexibility likely contributes to the variable patterns of $\delta^{13}C_{diet}$ value observed in four areas of the same ecoregion (Fig. 4.8). Equatorial regions of central Africa and Latin America both host extensive closed-canopy forests, exhibiting unimodal distributions of $\delta^{13}C_{diet}$ values with comparable medians (Tejada-Lara et al., 2020). Localities from western equatorial Africa are in Cameroon and Gabon; while having a primarily forested environment, these localities are close to relatively open habitats in the north and the south, and variable feeding locations by species likely explain the bimodal distribution of $\delta^{13}C_{diet}$ values in these localities. Forest habitats in East Africa occur in smaller areas surrounded by expansive tropical grasslands, and samples from this region exhibit a wide range of $\delta^{13}C_{diet}$ values, indicating consumption of both C_3 and C_4 plants by resident artiodactyls.

4.4.3 Future research

More isotopic data are needed for currently understudied regions and taxa to further explore the research questions posed in this study. In the current data compilation, tragulids are represented by only one species and moschids are absent. Both families are important forest dwellers in Asia, and their $\delta^{13}C_{diet}$ values can help us investigate the resource use and partitioning in artiodactyl faunas in tropical, subtropical, and temperate forests, which may be important analogues for some paleo-ecosystems. Better sampling records from Eurasia in general are also needed. Although some isotope data from other body tissues (e.g., hair) have been reported, tooth enamel data are lacking.

This dataset is potentially useful for addressing many questions beyond this study. For example, do some species track the variation in environmental $\delta^{13}C$ values better than other species that have similar geographic ranges? If so, what aspects of their ecology can explain the difference? How do species' $\delta^{13}C_{diet}$ values contract or expand from ecological interactions, such as co-occurrence with competitors for forage? What combination of isotopic signature and osteological characters can be used to improve paleoecological reconstructions? Some of these questions will need better sampling on targeted taxa, regions, or environmental settings, others will require more comparative data from plants.

4.5 Conclusion

I evaluated a global dataset of the carbon-isotope composition of artiodactyl tooth enamel in relation to diet, phylogeny, environmental setting, and geography. The herbivore dietary spectrum is expressed through a wide range of isotope values of ingested forage ($\delta^{13}C_{diet}$), with the most depleted mean value in frugivores and the most enriched in obligate grazers. In general, grazing taxa have a broader range of dietary isotope values than browsing taxa. Notably, variable grazers exhibit a bimodal distribution of $\delta^{13}C_{diet}$ values, with North American taxa consuming C_3 vegetation and African taxa consuming C_4, reflecting the different amounts of C_4 biomass available in temperate versus tropical environments. Variation in $\delta^{13}C_{diet}$ values also occurs among ecoregions, taxonomic groups, and geographic regions. Grassland ecoregions differ significantly in $\delta^{13}C_{diet}$ values from forest ecoregions. Some of the oldest ruminant lineages have maintained C_3 feeding, and pure C_4 dietary signals are restricted to two bovid clades. The $\delta^{13}C_{diet}$ values of species and faunas also vary across geographic regions and may be related to heterogeneity in the environmental setting. Detecting variation in $\delta^{13}C_{diet}$ values and decoupling contributing factors will help refine paleoecological and paleoenvironmental reconstructions.

4.6 Acknowledgments

I would like to thank Dr. Cody Thompson, Dr. Michael Cherney, and other members at the University of Michigan Museum of Zoology and the University of Michigan Museum of Paleontology for their kind assistance with museum access, data collection, and lab work. Isotope samples were analyzed in a timely manner by Lora Wingate and Dr. Kyger Lohmann at the University of Michigan Stable Isotope Laboratory. Benjamin Passey, Laura MacLatchy, and John Kingston provided helpful comments on the isotope data. Stable isotope analysis was supported by research funds from the Geological Society of America.

4.7 References

Badgley C, Barry JC, Morgan ME, Nelson SV, Behrensmeyer AK, Cerling TE, Pilbeam D, 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proc Nat Acad Sci USA* **105**:12145–12149.

Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger JJ, 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* **11**:306–318.

Boisserie J-R, Zazzo A, Merceron G, Blondel C, Vignaud P, Likius A, Mackaye HT, Brunet M, 2005. Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and microwear of tooth enamel. *Palaeogeogr Palaeoclim Palaeoecol* **221**:153–174.

Boutton TW, Harrison AT, Smith BN, 1980. Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in southeastern wyoming grassland. *Oecologia* **45**:287–298.

Bradham JL, DeSantis LRG, Jorge MLSP, Keuroghlian A, 2018. Dietary variability of extinct tayassuids and modern white-lipped peccaries (Tayassu pecari) as inferred from dental microwear and stable isotope analysis. *Palaeogeogr Palaeoclim Palaeoecol* **499**:93–101.

Cerling TE, Harris JM, 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* **120**:347–363.

Cerling T, Harris J, MacFadden, B. et al. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**:153–158.

Cerling TE, Harris JM, Leakey MG, 1999. Browsing and grazing in modern and fossil proboscideans. *Oecologia* **120**:364–374.

Cerling TE, Harris JM, Leakey MG, Mudida N, 2003. Stable isotope ecology of Northern Kenya, with emphasis on the Turkana Basin, Kenya. In: MG Leakey and JM Harris (eds). *Lothagam: the Dawn of Humanity in Africa*. Columbia Univ. Press. p. 583–603.

Cerling TE, Hart JA, Hart TB, 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* **138**: 5–12.

Cerling TE, et al. 2008. Stable isotope ecology of modern Hippopotamus amphibius in East Africa. *J Zool* **276**:204–212.

Cerling TE, et al. 2011. Diet of Paranthropus boisei in the early Pleistocene of East Africa. *Proc Nat Acad Sci* **108**: 9337–9341.

Copeland SR, Sponheimer M, Spinage CA, Lee-Thorp JA, 2008. Bulk and intra-tooth enamel stable isotopes of waterbuck *Kobus ellipsiprymnus* from Queen Elizabeth National Park, Uganda. *Afr J Ecol* **46**: 697–701.

DeSantis L, Feranec R, Southon J, Binder WJ, Cohen J, Farrell A, Lindsey E, Meachen J, O'Keefe FR, Takeuchi G, 2020. More tools and isotopes are better than one: Clarifying the ecology of ancient mammals at Rancho La Brea and beyond. *Soc Vertebr Paleontol Program and Abstracts*.

Drummond AJ, Suchard MA, Xie D, Rambaut A, 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol Biol Evol* **29**:1969–1973.

Ehleringer JR, Sage RF, Flanagan LB, Pearcy RW, 1991. Climate change and the evolution of C_4 photosynthesis. *Trends Ecol Evol* **6**:95–99.

Fenner JN, 2008. The use of stable isotope ratio analysis to distinguish multiple prey kill events from mass kill events. *J Archaeo Sci* **35**:704–716.

Jacobson AR, Schuldt KN, Miller JB, Oda T, Tans P, Andrews A, Mund J, Ott L, Collatz GJ, Aalto T, Afshar S, Aikin K, Aoki S, Apadula F, Baier B, Bergamaschi P, Beyersdorf A, Biraud SC, Bollenbacher A, et al. 2020. CarbonTracker CT2019B. NOAA Global Monitoring Laboratory. https://doi.org/10.25925/20201008.

Feranec RS, 2007. Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modern C_3-dominated ecosystems in North America. *Palaeogeogr Palaeoclim Palaeoecol* **252**:575–585.

Feranec RS, MacFadden BJ, 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes: *Palaeogeogr Palaeoclim Palaeoecol*, v. 162, p. 155–169.

Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfeld RL, Michel E, Steele LP, 1999. A 1000-year high precision record of $\delta^{13}C$ in atmospheric CO_2. *Tellus B Chem Phys Meteorol* **51**:170–193.

Gagnon M, Chew AE, 2000. Dietary preferences in extant African Bovidae. *J Mammal* **81**:490–511.

Gong Y, Wang Y, Wang Y, Mao F, Bai B, Wang H, Li Q, Jin X, Wang X, Meng J, 2020. Dietary adaptations and palaeoecology of Lophialetidae (Mammalia, Tapiroidea) from the Eocene of the Erlian Basin, China: combined evidence from mesowear and stable isotope analyses. *Palaeontology* **63**:547–564.

Hillson, S., 2005. *Teeth, Cambridge Manuals in Archaeology,* 2nd Ed. Cambridge University Press, Cambridge. 373 pp.

Harris JM, Cerling TE, 2002. Dietary adaptations of extant and Neogene African suids. *J Zool* **256**:45–54.

Higgins P, MacFadden BJ, 2004. “Amount Effect” recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. *Palaeogeogr Palaeoclimatol Palaeoecol* **206**: 337–353.

Hoppe KA, Paytan A, Chamberlain P, 2006. Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. *Geology* **34**:649–652.

IUCN (International Union for Conservation of Nature), 2008. *Odocoileus virginianus*. The IUCN Red List of Threatened Species. Version 2021-1.Jacobs BF, Kingston JD, Jacobs L, 1999. The origin of grass-dominated ecosystems. *Ann Missouri Bot Gard* **86**:590–643.

Kingston JD (2011) Stable isotopic analyses of Laetoli fossil herbivores. In: *Paleontology and geology of Laetoli: Human evolution in context*. Springer Netherlands, p. 293–328

Kingston JD, Harrison T, 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeogr Palaeoclimatol Palaeoecol* **243**:272–306.

Koch PL, Behrensmeyer AK, Fogel ML, 1991. The isotopic ecology of plants and animals in Amboseli National Park, Kenya. Annual Report of the Director Geophysical Laboratory 23:163–171.

Koch PL, Tuross N, Fogel ML, 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *J Archaeo Sci* **24**:417–429.

Kohn MJ, 2010. Carbon isotope compositions of terrestrial C_3 plants as indicators of (paleo)ecology and (paleo)climate. *Proc Nat Acad Sci USA* **107**:19691–19695.

Lee-Thorp J, 2002. Two decades of progress towards understanding fossilization processes and isotopic signals in calcified tissue minerals. *Archaeometry* **44**:435–446.

Landman M, Schoeman DS, Kerley GIH, 2013. Shift in black rhinoceros diet in the presence of elephant: evidence for competition? *PLoS One* **8**:e69771.

Lazzerini N, A. Coulon, L. Simon, C. Marchina, D. Fiorillo, Ts Turbat, N. Bayarkhuu, C. Noûs, S. Lepetz, A. Zazzo, 2021. The isotope record ($\delta^{13}C$, $\delta^{18}O$) of vertical mobility in incremental tissues (tooth enamel, hair) of modern livestock: A reference set from the Mongolian Altai. *Quat Int*, in press.

Levin NE, Simpson SW, Quade J, Cerling TE, Frost SR, 2008. Herbivore enamel carbon isotopic composition and the environmental context of Ardipithecus at Gona, Ethiopia. The Geology of Early Humans in the Horn of Africa: Geological Society of America Special Paper 446, eds Quade J, Wynn JG: Geological Society of America, pp 215–234.

Louys J, Ditchfield P, Meloro C, Elton S, Bishop LC, 2012. Stable isotopes provide independent support for the use of mesowear variables for inferring diets in African antelopes. *Proc R Soc B* **279**:4441–4446.

Luyt J, Sealy J, 2018. Inter-tooth comparison of δ^{13}C and δ^{18}O in ungulate tooth enamel from south-western Africa. *Quat Int* **495**:144–152.

Martin JE, Vance D, Balter V (2015) Magnesium stable isotope ecology using mammal tooth enamel. *Proc Nat Acad Sci USA* **112**:430–435.

Merceron G, Zazzo A, Spassov N, Geraads D, Kovachev D, 2006. Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: Evidence from dental microwear and stable isotopes. *Palaeogeogr Palaeoclimatol Palaeoecol* **241**:637–654.

Nelson SV, 2013. Chimpanzee fauna isotopes provide new interpretations of fossil ape and hominin ecologies. *Proc Roy Soc B* **280**:20132324.

O'Leary MH, 1988. Carbon isotopes in photosynthesis. Bioscience, v. 38,p. 328–336.

Olson DM, Dinerstein E, 2002. The Global 200: Priority ecoregions for global conservation. *Ann Missouri Bot Gard* **89**:199–224.

Rivera-Araya M, Birch SP, 2018. Stable isotope signatures in white-tailed deer as a seasonal paleoenvironmental proxy: A case study from Georgia, United States. *Palaeogeogr Palaeoclimatol Palaeoecol* **505**:53–62.

Pardi MI, DeSantis LRG, 2021. Dietary plasticity of North American herbivores: a synthesis of stable isotope data over the past 7 million years. *Proc Royal Soc B* **288**: 20210121.

Passey BH, Cerling TE, 2002. Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series. *Geochim Cosmochim Acta* **66**:3225–3234.

Secord R, Wing SL, Chew A, 2008. Stable isotopes in early Eocene mammals asindicators of forest canopy structure and resource partitioning. *Paleobiology* **34**:282–300.

Sponheimer M, Lee-Thorp JA, DeRuiter DJ, Smith JM, Van Der Merwe NJ et al. 2003. Diets of Southern African Bovidae: Stable isotope evidence. *J Mammal* **84**: 471–479.

Tejada-Lara, J.V., MacFadden, B.J., Bermudez, L., Rojas, G., Salas-Gismondi, R., Flynn, J.J., 2018. Body mass predicts isotope enrichment in herbivorous mammals. *Proc Roy Soc B* **285**:20181020.

Tejada-Lara, J.V., Flynn, J.J., Antoine, P.O., Pacheco, V., Salas-Gismondi, R., Cerling, T.E., 2020. Comparative isotope ecology of western Amazonian rainforest mammals. *Proc Nat Acad Sci USA* **117**:26263–26272.

Uno KT, Rivals F, Bibi F, Pante M, Njau M, de la Torre I, 2018. Large mammal diets and paleoecology across the Oldowan–Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses. *J Hum Evol* **120**:76–91.

Van der Merwe NJ (2013) Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *S Afr Jour Sci* **109**:1–14.

Wang B, Secord R, 2020. Paleoecology of Aphelops and Teleoceras (Rhinocerotidae) through an interval of changing climate and vegetation in the Neogene of the Great Plains, central United States. *Palaeogeogr Palaeoclimatol Palaeoecol* **542**:109411.

Wang Y, Kromhout E, Zhang C, Xu Y, Parker W, Deng T, Qiu Z, 2008. Stable isotopic variations in modern herbivore tooth enamel, plants and water on the Tibetan Plateau: Implications for paleoclimate and paleoelevation reconstructions. *Palaeogeogr Palaeoclimatol Palaeoecol* **260**:359–374.

West JB, Bowen GJ, Cerling TE, Ehleringer JR, 2006. Stable isotopes as one of nature's ecological recorders. *Trends Ecol Evol* **21**:408–414.

Winslow JC, Hunt Jr ER, Piper SC, 2003. The influence of seasonal water availability on global C_3 versus C_4 grassland biomass and its implications for climate change research. *Ecol Model* **163**:153–173.

Table 4.1 Summary statistics for $\delta^{13}C_{diet}$ values of 80 species of artiodactyls documented for this study.

Family	Taxon	N	Min	Max	Mean	Median	S.D.
Antilocapridae	*Antilocapra americana*	36	-25.68	-17.73	-19.80	-19.35	1.85
Bovidae	*Aepyceros melampus*	54	-23.54	-8.91	-16.46	-16.67	2.81
Bovidae	*Alcelaphus buselaphus*	49	-14.02	-8.26	-9.87	-9.55	1.28
Bovidae	*Antidorcas marsupialis*	35	-26.55	-20.32	-23.01	-22.50	1.56
Bovidae	*Beatragus hunteri*	2	-11.24	-10.71	-10.97	-10.97	0.38
Bovidae	*Bison bison*	88	-25.65	-13.49	-20.95	-22.39	3.44
Bovidae	*Bos grunniens*	7	-24.37	-21.31	-22.97	-22.79	1.29
Bovidae	*Bos* sp.	1	-16.34	-16.34	-16.34	-16.34	--
Bovidae	*Capra hircus*	17	-23.06	-19.90	-21.42	-21.46	0.72
Bovidae	*Capra nubiana*	3	-19.34	-17.57	-18.69	-19.15	0.97
Bovidae	*Capra walie*	1	-22.60	-22.60	-22.60	-22.60	NA
Bovidae	*Cephalophus callipygus*	4	-26.59	-17.67	-23.42	-24.71	3.94
Bovidae	*Cephalophus dorsalis*	4	-26.23	-24.94	-25.56	-25.53	0.71
Bovidae	*Cephalophus leucogaster*	4	-25.60	-24.22	-25.02	-25.13	0.66
Bovidae	*Cephalophus nigrifrons*	10	-28.16	-24.63	-26.41	-25.83	1.26
Bovidae	*Cephalophus* sp.	9	-27.26	-22.23	-25.51	-26.18	1.68
Bovidae	*Cephalophus sylvicultor*	3	-27.00	-24.97	-25.74	-25.23	1.11
Bovidae	*Cephalophus weynsi*	2	-25.96	-25.86	-25.91	-25.91	0.07
Bovidae	*Connochaetes gnou*	10	-10.96	-8.89	-9.84	-10.02	0.69
Bovidae	*Connochaetes taurinus*	42	-12.92	-8.39	-10.25	-9.97	1.20
Bovidae	*Damaliscus lunatus*	19	-13.46	-8.40	-10.26	-9.98	1.17
Bovidae	*Eudorcas thomsonii*	16	-18.77	-10.98	-13.71	-13.01	2.48
Bovidae	*Gazella dorcas*	8	-23.37	-19.86	-21.75	-21.49	1.16
Bovidae	*Hippotragus equinus*	5	-15.18	-8.30	-11.16	-10.16	2.67
Bovidae	*Hippotragus niger*	3	-11.46	-9.66	-10.41	-10.11	0.93
Bovidae	*Kobus ellipsiprymnus*	76	-14.35	-8.90	-11.39	-11.19	1.25
Bovidae	*Kobus kob*	11	-12.59	-8.88	-10.74	-10.42	1.10
Bovidae	*Litocranius walleri*	8	-24.27	-21.20	-23.32	-23.50	1.02
Bovidae	*Madoqua guentheri*	2	-18.92	-18.43	-18.68	-18.68	0.35
Bovidae	*Madoqua kirkii*	33	-24.33	-17.62	-22.06	-22.27	1.60
Bovidae	*Madoqua saltiana*	5	-24.27	-19.81	-21.79	-21.79	1.78
Bovidae	*Nanger granti*	57	-28.00	-13.60	-21.34	-22.11	3.02
Bovidae	*Nanger soemmerringii*	1	-22.70	-22.70	-22.70	-22.70	--
Bovidae	*Neotragus batesi*	4	-35.07	-29.64	-33.43	-34.52	2.55
Bovidae	*Oreamnos americanus*	2	-22.60	-21.92	-22.26	-22.26	0.48
Bovidae	*Oreotragus oreotragus*	3	-24.65	-19.99	-22.61	-23.20	2.39
Bovidae	*Oryx beisa*	30	-17.05	-9.67	-12.12	-12.10	1.62
Bovidae	*Ourebia ourebi*	1	-16.33	-16.33	-16.33	-16.33	--
Bovidae	*Ovibos moschatus*	2	-22.92	-15.20	-19.06	-19.06	5.46
Bovidae	*Ovis aries*	3	-22.53	-20.69	-21.51	-21.31	0.94
Bovidae	*Ovis canadensis*	2	-23.20	-15.27	-19.24	-19.24	5.61
Bovidae	*Ovis dalli*	1	-22.10	-22.10	-22.10	-22.10	--
Bovidae	*Philantomba monticola*	11	-25.68	-21.35	-23.78	-23.97	1.42
Bovidae	*Raphicerus campestris*	33	-26.02	-18.31	-22.81	-23.36	2.05
Bovidae	*Redunca fulvorufula*	2	-11.07	-10.39	-10.73	-10.73	0.48
Bovidae	*Redunca redunca*	13	-18.03	-7.92	-10.62	-9.53	2.75
Bovidae	*Sylvicapra grimmia*	13	-27.83	-21.50	-24.99	-25.16	1.89
Bovidae	*Syncerus caffer*	118	-28.56	-9.67	-13.24	-12.12	3.50
Bovidae	*Taurotragus oryx*	29	-25.26	-18.02	-22.22	-22.50	1.84
Bovidae	*Tragelaphus buxtoni*	5	-25.79	-23.63	-24.66	-24.45	1.00
Bovidae	*Tragelaphus euryceros*	2	-27.50	-26.92	-27.21	-27.21	0.40
Bovidae	*Tragelaphus imberbis*	6	-24.53	-19.55	-22.92	-23.41	1.72
Bovidae	*Tragelaphus scriptus*	16	-28.12	-21.76	-24.90	-25.31	1.60
Bovidae	*Tragelaphus spekei*	5	-29.38	-26.60	-28.06	-28.30	1.08
Bovidae	*Tragelaphus strepsiceros*	26	-27.92	-20.65	-23.31	-23.26	1.49
Camelidae	*Llama guanaco*	6	-26.87	-25.97	-26.45	-26.50	0.35
Cervidae	*Alces americanus*	3	-28.08	-27.48	-27.73	-27.63	0.31
Cervidae	*Capreolus capreolus*	1	-22.37	-22.37	-22.37	-22.37	--
Cervidae	*Cervus elaphus*	32	-28.40	-23.21	-24.64	-24.67	0.96
Cervidae	*Hydropotes inermis*	1	-25.17	-25.17	-25.17	-25.17	-
Cervidae	*Mazama americana*	10	-26.97	-24.60	-25.53	-25.51	0.64
Cervidae	*Mazama gouazoubira*	9	-24.67	-17.37	-21.74	-21.45	2.41
Cervidae	*Mazama rufina*	1	-26.02	-26.02	-26.02	-26.02	-
Cervidae	*Mazama temama*	3	-25.72	-24.38	-24.97	-24.81	0.69
Cervidae	*Muntiacus reevesi*	1	-21.84	-21.84	-21.84	-21.84	--

Cervidae	*Odocoileus hemionus*	29	-26.44	-19.59	-24.26	-24.47	1.44
Cervidae	*Odocoileus virginianus*	28	-28.20	-15.96	-24.97	-25.82	3.23
Cervidae	*Rangifer tarandus*	2	-21.11	-20.78	-20.94	-20.94	0.24
Giraffidae	*Giraffa camelopardalis*	53	-28.64	-20.66	-25.09	-25.22	1.58
Giraffidae	*Okapia johnstoni*	4	-34.00	-31.73	-32.52	-32.18	1.03
Hippopotamidae	*Choeropsis liberiensis*	1	-28.40	-28.40	-28.40	-28.40	--
Hippopotamidae	*Hippopotamus amphibius*	193	-25.48	-10.70	-16.73	-16.24	2.38
Suidae	*Hylochoerus meinertzhageni*	13	-34.30	-24.65	-28.70	-27.89	2.84
Suidae	*Phacochoerus aethiopicus*	59	-24.37	-8.96	-12.98	-12.03	2.87
Suidae	*Phacochoerus africanus*	33	-15.04	-9.83	-12.61	-12.16	1.22
Suidae	*Potamochoerus larvatus*	23	-26.05	-13.23	-21.86	-22.29	4.19
Suidae	*Potamochoerus porcus*	23	-28.22	-19.70	-25.63	-26.11	1.96
Tayassuidae	*Pecari tajacu*	4	-24.96	-23.97	-24.49	-24.51	0.45
Tayassuidae	*Tayassu pecari*	5	-26.13	-24.65	-25.48	-25.54	0.53
Tragulidae	*Hyemoschus aquaticus*	3	-25.69	-24.80	-25.26	-25.29	0.45

Data sources: Bocherens et al. (1996), Cerling and Harris (1999), Cerling et al. (1999), Harris and Cerling (2002), Cerling et al. (2003), Cerling et al. (2004), Higgins and MacFadden (2004), Boisserie et al. (2005), Hoppe et al. (2006), Feranec (2007), Kingston and Harrison (2007), Cerling et al. (2008), Copeland et al. (2008), Fenner (2008), Levin et al. (2008), Wang et al. (2008), Cerling et al. (2011), Nelson (2013), Van der Merwe (2013), Martin et al. (2015), Luyt and Seely (2018), Rivera-Araya and Birch (2018), Lazzerini et al. (2021), and this study.

Table 4.2 Eighty new samples of artiodactyl tooth enamel collected from specimens housed in the University of Michigan Museum of Zoology (UMMZ) and analyzed for carbon-isotope composition ($\delta^{13}C_E$).

Taxon	Collection No.	Element	Region	Country	Lat	Long	Year	$\delta^{13}C_E$
Antilocapra americana oregona	UMMZ 44370	Lm3	Montana	US	45.78	-108.5	1891	-10.14
Antilocapra americana oregona	UMMZ 44372	Lm3	Montana	US	45.78	-108.5	1891	-9.19
Antilocapra americana oregona	UMMZ 65026	Rm3	Michigan	US	42.46	-84.01	1931	-13.92
Antilocapra americana oregona	UMMZ 65502	Rm3	Michigan	US	42.46	-84.01	1932	-13.69
Antilocapra americana oregona	UMMZ 67482	Lm3	Michigan	US	42.46	-84.01	1932	-12.69
Capra nubiana	UMMZ 163513	Lm3	Red Sea	Egypt	26.57	32.2	1983	-6.19
Capra nubiana	UMMZ 164923	Lp4	Red Sea	Egypt	28.7	32.37	1986	-7.91
Capra nubiana	UMMZ 164942	Lm3	Red Sea	Egypt	27.15	32.53	1986	-8.11
Cephalophus sp.	UMMZ 38376	Lm3	Kribi	Cameroon	2.95	9.917	1908	-12.05
Gazella dorcas	UMMZ 158959	Lm3	Hunter's Camp	Egypt			1983	-12.13
Gazella dorcas	UMMZ 158960	Lm3	Hunter's Camp	Egypt			1983	-10.06
Gazella dorcas	UMMZ 158962	Rm3	Hunter's Camp	Egypt			1983	-10.97
Gazella dorcas	UMMZ 158966	Lm3	Hunter's Camp	Egypt			1983	-8.7
Gazella dorcas	UMMZ 158967	Lm3	Hunter's Camp	Egypt			1983	-10.63
Gazella dorcas	UMMZ 158969	Rm3	Hunter's Camp	Egypt			1983	-10.05
Gazella dorcas	UMMZ 158970	Lm3	Hunter's Camp	Egypt			1983	-10.07
Gazella dorcas	UMMZ 158972	Lp4	Hunter's Camp	Egypt			1983	-12.25
Neotragus batesi	UMMZ 39516	Rm3	Efulan, Kribi	Cameroon	2.783	10.53	1908	-24.6
Neotragus batesi	UMMZ 39517	Rm3	Efulan, Kribi	Cameroon	2.783	10.53	1908	-19.43
Oreamnos americanus missoulae	UMMZ 60546	Rm3	Mt. Hammel	Canada			1929	-9.76
Oreamnos americanus missoulae	UMMZ 87772	Rm3	Montana	US	47.77	-112.7	1942	-10.47
Oryx beisa	UMMZ 124068	Rm3		(Africa)			~1909	3.17
Ovibos moschatus	UMMZ 116376	Lm3	NW Territories	Canada	75.7	-84.4	1967	-2.29
Ovibos moschatus	UMMZ 112377	Lm3	Greeland	Denmark	72.18	-23.75	1962	-10.11
Ovis canadensis canadensis	UMMZ 167428	RM3	Colorado	US	40.38	-105.5	1942	-2.94
Ovis canadensis canadensis	UMMZ 42316	RM3	Idaho	US	43.61	-116.2	1899	-10.78
Ovis dalli stonei	UMMZ 53659	Lm3	British Columbia	Canada	59	-129	~1948	-10.18
Philantomba monticola monticola	UMMZ 39515	Lm3	Efulai	Cameroon	2.783	10.53	1908	-14.78
Alces americanus	UMMZ 60536	Lp4	Michigan	US	48.1	-88.7	1929	-14.42
Alces americanus	UMMZ 61782	Rm3	Michigan	US	47.37	-88.11	1930	-14.88
Alces americanus	UMMZ 64975	Lm3	Michigan	US	48.03	-88.77	1931	-14.27
Capreolus capreolus	UMMZ 125684	Lm3	Thetford Chase	UK			1966	-11.11
Cervus elaphus canadensis	UMMZ 57713	Lm3	Michigan	US	42.81	-83.78	1926	-11.75
Cervus elaphus canadensis	UMMZ 57755	Lm3	Michigan	US	44.85	-83.96	1926	-12
Cervus elaphus canadensis	UMMZ 59189	Lm3	Utah	US	40.85	-109.9	1928	-11.04
Cervus elaphus canadensis	UMMZ 59798	Rm3	Wyoming	US	43.48	-110.8	1927	-11.24
Cervus elaphus canadensis	UMMZ 59799	Rm3	Wyoming	US	43.48	-110.8	1927	-10.77
Cervus elaphus canadensis	UMMZ 62121	Lm3	Wyoming	US	44	-110.4	1930	-11.31
Cervus elaphus canadensis	UMMZ 62122	RM3	Wyoming	US	43.48	-110.8	1930	-10.59
Hydropotes inermis inermis	UMMZ 56527	Rm3	Kiangsu	China	32.07	118.8	1923	-14.23
Mazama americana	UMMZ 126854	Lm3	La Paz	Bolivia	-15.52	-67.82	1978	-13.98
Mazama americana	UMMZ 126128	Rm3	Canindeyu	Paraguay	-24.45	-55.65	1978	-14.78
Mazama americana	UMMZ 146493	Rm3	Canindeyu	Paraguay	-24.45	-55.65	1979	-14.5
Mazama americana	UMMZ 146494	RM3	Canindeyu	Paraguay	-24.45	-55.65	1979	-14.97
Mazama americana gualea	UMMZ 77816	RM3	Imbabura	Ecuador	0.35	-78.53	1934	-14.15
Mazama americana zamora	UMMZ 82862	Rm3	Napo	Ecuador	-0.983	-77.82	1936	-14.05
Mazama gouazoubira	UMMZ 124699	Lm3	Nueva Asuncion	Paraguay	-22.1	-59.9	1976	-6.58
Mazama gouazoubira	UMMZ 124700	Lm3	Chaco	Paraguay	-20.63	-60.32	1976	-10.67
Mazama gouazoubira	UMMZ 124701	Lm3	Nueva Asuncion	Paraguay	-20.7	-60	1976	-9.01
Mazama gouazoubira	UMMZ 125569	Lm3	Chaco	Paraguay	-20.63	-60.32	1977	-10.02
Mazama gouazoubira	UMMZ 125572	Lm3	Chaco	Paraguay	-20.13	-60.15	1977	-9.6
Mazama gouazoubira	UMMZ 125573	Lm3	Chaco	Paraguay	-20.4	-60.1	1977	-11.88
Mazama rufina	UMMZ 126126	Lm3	Itapua	Paraguay	-27.33	-56.42	1978	-15.81
Mazama temama cerasina	UMMZ 63500	Lm3	Peten	Guatemala	17.39	-89.63	1931	-13.57
Mazama temama cerasina	UMMZ 63502	Lm2	PETEN	Guatemala	17.39	-89.63	1931	-13.14
Mazama temama cerasina	UMMZ 76637	Rm2	Peten?	Guatemala			1924	-14.44
Muntiacus reevesi roberti	UMMZ 97617	Lm3	Taipei	Taiwan	25.02	121.5	1950	-11.16
Odocoileus hemionus crooki	UMMZ 46190	Rm3	Texas	US	30.6	-103.9		-7.45
Odocoileus hemionus crooki	UMMZ 79419	Lm3	Texas	US	30.6	-103.9	1937	-10.05

Odocoileus hemionus hemionus	UMMZ 59187ave	Rm3	Utah	US	40.64	-109.7	1928	-12.28
Odocoileus hemionus hemionus	UMMZ 59638	Lm3	Arizona	US	35.92	-112.1	1928	-11.49
Odocoileus hemionus sitkensis	UMMZ 103357	Lm3	Alaska	US	57.86	-152.4		-14.37
Odocoileus virginianus borealis	UMMZ 5240	Rm3	Michigan	US				-12.48
Odocoileus virginianus borealis	UMMZ 59029	Rm3	Michigan	US	44.66	-84.71	1927	-13.44
Odocoileus virginianus borealis	UMMZ 60964	Lm3	Michigan	US	46.24	-84.18	1929	-13.65
Odocoileus virginianus borealis	UMMZ 61004ave	Lm3	Michigan	US	46.09	-88.64	1929	-12.15
Odocoileus virginianus borealis	UMMZ 61038	Lm3	Michigan	US	45.27	-84.58	1929	-13.83
Odocoileus virginianus borealis	UMMZ 61048	Lm3	Michigan	US	46	-83.85	1929	-14.49
Odocoileus virginianus borealis	UMMZ 61147	Lm3	Michigan	US	46.46	-90.17	1929	-13.72
Odocoileus virginianus borealis	UMMZ 80213	Lm3	Michigan	US	42.46	-84.01	1937	-14.08
Odocoileus virginianus thomasi	UMMZ 76630	Rm3	Peten?	Guatemala			1924	-13.21
Odocoileus virginianus thomasi	UMMZ 76631	Rm3	Peten?	Guatemala			1924	-11.86
Odocoileus virginianus thomasi	UMMZ 76632	Rm3	Peten?	Guatemala			1924	-12.38
Odocoileus virginianus thomasi	UMMZ 76634	Rm3	Peten?	Guatemala			1924	-12.7
Odocoileus virginianus thomasi	UMMZ 76638	Rm3	Peten?	Guatemala			1924	-14.1
Odocoileus virginianus thomasi	UMMZ 76641	Rm3	Peten?	Guatemala			1924	-12.52
Odocoileus virginianus thomasi	UMMZ 76648	Rm3	Peten?	Guatemala			1924	-14.05
Odocoileus virginianus thomasi	UMMZ 76654ave	Rm3	Peten?	Guatemala			1924	-13.2
Rangifer tarandus groenlandicus	UMMZ 97462	Rm3	Northwest Territories	Canada	62.71	-109.2	1949	-8.64
Rangifer tarandus osborni	UMMZ 53658	Lm3	British Columbia	Canada	59	-129	1920	-8.81

Table 4.3 Comparison of $\delta^{13}C_{diet}$ values among seven feeding categories of artiodactyls.

(a) Summary statistics

Feeding category	**N**	**Min**	**Max**	**Mean**	**Median**	**S.D.**
Frugivore	72	-28.16	-17.37	-24.75	-25.30	2.08
Browser	312	-35.07	-15.96	-23.53	-23.75	3.05
Browser-grazer intermediate	155	-28.00	-8.91	-20.06	-21.31	3.79
Generalist	39	-28.40	-19.86	-23.14	-23.20	1.84
Variable grazer	313	-29.38	-8.89	-17.64	-16.66	5.60
Obligate grazer	533	-28.56	-7.92	-13.42	-12.36	3.59
Omnivore	68	-34.30	-13.23	-24.87	-25.57	3.83

(b) P-values from post-hoc pairwise tests. Above diagonal line: Tukey's HSD post hoc test. Below diagonal line: Mann−Whitney U test. Both ANOVA and Kruskal−Wallis tests yielded $p < 0.001$.

	Frugivore	Brower	Intermediate	Generalist	Variable grazer	Obligate grazer	Omnivore
Frugivore		0.21	**0.00**	0.38	**0.00**	**0.00**	1.00
Brower	**0.00**		**0.00**	1.00	**0.00**	**0.00**	0.15
Intermediate	**0.00**	**0.00**		**0.00**	**0.00**	**0.00**	**0.00**
Generalist	**0.00**	0.15	**0.00**		**0.00**	**0.00**	0.31
Variable grazer	**0.00**	**0.00**	**0.00**	**0.00**		**0.00**	**0.00**
Obligate grazer	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**		**0.00**
Omnivore	0.20	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	

Table 4.4 Comparison of $\delta^{13}C_{diet}$ values of artiodactyls among eleven ecoregions.

(a) Summary statistics

Ecoregion	N	Min	Max	Mean	Median	S.D.
1) Tropical and subtropical moist broadleaf forests	208	-35.07	-7.92	-22.55	-24.78	5.89
2) Temperate broadleaf and mixed forests	30	-28.20	-15.96	-25.11	-25.82	3.25
3) Temperate coniferous forests	107	-28.40	-19.75	-24.00	-24.25	1.44
4) Boreal forests/taiga	10	-26.44	-15.27	-22.32	-22.90	2.97
5) Tropical and subtropical grasslands, savannas, and shrublands	812	-28.64	-8.21	-15.47	-14.00	5.16
6) Temperate grasslands, savannas, and shrublands	49	-26.87	-13.49	-19.60	-20.42	4.11
7) Flooded grasslands and shrublands	8	-21.15	-12.35	-16.46	-15.58	2.97
8) Montane grasslands and shrublands	51	-29.16	-12.03	-22.12	-21.90	2.77
9) Tundra	2	-22.92	-15.20	-19.06	-19.06	5.46
10) Mediterranean forests, woodlands, and scrub	72	-27.83	-17.27	-23.50	-23.58	2.04
11) Deserts and xeric shrublands	143	-26.55	-8.40	-19.25	-19.94	4.35

(b) P-values from post-hoc pairwise tests. Above diagonal line: Tukey's HSD post hoc test. Below diagonal line: Mann−Whitney U test. Both ANOVA and Kruskal−Wallis tests yielded $p < 0.001$.

	1)	2)	3)	4)	5)	6)	7)	8)	9)	10)	11)
1)		0.18	0.27	1.00	**0.00**	**0.00**	**0.02**	1.00	0.99	0.94	**0.00**
2)	**0.01**		0.99	0.88	**0.00**	**0.00**	**0.00**	0.19	0.81	0.90	**0.00**
3)	0.25	**0.00**		0.99	**0.00**	**0.00**	**0.00**	0.42	0.93	1.00	**0.00**
4)	0.27	**0.00**	**0.01**		**0.00**	0.86	0.25	1.00	1.00	1.00	0.67
5)	**0.00**	**0.00**	**0.00**	**0.00**		**0.00**	1.00	0.00	0.99	**0.00**	**0.00**
6)	**0.00**	**0.00**	**0.00**	**0.02**	**0.00**		0.82	0.23	1.00	**0.00**	1.00
7)	**0.00**	**0.00**	**0.00**	**0.00**	0.26	0.06		0.07	1.00	**0.00**	0.88
8)	**0.02**	**0.00**	**0.00**	0.58	**0.00**	**0.00**	**0.00**		1.00	0.89	**0.01**
9)	0.24	**0.05**	**0.03**	0.33	0.28	0.83	0.51	0.50		0.97	1.00
10)	0.30	**0.00**	**0.03**	0.23	**0.00**	**0.00**	**0.00**	**0.00**	**0.10**		**0.00**
11)	**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	0.87	**0.04**	**0.00**	0.95	**0.00**	

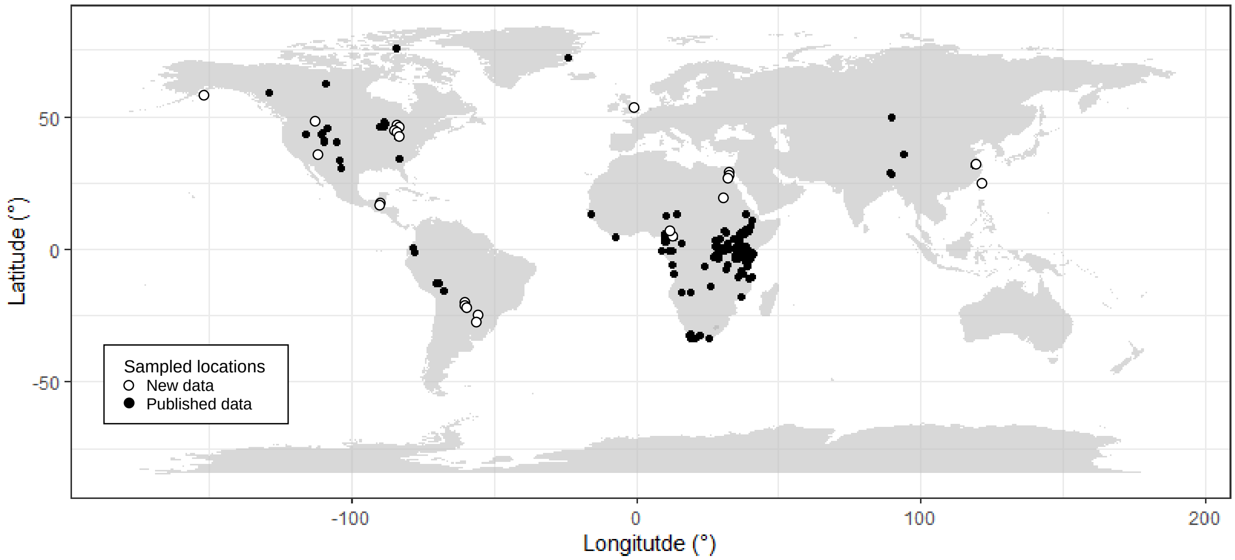


Figure 4.1 Collecting locations of tooth enamel samples compiled from the literature and collected in this study.

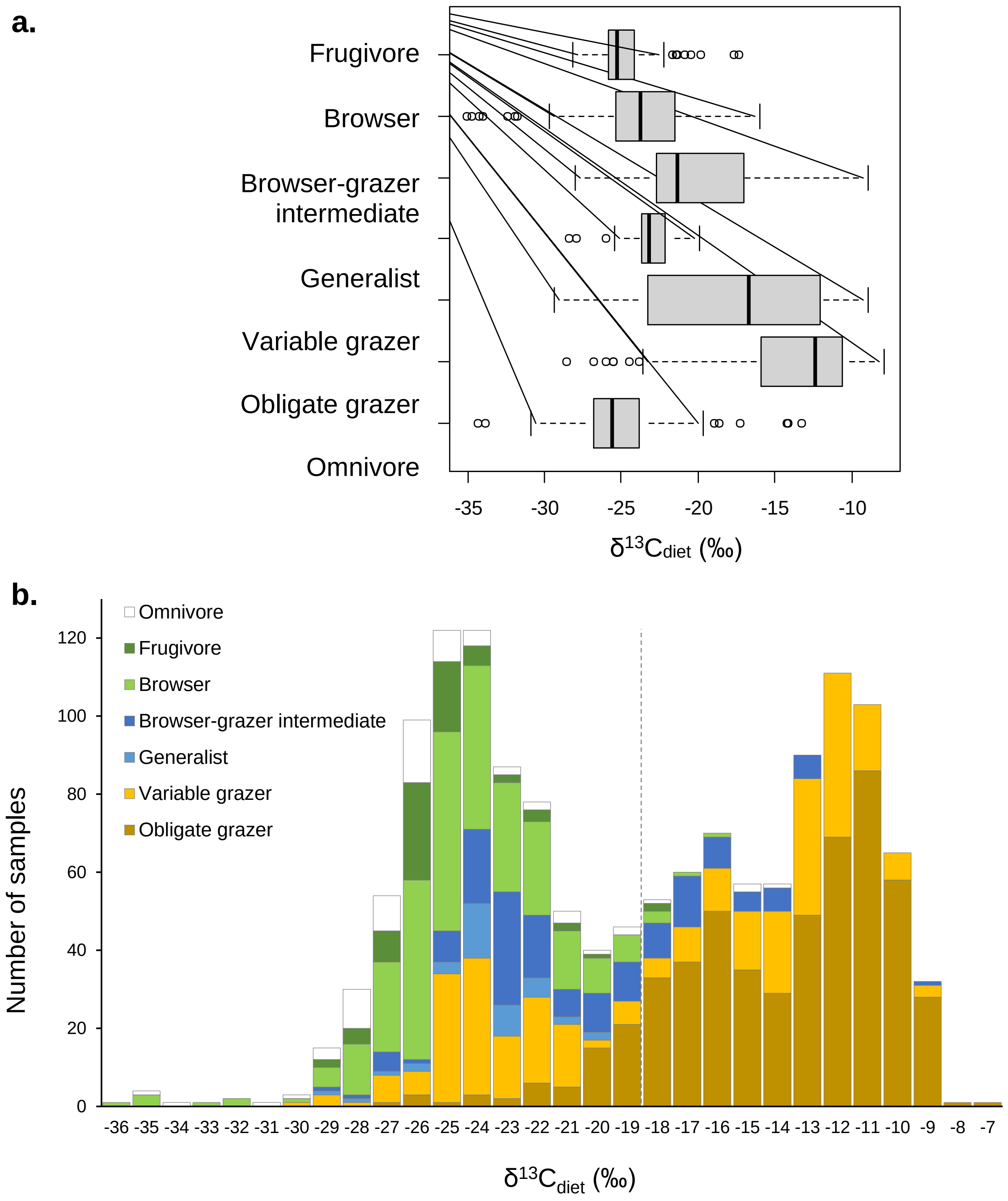


Figure 4.2 Comparison of δ^{13}C$_{diet}$ values of seven artiodactyl feeding categories. Dashed line is the C$_3$-C$_4$ boundary.

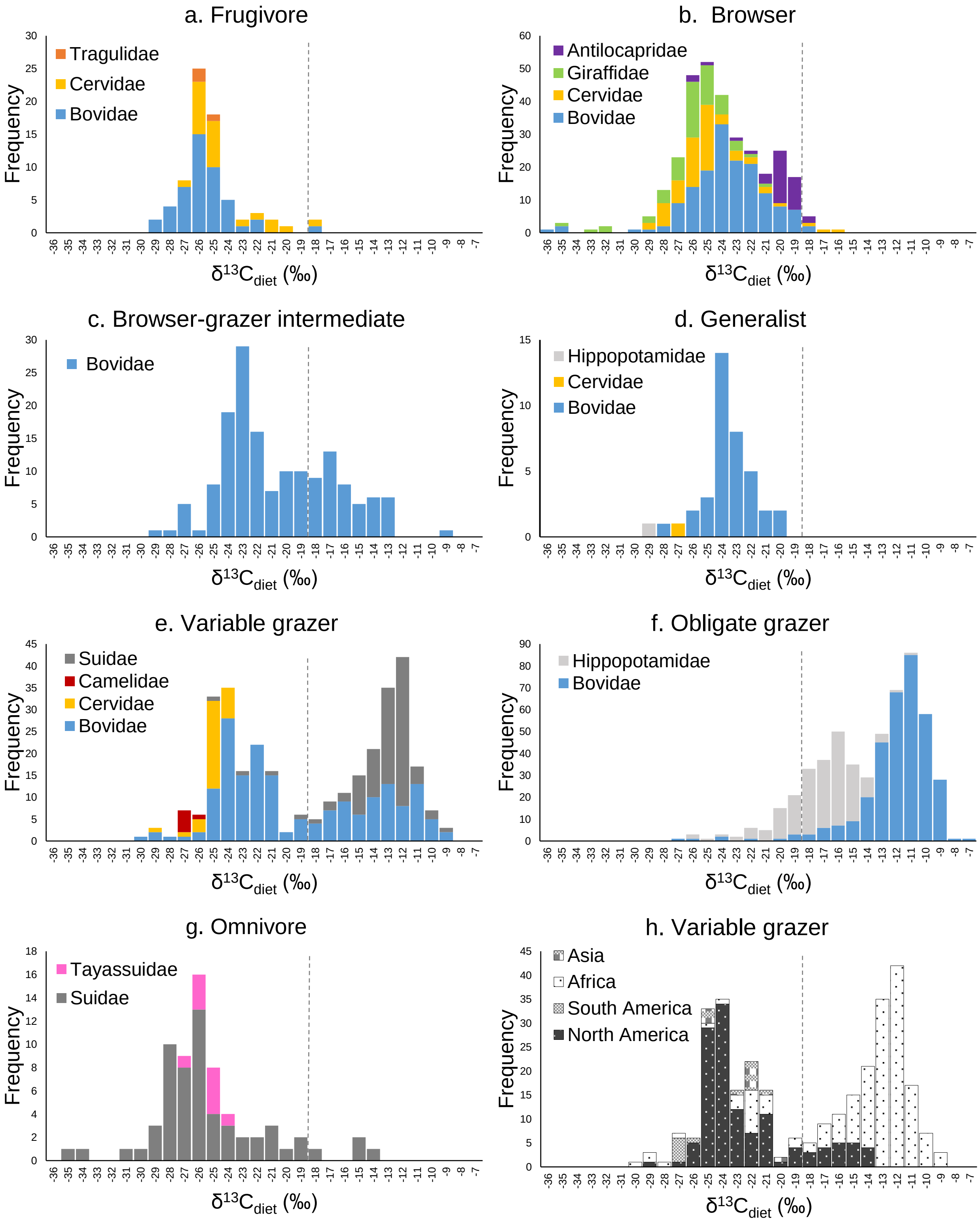


Figure 4.3 Frequency of $\delta^{13}C_{diet}$ values and taxonomic composition in each of the seven artiodactyl feeding categories. Dashed line is the C_3-C_4 boundary.

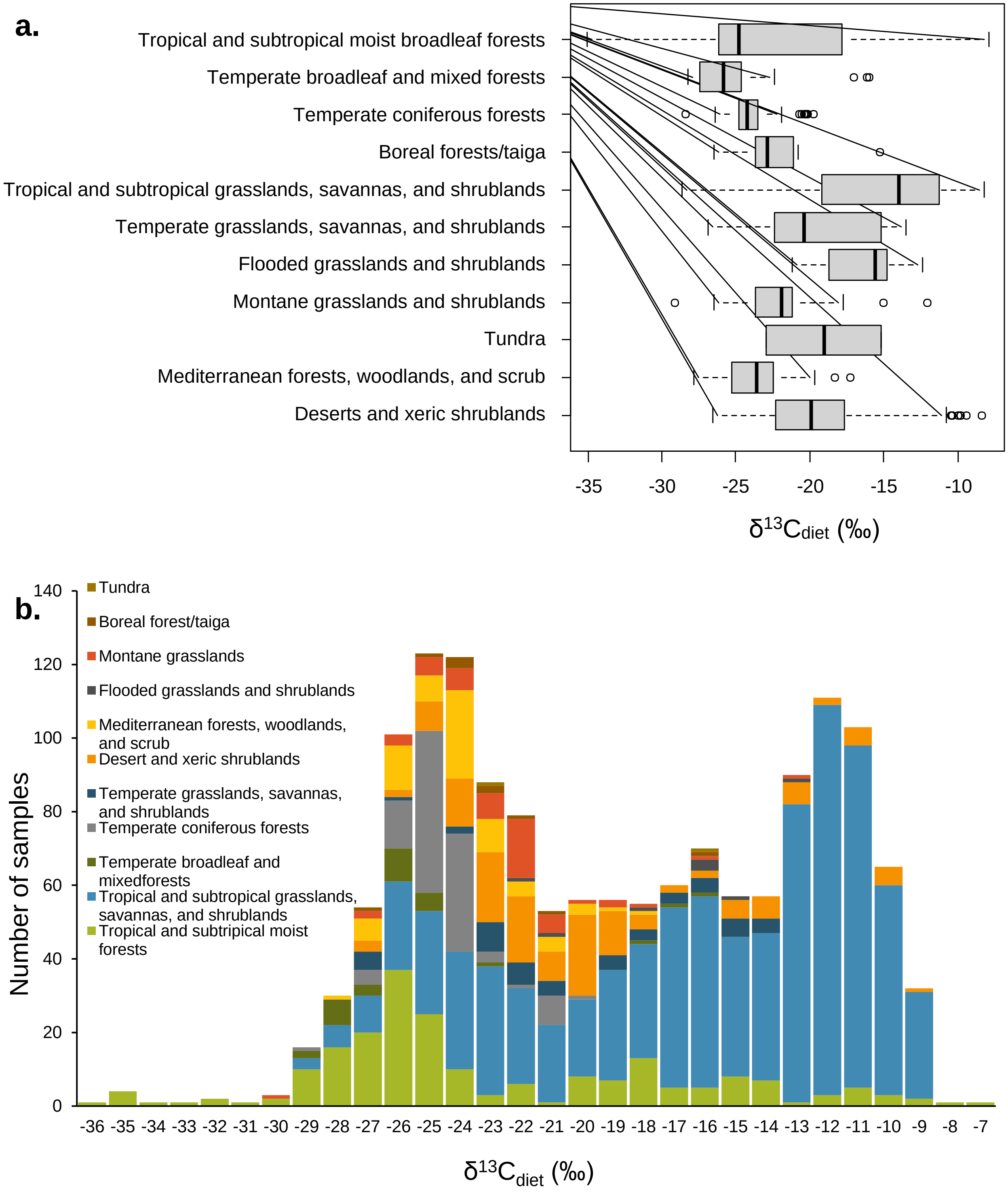


Figure 4.4 Comparison of the $\delta^{13}C_{diet}$ values of eleven terrestrial ecoregions.

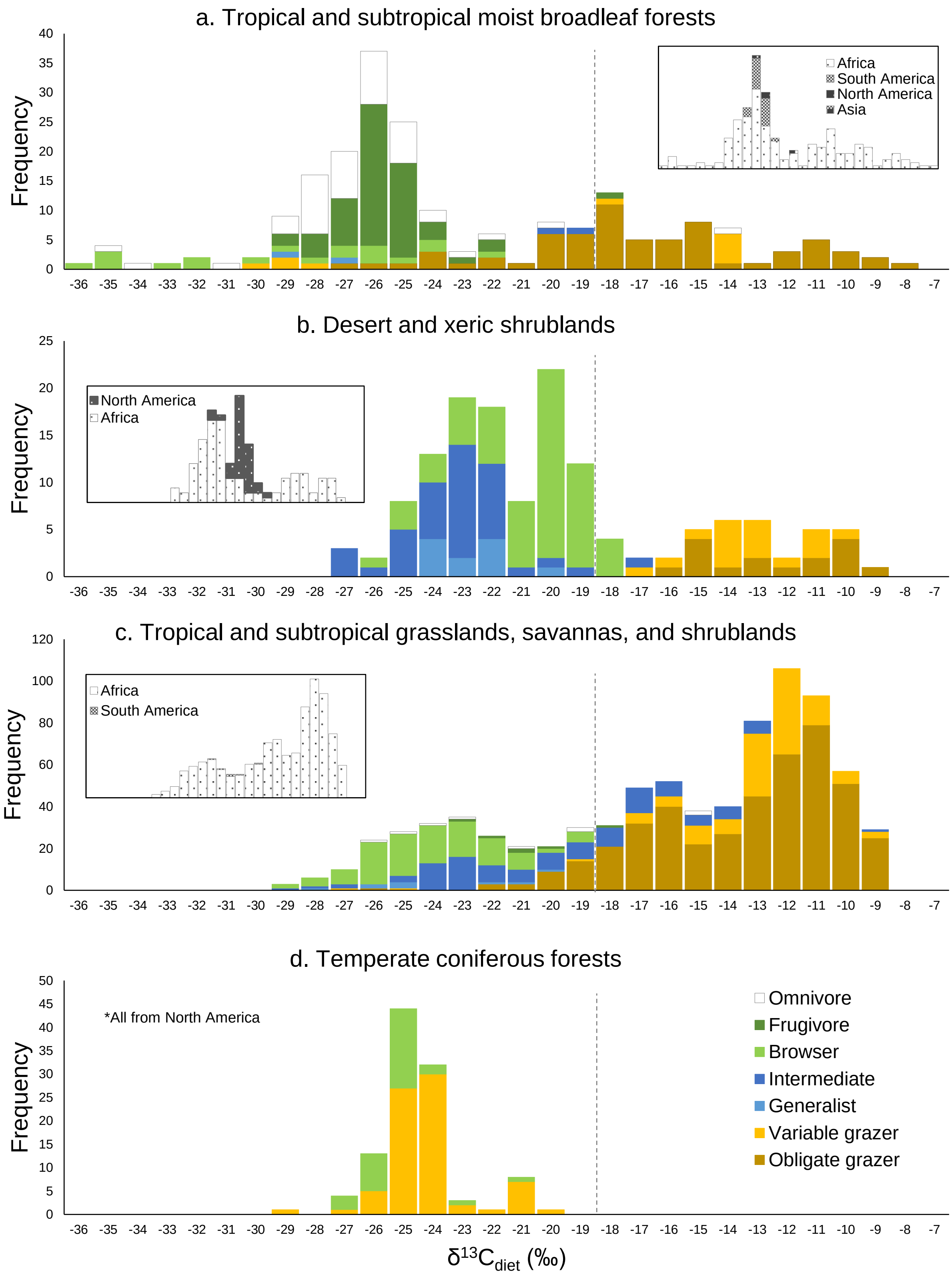


Figure 4.5 Frequency of $\delta^{13}C_{diet}$ values in the four best-sampled ecoregions. Dashed line is the C_3-C_4 boundary.

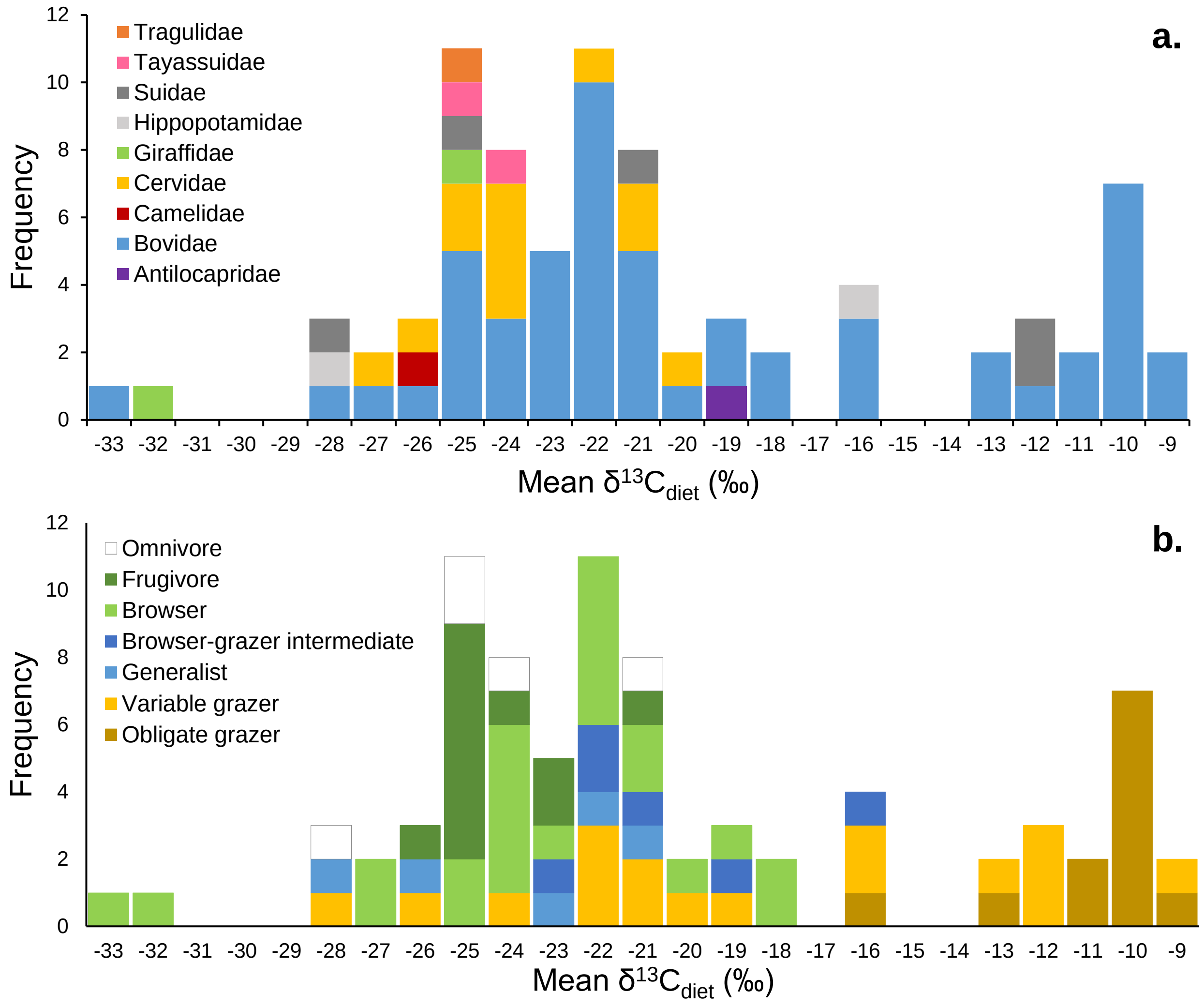


Figure 4.6 Frequency of mean $\delta^{13}C_{diet}$ values in 80 artiodactyl species.

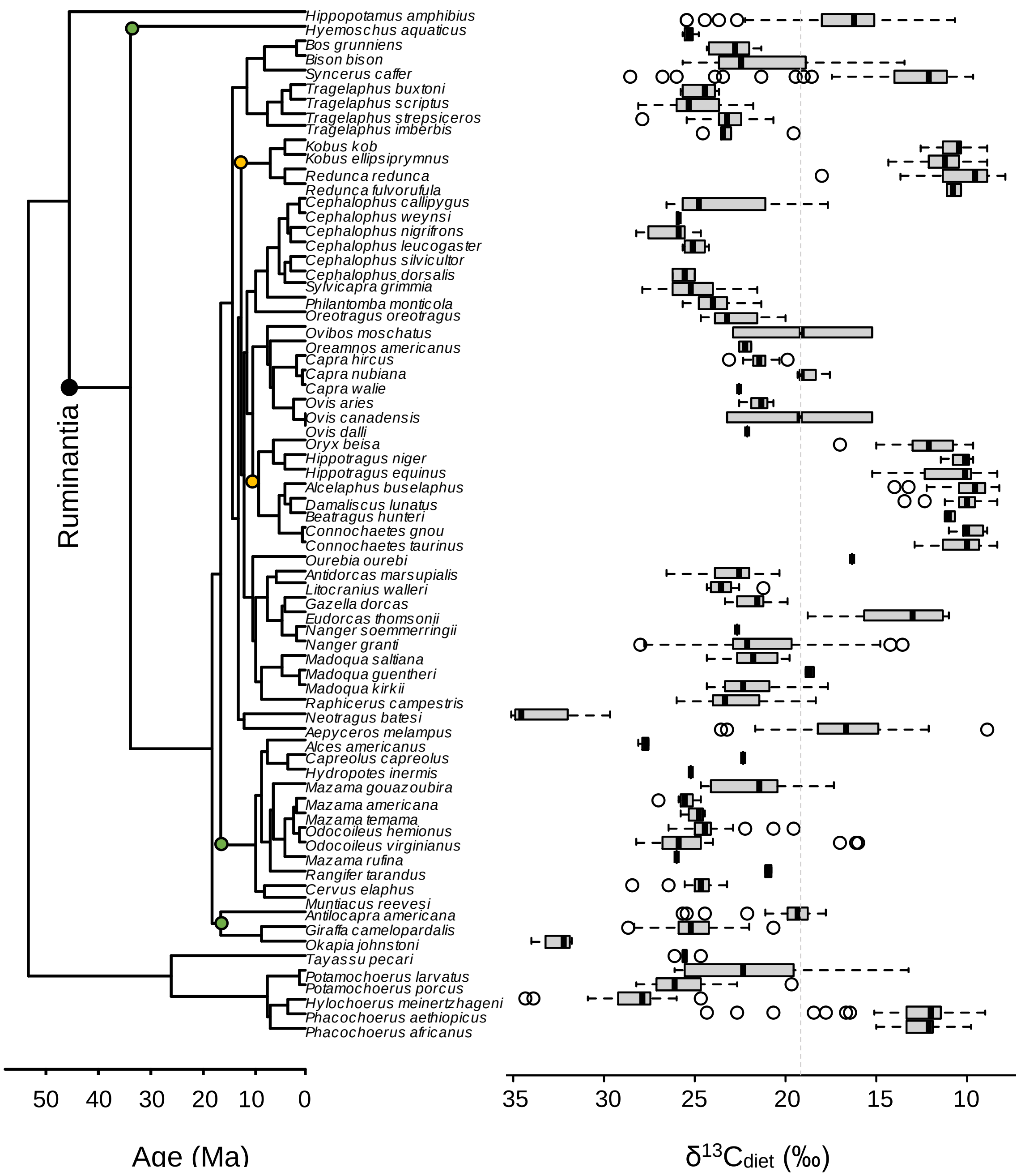


Figure 4.7 Summary statisitcs of $\delta^{13}C_{diet}$ values in relation to the phylogentic relationship of 72 artiodactyl species. Labeled nodes mark clades that are mentioned in the text. Green nodes = C_3 feeders. Yellow nodes = C_4 feeders. Dashed vertical line = C_3-C_4 cutoff.

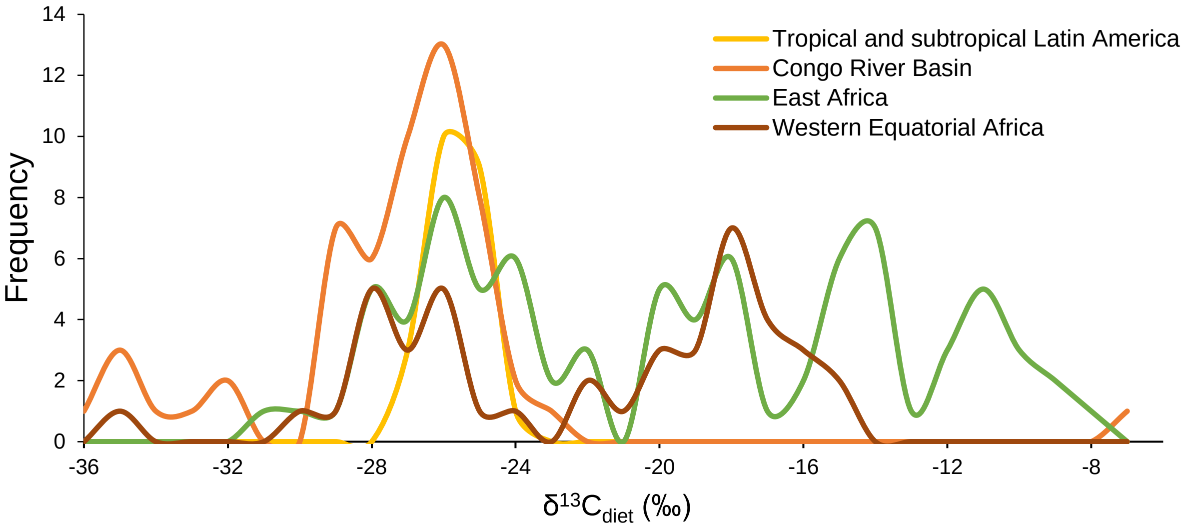


Figure 4.8 Distribution of $\delta^{13}C_{diet}$ values of artiodactyls from four well sampled areas of the same ecoregion: tropical and subtropical moist broadleaf forests. Note the generally unimodal distribution in Congo and Latin America, the generally bimodal distribution in western Africa, and the generally multimodal distribution in East Africa.

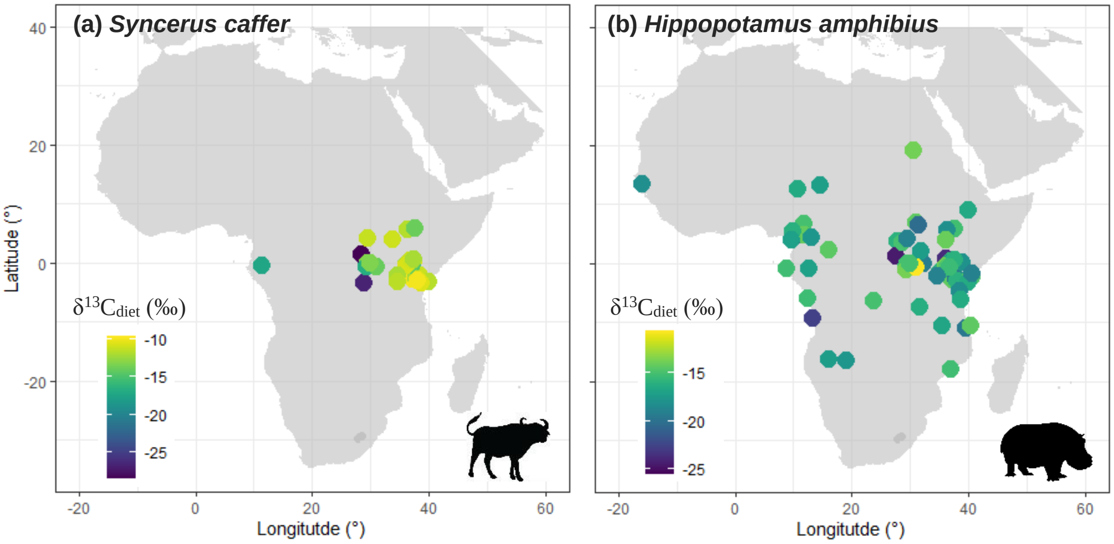


Figure 4.9 Geographic variation in the $\delta^{13}C_{diet}$ values of (a) the Cape buffalo (*Syncerus caffer*) and (b) the hippopotamus (*Hippopotamus amphibius*). Both species are well-sampled and exhibit a wide range of $\delta^{13}C_{diet}$ values, primarily in the C_4 range, reflecting the variability in their diet and the variation in ecoregion.

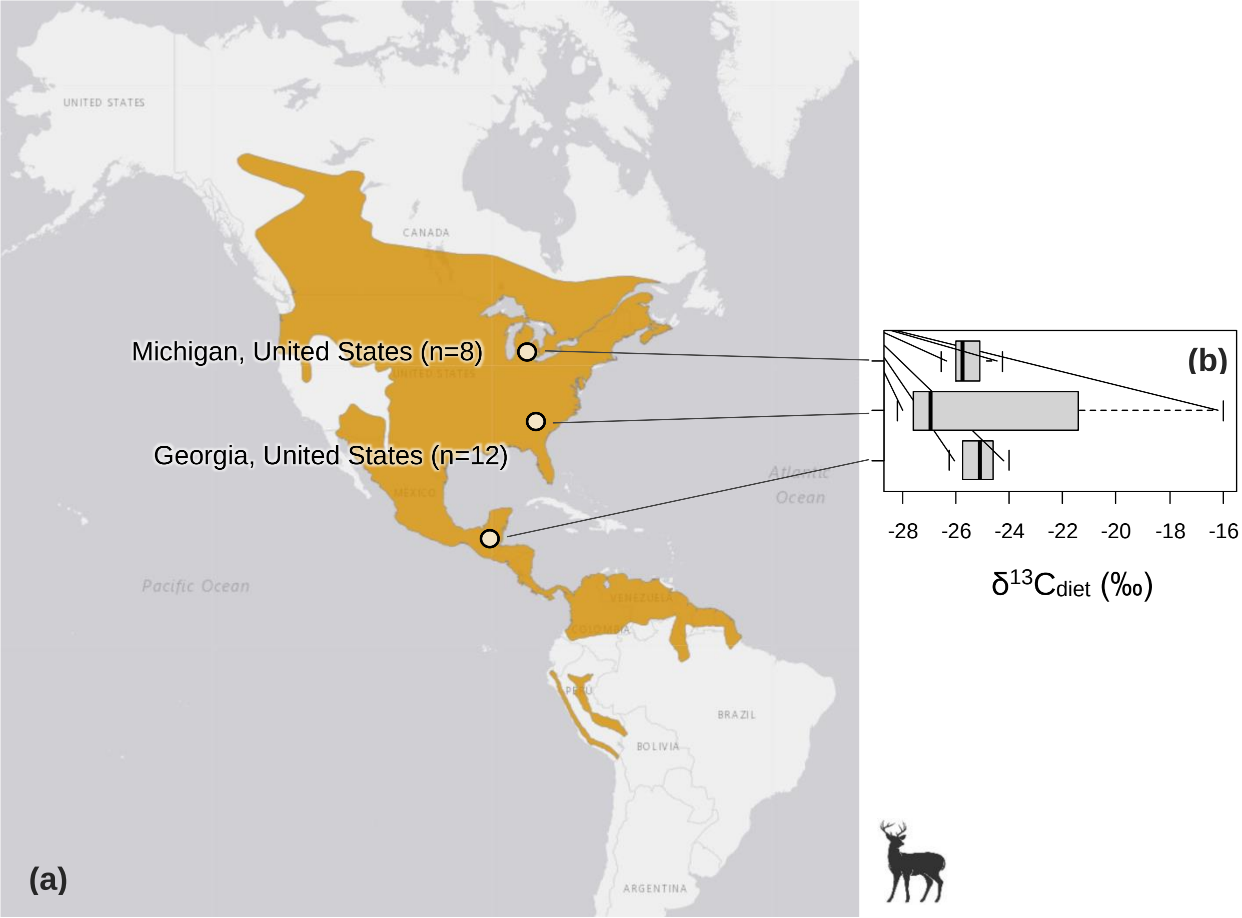


Figure 4.10 The white-tailed deer (*Odocoileus virginianus*), a C_3 feeder, exhibit relatively narrow ranges of $\delta^{13}C_{diet}$ values across a large latitudinal gradient. (a) Range map from IUCN (2008), showing the three areas where tooth specimens were collected. (b) Box and whisker plot of $\delta^{13}C_{diet}$ values for the three sampled areas.

Chapter 5

Cross-Method Integration of Dietary Data

Motivated by the potential applicability of a finer, quantitatively defined dietary classification in the study of fossil ungulates, I analyzed the dietary ecology of a wide range of extant artiodactyls with respect to biogeography, functional morphology, and stable isotopes. I found that frugivores and obligate grazers differ from other species in living in restricted climatic envelopes and exhibiting diagnostic mandibular morphologies. Both dietary extremes occur in warm climates; frugivores prefer wet conditions while obligate grazers prefer moderately dry conditions. Obligate grazers, feeding almost exclusively on monocots, have the highest $\delta^{13}C_{diet}$ values, and most of them can be differentiated from other groups based on their isotopic signatures. These findings justify application of a finer dietary classification than what is commonly used to paleoecological and paleoenvironmental reconstructions. Below, I discuss several important considerations when applying findings of this research to the study of fossil ungulates.

5.1 The scope of dietary information

Three markedly different types of data are used in this dissertation to describe or infer the dietary preferences of artiodactyls. These data sources contain information about dietary habits that is manifested over different time scales and at different taxonomic levels.

The pre-defined feeding categories used in the three data chapters were assigned based on dietary information compiled primarily from direct-observation studies and rumen and fecal analyses. These data record species' diet across months and years, that is, in ecological time. A spatially and seasonally averaged dietary intake was determined for each species. Variability in forage selection among individuals and populations is, therefore, removed from the data compilation.

Morphology provides information about dietary adaptations over the evolutionary time scale. Changes in the shape of craniomandibular or dental features usually occur over million-year time scales, lagging the time scale of environmental variability and ecological responses (e.g., Padilla and Adolph, 1996). Additionally, because force is applied to food during processing by jaw-lever mechanics and dental occlusal surfaces, morphology dictates the most biomechanically demanding food that a species is able to consume. Such food, however, may be nutritionally or biomechanically unfavorable and only rarely consumed (Liem's paradox). Species with highly specialized morphology may sometimes act as generalist or opportunistic feeders (Robinson and Wilson, 1998; Tütken et al., 2013), thereby weakening the relationship between morphology and average diet explored in Chapter 3.

Stable isotopes of tooth enamel record an individual's diet during the time of formation of the sampled tooth, which varies between months to over a year among different ungulate species (Kohn and Cerling, 2002; Kohn et al., 2002). Teeth erupted early in the sequence can have more depleted $\delta^{13}C_E$ values, through influence by the consumption of milk, while those erupted after weaning fully reflect the animal's dietary signal (e.g., Boisserie et al., 2005; Zazzo et al., 2010; Luyt and Sealy, 2018). While morphology provides approximation of diets, stable isotopes provide insights into the realized diets of animals. Stable isotopes allow comparisons of diets among herbivore communities (faunas), populations, individuals, and within individuals across seasons.

Few studies have simultaneously analyzed morphological traits (either with linear measurements or geometric morphometrics) and isotopes. In such studies, researchers were able not only to make robust dietary inferences, but also to further explore the relationship between phenotypic specialization and dietary niche breadth (e.g., Sponheimer et al., 1999; Pardi and DeSantis, 2021). Although combining methods poses some challenges, it also provides opportunities to take advantage of the strengths and overcome the weaknesses of each data type.

5.2 Integrating morphometric and isotopic data

Here, I depict the $\delta^{13}C_{diet}$ values from Chapter 3 in the mandibular morphospace of Chapter 2 (Fig. 5.1). The morphospace shows an ordination of the mandibular shapes of 100 bovid species. The frugivore–browser–grazer dietary spectrum is expressed primarily on the first principal component axis and in part on the second axis. Each data point represents the mean mandibular shape of one species and is color-coded by the species' mean $\delta^{13}C_{diet}$ values. Seventy-two species are shared between the two datasets. The figure simultaneously presents results from both analyses. C_3 and C_4 feeders are well differentiated in the diagonal direction of the morphospace, with the more depleted values (higher proportion of C_3 consumption) generally associated with frugivores and browsers; the more enriched values (higher proportion of C_4 consumption) are generally associated with obligate grazers and certain variable grazers (Fig. 5.1).

A few species appear to deviate from this broad trend. For example, the sitatunga (*Tragelaphus spekii*), a swamp-dwelling antelope in central Africa, has an average diet of a variable grazer (Gagnon and Chew, 2000). As discussed in Chapter 3, the species has a mandibular morphology that diverges notably from other *Tragelaphus* species, which are browsers or browser–grazer intermediates, and converges with grazing bovids, aligning with its dietary behavior. The $\delta^{13}C_{diet}$ values of *T. spekii*, however, are more depleted than for species with similar mandibular morphology. This discrepancy could be due to the small sample isotope sample size (N = 4) of the species, collected from the more closed-canopy part of its geographic range (Congo), or reflect the scarcity of C_4 vegetation in wetland-edge habitats where this species primarily feeds (Ndawula et al., 2011). A better sampling record or a deeper look into the feeding behavior of this species would help refine the relationship between mandibular morphology and the isotopic signature of tooth enamel.

Incorporating different data types has proven valuable to studying paleoecology, and when reconstructing the diet of fossil species, more proxies are better than one. In addition to mandibular morphology and tooth-enamel isotopes, tooth-wear proxies should also be incorporated. The microscopic wear patterns on the occlusal surface of teeth (microwear), for example, records feeding habits with the finest temporal resolution (daily or weekly) and can be used to detect subtle dietary variations in broadly similar diets (e.g., Louail et al., 2021) and can reveal ecological responses to short-term environmental changes that would not be reflected in tooth-wear measurements (such as mesowear) or from dental morphology (such as hyposodonty) (Mihlbachler et al., 2018).

5.3 Body size, diet, and isotopes

In extant artiodactyls, the frugivore-browser-grazer dietary spectrum is associated with a general increase in body mass, in the centroid size of mandibles, and in $\delta^{13}C_{diet}$ values (Fig. 5.2). The body size of mammalian herbivores has implications for the minimal quality of food necessary for survival (Bell, 1971; Jarman, 1974; Geist, 1974), as gut volume scales isometrically with body mass ($BM^{1.0}$) while metabolism scales as a fractional power of body mass ($BM^{0.75}$). Hence, larger herbivores have a greater capacity to process and survive on low-quality (high-fiber) forages, such as grasses (Demment and Van Soest, 1985). However, it is worth noting that a range of body size can be present within a feeding category, and species with comparable body sizes may have different diets. At the species level, body size is found to have no significant effect on fiber digestibility (fiber to lignin ratio) in ruminant diets (Pérez-Barbería et al., 2004). I also found no significant correlation of $\delta^{13}C_{diet}$ values with body mass or centroid size of mandibles at the species level, although the group means for the six feeding categories are correlated (Fig. 5.2). Therefore, although the general relationship among foraging behavior, body size, and nutritional needs is well documented and has been a fundamental principle in herbivore ecology, body size does not appear to be predictive of species' realized diet at a more refined level.

5.4 The herbivore dietary spectrum: terminology and application

Since the initial proposal of the three broad ruminant feeding types by Hofmann (1973, 1989), categorizing herbivore species into either browser ("concentrate" selectors), grazer, or mixed feeder has informed many studies in ecology and paleoecology. In reviewing the literature about the dietary ecology and ecomorphology of artiodactyls, I found various attempts to classify herbivore diets into finer categories. However, each of these classification schemes is used by few groups of researchers. One reason may be that these classifications lack detailed defining criteria of the categories, and making dietary assignments based on broad, qualitative definitions sometimes depends on expert opinion. Therefore, application of these classification schemes to species beyond those in the original studies is limited. Different dietary classifications also cover slightly different aspects of feeding ecology. Some classifications are based on the consumption of browse, forbs, shrubs, and grasses, while others are based on proportional consumption of fruits, dicots, and monocots. Some classifications consider feeding level (height from the ground) and the canopy cover of habitats in which feeding takes place (e.g., Spencer, 1995; Janis and Ehrhardt, 1998; Mendoza et al., 2002). There is also one classification scheme based solely on $\delta^{13}C_E$ values, which reflect the proportional consumption of C_3 and C_4 plants but reveal little information about the specific plant types in species' diets (Cerling and Harris, 1999; Table 1.1).

Another problem in this literature is related to the ambiguous use of "selectivity" to describe dietary choices. Aside from the word's conventional meaning in nutritional ecology (i.e., species selecting for or against foods of different nutritional levels), it has also been used to describe cropping mechanism (i.e., species plucking certain plant parts, such as fruits, from surrounding plant material), and the range of plants consumed (i.e., species selecting for or against certain plant species).

Future research could benefit from better-defined feeding categories and more precise descriptive terminologies. It would also be useful to evaluate what categories from different classification schemes have in common or in contrast. For example, hypergrazers as identified by Cerling et al. (2015) based on $\delta^{13}C_E$ values largely correspond to obligate grazers by the definition of Gagnon and Chew (2000), as shown in Chapter 4, and they can be studied in association with each other. Different classification schemes may also be combined with different types of morphological proxies or be suitable for addressing different types of research questions, as they capture slightly different aspects of dietary ecology. Figure 3.S1 illustrates an example: one classification scheme more effectively differentiates subsets of browsing taxa (frugivores and browsers), while the other scheme more effectively differentiates subsets of grazing taxa (fresh grass feeder and grass feeder).

5.5 The modern (non-)analogue

The observed geographic ranges and dietary niches of extant artiodactyls are a result of diversification, extinction, and geographic-range shifts over evolutionary time scales in response to landscape changes (e.g., Barnosky et al., 2016), as well as of impacts by anthropogenic activities and recent global change (e.g., Rivals et al., 2007; Pineda-Munoz et al., 2021). The degree to which modern ecosystems are representative of paleoenvironment varies, but there is mounting evidence that modern climates and faunas are not analogous to many ancient environments (Janis et al., 2000; Williams and Jackson, 2007; Faith et al., 2019). To that end, trait- and process-based evaluations of extant faunas, in combination with geological and paleontological data, are essential components of paleoecological and paleoenvironmental reconstructions.

5.6 Conclusions

Combining the dietary information, biogeography, mandibular morphology, and carbon-isotope composition of tooth enamel of extant artiodactyls, I found that: (1) frugivores and obligate grazers can be identified by mandibular shape and occupy the most restricted climatic conditions, (2) frugivores are a distinct dietary group and their functional morphology needs further investigation, (3) carbon isotopes show variable feeding preferences and dietary niche breadths of artiodactyl species, which reflect the vegetation heterogeneity in their environment, and grazing taxa have more variable isotopic signals than browsing taxa do as a result of feeding on C_4 graze, C_3 browse, and C_3 graze materials. Findings of this research suggest that the more detailed dietary classifications can be useful for studying fossil artiodactyls. In addition, integration of multiple approaches provides deeper insights into species' ecology.

5.7 References

Barnosky AD, Lindsey EL, Villavicenci o NA, Bostelmann E, Hadly EA, Wanket J, Marshall CR, 2016. Variable impact of late Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proc Natl Acad Sci* 113:856-861.

Bell RHV, 1971. A grazing ecosystem in the Serengeti. *Scientific American* **225**: 86–93.

Boisserie J-R, Zazzo A, Merceron G, Blondel C, Vignaud P, Likius A, Mackaye HT, Brunet M, 2005. Diets of modern and late Miocene hippopotamids: Evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeogr Palaeoclimatol Palaeoecol* **221**:153–174.

Cerling TE, Harris JM, 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* **120**:347–363.

Clauss M, Steuer P, Müller DWH, Codron D, Hummel J, 2013. Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PLoS One* **8**: e68714.

Faith T, Rowan J, Du A, 2019. Early hominins evolved within non-analog ecosystems. *Proc Natl Acad Sci* **116**: 21478-21483.

Forrest F, Plummer T, Raaum R, 2018. Ecomorphological analysis of bovid mandibles from Laetoli Tanzania using 3D geometric morphometrics: Implications for hominin paleoenvironmental reconstruction. *J Hum Evol* **114**:20–34.

Geist V, 1974. On the relationship of social evolution and ecology in ungulates. *Am Zool* **14**: 205–220.

Hofmann RR, 1973. The ruminant stomach (stomach structure and feeding habits of East Afrcian game ruminants). *East African Monographs in Biology, vol 2*. East African Literature Bureau: Nairobi.

Hofmann RR, 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* **78**:443-457.

Janis CM, Damuth J, Theodor JM. 2000 Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc Natl Acad Sci USA* **97**:7899–7904.

Jarman PJ, 1974. The social organization of antelope in relation to their ecology. *Behaviour* **48**: 215–266.

Kohn MJ, Cerling TE, 2002. Stable isotope compositions of biological apatite. *Rev Mineral Geochem* **48**:455–488.

Kohn MJ, Miselis JL, Fremd TJ, 2002. Oxygen isotope evidence for progressive uplift of the Cascade Range, Oregon. *Earth Planet Sci Lett* **204**:151–165.

Louail M, Ferchaud S, Souron A, Walker AEC, Merceron G, 2021. Dental microwear textures differ in pigs with overall similar diets but fed with different seeds. *Palaeogeogr Palaeoclimatol Palaeoecol* **572**:110415.

Luyt J, Sealy J, 2018. Inter-tooth comparison of δ^{13}C and δ^{18}O in ungulate tooth enamel from south-western Africa. *Quat Int* **495**:144–152.

Mihlbachler, M.C., Campbell, D., Chen, C., Ayoub, M., Kaur, P., 2018. Microwear-mesowear congruence and mortality bias in rhinocerotid mass death assemblages. *Paleobiology* **44**: 131–154.

Müller DWH, Codron D, Meloro C, Munn A, Schwarm A, Hummel J, Clauss M, 2013. Assessing the Bell-Jarman principle: scale of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology, Part A* **164**:129-140.

Ndawula J, Tweheyo M, Tumusiime DM, Eilu G, 2011. Understanding sitatunga (*Tragelaphus spekii*) habitats through diet analysis in Rushebeya-Kanyabaha wetland, Uganda. *Afr J Ecol* **49**:481–489.

Padilla DK, Adolph SC, 1996. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol Ecol* **10**:105–117.

Pardi MI, DeSantis LRG, 2021. Dietary plasticity of North American herbivores: a synthesis of stable isotope data over the past 7 million years. *Proc Royal Soc B* **288**: 20210121.

Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius WA, 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proc R Soc Lond B* **271**:1081–1090.

Pineda-Muzos S, Wang Y, Lyons SK, Tóth AB, McGuire JL, 2021. Mammal species occupy different climates following the expansion of human impacts. *Proc Natl Acad Sci* **118**:e1922859118

Rivals F, Solounias N, Mihlbachler MC, 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. *Quat Res* **68**:338–346.

Robbins CT, Spalinger DE, van Hoven W, 1995. Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia* **103**:208–213.

Sponheimer M, Reed KE, Lee-Thorp JA, 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J Hum Evol* **36**:705–718.

Sridhara S, McConkey K, Prasad S, Corlett RT, 2016. Frugivory and seed dispersal by large herbivores of Asia. In: Ahrestani F, Sankaran M, (eds) *The Ecology of Large Herbivores in South and Southeast Asia*. Ecological Studies (Analysis and Synthesis), vol 225. Springer: Dordrecht. https://doi.org/10.1007/978-94-017-7570-0_5

Stevens RD, Rowe R, Badgley C, 2019. Gradients of mammalian biodiversity through space and time. *J Mammal* **100**:1069–1086.

Robinson BW, Wilson DS, 1998. Optimal foraging, specialization, and a solution to Liem's Paradox. *Am Nat* **151**: 223-235.

Tütken T, Kaiser TM, Vennemann T, Merceron G., 2013. Opportunistic feeding strategy for the earliest Old World hypsodont equids: Evidence from stable isotope and dental wear proxies. *PLoS One* **8**: e74463.

Williams JW.; Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment **5** (9): 475–482.

Zazzo A, Balasse M, Passey BH, Moloney AP, Monahan FJ, Schmidt O, 2010. The isotope record of short- and long-term dietary changes in sheep tooth enamel: Implications for quantitative reconstruction of paleodiets. *Geochim Cosmochim Acta* **74**: 3571–3586.

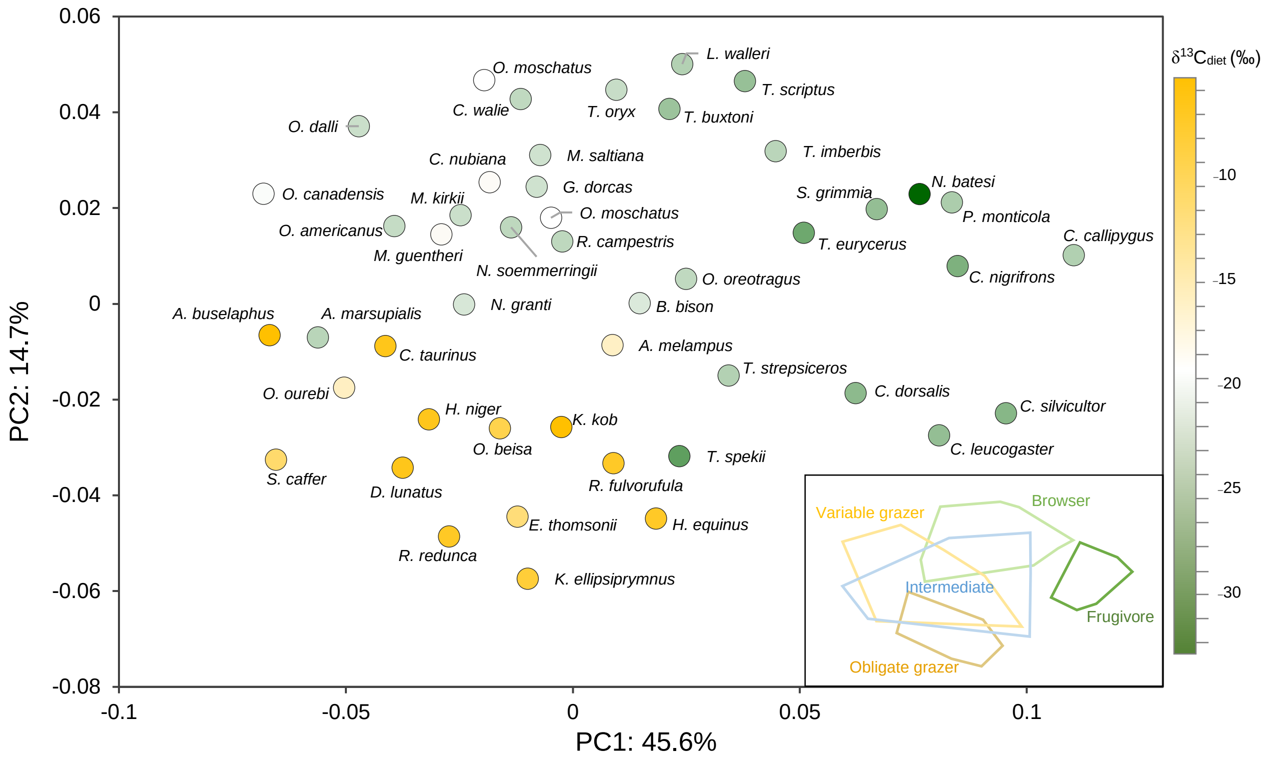


Figure 5.1 Relationship between mandibular morphology and $\delta^{13}C_{diet}$ values in 47 species of bovids. Principal component scores are derived from a Procrustes principal component analysis of the mandibular morphology of 100 bovid species (Chapter 3). Data points are color-coded by the mean $\delta^{13}C_{diet}$ values of the species (Chapter 4). See Table 1 in Chapter 4 for full species names. Higher $\delta^{13}C_{diet}$ values indicate greater proportions of C_4 consumption. Inset figure shows convex hulls of five herbivorous feeding categories. Note that the browser-grazer continuum generally goes diagonally from top-right to bottom-left in the morphospace.

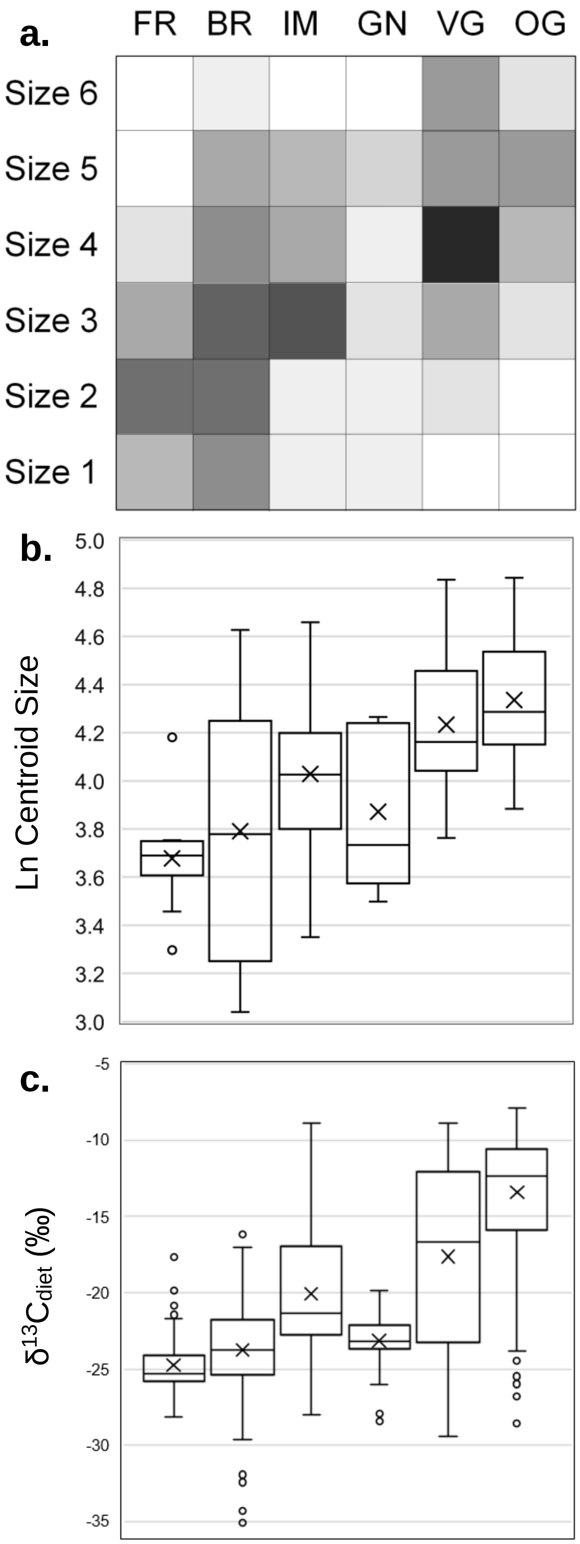


Figure 5.2 Relationships between herbivore feeding categories and (a) body size (N species = 161), (b) ln-transformed centroid size of mandibles (N species = 100), and (c) carbon-isotope composition of forage derived from tooth enamels (N species = 80). FR, frugivore; BR, browser; IM, browser-grazer intermediate; GN, generalist; VG, variable grazer; OG, obligate grazer.

Appendix A

Artiodactyl species analyzed in this work and their dietary classifications.

Table A 1 Dietary classification of artiodactyl species analyzed in this research.

Family	**Genus**	**Species**	**Dietary Classification**	**References**
Antilocapridae	*Antilocapra*	*americana*	Browser	Smith et al. (1998); Jacques et al. (2006); Clemente et al. (2009)
Bovidae	*Addax*	*nasomaculatus*	Variable Grazer	Gagnon and Chew (2000)
Bovidae	*Aepyceros*	*melampus*	Browser-Grazer Intermediate	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Codron et al. (2007); Hofmann et al. (2008); Steuer et al. (2014)
Bovidae	*Alcelaphus*	*buselaphus*	Obligate Grazer	Schuette et al. (1998); Gagnon and Chew (2000); Sponheimer et al. (2003); Djagoun et al. (2013); Steuer et al. (2014); Tolcha et al. (2019)
Bovidae	*Alcelaphus*	*lichtensteinii*	Obligate Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Ammodorcas*	*clarkei*	Browser	Gagnon and Chew (2000); Wilhelmi (2013)
Bovidae	*Ammotragus*	*lervia*	Variable Grazer	Gray and Simpson (1980); Mimoun and Nouira (2015)
Bovidae	*Antidorcas*	*marsupialis*	Browser-Grazer Intermediate	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Antilope*	*cervicapra*	Variable Grazer	Solanki and Naik (1998); Baskaran et al. (2016); Jhala and Isvaran (2016)
Bovidae	*Arabitragus*	*jayakari*	Browser	Munton (1985); Al Majaini (1999)
Bovidae	*Bison*	*bison*	Variable Grazer	Peden et al. (1974); Coppedge et al. (1998); Meagher (1986); Fortin et al. (2002); Craine et al. (2015); Sanderson et al. (2008)
Bovidae	*Bison*	*bonasus*	Variable Grazer	Borowski et al. (1967); Gębczyńska et al. (1991); Larter and Gates (1991); Cromsigt et al. (2017)
Bovidae	*Bos*	*frontalis*	Variable Grazer	Ahrestani (2018)
Bovidae	*Bos*	*gaurus*	Variable Grazer	Ahrestani (2018); but see McShea et al. (2019)
Bovidae	*Bos*	*grunniens*	Variable Grazer	Leslie and Schaller (2009)
Bovidae	*Bos*	*javanicus*	Variable Grazer	Pérez-Barbería and Gordon (2005); Matsubayashi et al. (2007); Hofmann et al. (2008); Clauss et al. (2008); Phillipps (2016); but see McShea et al. (2019)
Bovidae	*Bos*	*sauveli*	Variable Grazer	Melletti et al. (2014); Castelló (2016)
Bovidae	*Bos*	*taurus*	Variable Grazer	Elliot and Barrett (1985)
Bovidae	*Boselaphus*	*tragocamelus*	Browser-Grazer Intermediate	Leslie (2008)
Bovidae	*Bubalus*	*bubalis*	Variable Grazer	Gurung and Singh (1996); Lekagul and McNeely (1988); Macdonald (2001); Shackleton and Harestad (2003)
Bovidae	*Bubalus*	*depressicornis*	Browser-Grazer Intermediate	Flores-Miyamoto et al. (2005); Clauss et al. (2009); Pujaningsih et al. (2009)

Bovidae	*Bubalus*	*mindorensis*	Browser-Grazer Intermediate	Pujaningsih et al. (2009); Groves and Leslie (2011)
Bovidae	*Budorcas*	*taxicolor*	Browser	Wangchuck et al. (2015)
Bovidae	*Capra*	*caucasica*	Variable Grazer	Groves and Leslie (2011)
Bovidae	*Capra*	*falconeri*	Browser-Grazer Intermediate	Groves and Leslie (2011); Bashir et al. (2020)
Bovidae	*Capra*	*ibex*	Variable Grazer	Parrini et al. (2009)
Bovidae	*Capra*	*nubiana*	Browser	Hakham and Ritte (1993); Groves and Leslie (2011)
Bovidae	*Capra*	*pyrenaica*	Browser-Grazer Intermediate	García-Gonzalez and Cuartas (1989); Martínez (2002); Acevedo and Cassinello (2009); Martínez and Martínez (1987); Moço et al. (2013)
Bovidae	*Capra*	*sibirica*	Variable Grazer	Fodosenko and Blank (2001); Han et al. (2020)
Bovidae	*Capra*	*walie*	Browser	Dunbar (1978); Groves and Leslie (2011); Gebremedhin et al. (2016); Wale (2016)
Bovidae	*Capricornis*	*sumatraensis*	Browser	Santiapillai and Ramono (1994); Chen et al. (2009)
Bovidae	*Cephalophus*	*callipygus*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*dorsalis*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*harveyi*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*jentinki*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*leucogaster*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*natalensis*	Frugivore	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Cephalophus*	*niger*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*nigrifrons*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*ogilbyi*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*rufilatus*	Frugivore	Gagnon and Chew (2000); Djagoun et al. (2013)
Bovidae	*Cephalophus*	*silvicultor*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*sp.*	Frugivore	
Bovidae	*Cephalophus*	*spadix*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*weynsi*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Cephalophus*	*zebra*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Connochaetes*	*gnou*	Variable Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Connochaetes*	*taurinus*	Obligate Grazer	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Condron et al. (2007)
Bovidae	*Damaliscus*	*lunatus*	Obligate Grazer	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Condron et al. (2007); Djagoun et al. (2013)

Bovidae	*Damaliscus*	*pygargus*	Obligate Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003); Clauss et al. (2008)
Bovidae	*Dorcatragus*	*megalotis*	Browser	Gagnon and Chew (2000); Giotto et al. (2008); Giotto et al. (2016)
Bovidae	*Eudorcas*	*rufifrons*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Eudorcas*	*thomsonii*	Variable Grazer	Tieszen and Imbamba (1980); Gagnon and Chew (2000)
Bovidae	*Gazella*	*arabica*	Generalist	Shalmon (1989)
Bovidae	*Gazella*	*cuvieri*	Browser-Grazer Intermediate	Benamor et al. (2019)
Bovidae	*Gazella*	*dorcas*	Generalist	Gagnon and Chew (2000)
Bovidae	*Gazella*	*gazella*	Browser-Grazer Intermediate	Baharav (1981); Mendelssohn et al. (1995)
Bovidae	*Gazella*	*leptoceros*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Gazella*	*spekei*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Gazella*	*subgutturosa*	Browser	Mohamed et al. (1991); Cunningham (2009); Xu et al. (2012)
Bovidae	*Hemitragus*	*jemlahicus*	Variable Grazer	Schaller (1973); Green (1978); Clauss et al. (2005); Bhattacharya et al. (2012)
Bovidae	*Hippotragus*	*equinus*	Obligate Grazer	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Codron et al. (2007); Djagoun et al. (2013)
Bovidae	*Hippotragus*	*niger*	Obligate Grazer	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Codron et al. (2007)
Bovidae	*Kobus*	*ellipsiprymnus*	Obligate Grazer	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Codron et al. (2007); Djagoun et al. (2013); Steuer et al. (2014)
Bovidae	*Kobus*	*kob*	Obligate Grazer	Gagnon and Chew (2000); Djagoun et al. (2013)
Bovidae	*Kobus*	*leche*	Obligate Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Kobus*	*megaceros*	Obligate Grazer	Gagnon and Chew (2000)
Bovidae	*Kobus*	*vardonii*	Obligate Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Litocranius*	*walleri*	Browser	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Steuer et al. (2014)
Bovidae	*Madoqua*	*guentheri*	Browser	Gagnon and Chew (2000)
Bovidae	*Madoqua*	*kirkii*	Browser	Gagnon and Chew (2000)
Bovidae	*Madoqua*	*saltiana*	Browser	Gagnon and Chew (2000)
Bovidae	*Naemorhedus*	*baileyi*	Browser	Zhang (1987); Sheng et al. (1999)
Bovidae	*Naemorhedus*	*goral*	Variable Grazer	Green (1987); Mead (1989); Chaiyarat et al. (1999); Ilyas and Khan (2003); Fukhar-I-Abbas et al. (2008); Ashraf et al. (2017); Dar et al. (2020)

Bovidae	*Nanger*	*dama*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Nanger*	*granti*	Browser-Grazer Intermediate	Spinage et al. (1980); Tieszen and Imbamba (1980); Gagnon and Chew (2000); Müller et al. (2011); Steuer et al. (2014)
Bovidae	*Nanger*	*soemmerringii*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Neotragus*	*batesi*	Browser	Gagnon and Chew (2000)
Bovidae	*Neotragus*	*pygmaeus*	Browser	Gagnon and Chew (2000)
Bovidae	*Nesotragus*	*moschatus*	Browser	Gagnon and Chew (2000)
Bovidae	*Nilgiritragus*	*hylocrius*	Variable Grazer	Groves and Leslie (2011)
Bovidae	*Oreamnos*	*americanus*	Variable Grazer	Rideout and Hoffmann (1975); Dailey et al. (1984); Fox and Smith (1988); Groves and Leslie (2011); Müller et al. (2011)
Bovidae	*Oreotragus*	*oreotragus*	Generalist	Gagnon and Chew (2000); Steuer et al. (2014)
Bovidae	*Oryx*	*beisa*	Variable Grazer	Tieszen and Imbamba (1980); Groves and Leslie (2011); Steuer et al. (2014)
Bovidae	*Oryx*	*dammah*	Variable Grazer	Gagnon and Chew (2000)
Bovidae	*Oryx*	*gazella*	Variable Grazer	Smith et al. (1998); Gagnon and Chew (2000); Sponheimer et al. (2003); Clauss et al. (2008)
Bovidae	*Oryx*	*leucoryx*	Variable Grazer	Gagnon and Chew (2000)
Bovidae	*Ourebia*	*ourebi*	Variable Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003); Cerling et al. (2003); but see Djagoun et al. (2013)
Bovidae	*Ovibos*	*moschatus*	Browser-Grazer Intermediate	Lent (1988); Klein (1991); Klein and Bay (1994); Ihl and Klein (2001); Larter and Nagy (2004); Groves and Leslie (2011)
Bovidae	*Ovis*	*ammon*	Variable Grazer	Harris and Miller (1995); Fedosenko and Blank (2005); Pérez-Barbería and Gordon (2005); Shrestha et al. (2005); Clauss et al. (2008); Groves and Leslie (2011); Li et al. (2018)
Bovidae	*Ovis*	*canadensis*	Variable Grazer	Dailey et al. (1984); Shackleton (1985); Festa-Bianchet (1999)
Bovidae	*Ovis*	*dalli*	Variable Grazer	Bowyer and Leslie (1992); Nichols and Bunnell (1999); Jung et al. (2015)
Bovidae	*Ovis*	*nivicola*	Variable Grazer	Baskin and Danell (2003); Groves and Leslie (2011)
Bovidae	*Ovis*	*orientalis*	Variable Grazer	Hoefs (1985); Kaya et al. (2004); Müller et al. (2011)
Bovidae	*Pantholops*	*hodgsonii*	Browser-Grazer Intermediate	Harris and Miller (1995); Leslie and Schaller (2008)
Bovidae	*Pelea*	*capreolus*	Browser	Gagnon and Chew (2000)
Bovidae	*Philantomba*	*maxwellii*	Frugivore	Gagnon and Chew (2000)
Bovidae	*Philantomba*	*monticola*	Frugivore	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Procapra*	*gutturosa*	Variable Grazer	Jiang et al. (1998); Jiang et al. (2002); Olsen et al. (2010)

Bovidae	*Procapra*	*picticaudata*	Browser	Harris and Miller (1995); Yin et al. (2007); Leslie (2010)
Bovidae	*Pseudois*	*nayaur*	Variable Grazer	Wang and Hoffman (1987); Mishra et al. (2004); Shrestha et al. (2005); Suryawanshi et al. (2010); Groves and Leslie (2011); Bhattacharya et al. (2012)
Bovidae	*Raphicerus*	*campestris*	Browser	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Pérez-Barbería and Gordon (2005); Codron et al. (2007)
Bovidae	*Raphicerus*	*sharpei*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Redunca*	*arundinum*	Obligate Grazer	Gagnon and Chew (2000)
Bovidae	*Redunca*	*fulvorufula*	Obligate Grazer	Gagnon and Chew (2000); Sponheimer et al. (2003)
Bovidae	*Redunca*	*redunca*	Obligate Grazer	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003)
Bovidae	*Rupicapra*	*pyrenaica*	Browser-Grazer Intermediate	Garcia-Gonzalez and Cuartas (1996); Pérez-Barbería et al. (1997); La Morgia and Bassano (2009)
Bovidae	*Rupicapra*	*rupicapra*	Variable Grazer	Schaller (1998); Pérez-Barbería and Gordon (2005); Hofmann et al. (2008); La Morgia and Bassano (2009); Groves and Leslie (2011)
Bovidae	*Saiga*	*tatarica*	Browser-Grazer Intermediate	Sokolov (1974); Heptner et al. (1988); Baskin and Danell (2003); Müller et al. (2011)
Bovidae	*Sylvicapra*	*grimmia*	Browser	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003); Pérez-Barbería and Gordon (2005); Codron et al. (2007); Djagoun et al. (2013)
Bovidae	*Syncerus*	*caffer*	Obligate Grazer	Tieszen and Imbamba (1980); Gagnon and Chew (2000); Sponheimer et al. (2003); Pérez-Barbería et al. (2004); Codron et al. (2007); Djagoun et al. (2013); Steuer et al. (2014)
Bovidae	*Taurotragus*	*derbianus*	Browser	Gagnon and Chew (2000)
Bovidae	*Taurotragus*	*oryx*	Browser	Gagnon and Chew (2000); Codron et al. (2003); Sponheimer et al. (2003); Djagoun et al. (2013); Steuer et al. (2014); Hejcmanová et al. (2020)
Bovidae	*Tetracerus*	*quadricornis*	Browser	Solanki and Naik (1998); Krishna et al. (2009); Leslie and Sharma (2009); Baskaran et al. (2011)
Bovidae	*Tragelaphus*	*angasii*	Generalist	Gagnon and Chew (2000); Sponheimer et al. (2003); Codron et al. (2007)
Bovidae	*Tragelaphus*	*buxtoni*	Browser	Gagnon and Chew (2000)
Bovidae	*Tragelaphus*	*eurycerus*	Browser	Gagnon and Chew (2000)
Bovidae	*Tragelaphus*	*imberbis*	Browser-Grazer Intermediate	Gagnon and Chew (2000)
Bovidae	*Tragelaphus*	*scriptus*	Browser	Gagnon and Chew (2000); Sponheimer et al. (2003); Codron et al. (2007); Djagoun et al. (2013); Steuer et al. (2014)
Bovidae	*Tragelaphus*	*spekii*	Variable Grazer	Gagnon and Chew (2000)
Bovidae	*Tragelaphus*	*strepsiceros*	Generalist	Gagnon and Chew (2000); Sponheimer (2003); Steuer et al. (2014)

Camelidae	*Camelus*	*bactrianus*	Variable Grazer	Zhao et al. (2006); Sigomoto et al. (2018)
Camelidae	*Camelus*	*dromedarius*	Browser-Grazer Intermediate	Gauthier-Pilters (1984); Kohler-Rollefson (1991)
Camelidae	*Lama*	*glama*	Browser-Grazer Intermediate	Groves and Leslie (2011)
Camelidae	*Vicugna*	*vicugna*	Variable Grazer	Borgnia et al. (2010); Mosca Torres and Puig (2010); Groves and Leslie (2011); Castellaro et al. (2020)
Cervidae	*Alces*	*alces*	Browser	Hodder et al. (2013); Jung et al. (2015); Spitzer et al. (2020)
Cervidae	*Axis*	*axis*	Variable Grazer	Elliot and Barrett (1985); Khan (1994); Clauss et al. (2008); Hofmann et al. (2008)
Cervidae	*Axis*	*porcinus*	Browser-Grazer Intermediate	Dhungel and O'Gara (1991); Clauss et al. (2008); Hofmann et al. (2008); Tripathi et al. (2019)
Cervidae	*Blastocerus*	*dichotomus*	Browser-Grazer Intermediate	Redford and Eisenberg (1992); Tomas and Salis (2000); Piovezan et al. (2012)
Cervidae	*Capreolus*	*capreolus*	Browser	Cornelis et al. (1999); Spitzer et al. (2020)
Cervidae	*Capreolus*	*pygargus*	Browser	Danilkin (1995); Adhikari et al. (2016)
Cervidae	*Cervus*	*canadensis*	Variable Grazer	McCracken and Hansen (1981); Groves and Leslie (2011); Kohl et al. (2012); Jung et al. (2015)
Cervidae	*Cervus*	*elaphus*	Browser-Grazer Intermediate	Hodder et al. (2013); Spitzer et al. (2020)
Cervidae	*Cervus*	*nippon*	Browser-Grazer Intermediate	Feldhamer (1980); Yokoyama et al. (2000)
Cervidae	*Dama*	*dama*	Browser-Grazer Intermediate	Elliot and Barrett (1985); Spitzer et al. (2020)
Cervidae	*Elaphodus*	*cephalophus*	Browser-Grazer Intermediate	Sheng and Lu (1982); Leslie et al. (2013)
Cervidae	*Hippocamelus*	*antisensis*	Browser-Grazer Intermediate	Barrio (2013); Gazzolo and Barrio (2016)
Cervidae	*Hippocamelus*	*bisulcus*	Browser	Galende et al. (2005); Vila et al. (2009)
Cervidae	*Hydropotes*	*inermis*	Browser	Guo and Zhang (2005); Kim et al. (2011)
Cervidae	*Mazama*	*americana*	Frugivore	Branan et al. (1985); Redford and Eisenberg (1992); Gayot et al. (2004); Pérez-Barbería and Gordon (2005); Cassini and Toledo (2021)
Cervidae	*Mazama*	*chunyi*	Browser	Rumiz et al. (2007); Rumiz and Pardo (2010)
Cervidae	*Mazama*	*gouazoubira*	Frugivore	Stallings (1984); Redford and Eisenberg (1992); Gayot et al. (2004); Pérez-Barbería and Gordon (2005); Black-Décima et al. (2010); Serbent et al. (2011); Prado (2013); Gallina-Tessaro et al. (2019)
Cervidae	*Mazama*	*rufina*	Generalist	Redford and Eisenberg (1992); Lizcano and Alvarez (2008)
Cervidae	*Mazama*	*sp.*	Frugivore	

Cervidae	*Muntiacus*	*atherodes*	Browser	Payne et al. (1985); Payne and Francis (2005)
Cervidae	*Muntiacus*	*crinifrons*	Browser	Sheng and Lu (1980); Timmins and Chan (2016)
Cervidae	*Muntiacus*	*muntjak*	Browser	Oka (1998); Ilyas and Khan (2003); Farida et al. (2006); Hofmann et al. (2008)
Cervidae	*Muntiacus*	*reevesi*	Browser	Jackson and Chapman (1977); Van Wieren (1996)
Cervidae	*Odocoileus*	*hemionus*	Browser	Anthony and Smith (1974); MacCracken and Hansen (1981); Anderson and Wallmo (1984); Elliot and Barrett (1985); Marshal et al. (2012); Hodder et al. (2013)
Cervidae	*Odocoileus*	*sp.*	Browser	
Cervidae	*Odocoileus*	*virginianus*	Browser	Anthony and Smith (1974); Henke et al. (1988); Smith (1991); Daigle et al. (2004); Arceo et al. (2005); Vasquez et al. (2015)
Cervidae	*Ozotoceros*	*bezoarticus*	Browser-Grazer Intermediate	Jackson and Giulietti (1988); Cosse et al. (2009); Vila (2010); Desbiez et al. (2011)
Cervidae	*Pudu*	*mephistophiles*	Generalist	Pérez-Barbería and Gordon (2005); Weber and Gonzales (2016); Cassini and Toledo (2021)
Cervidae	*Pudu*	*puda*	Browser	Eldridge et al. (1987); Cassini et al. (2021)
Cervidae	*Rangifer*	*tarandus*	Browser	Klein (1991); Bjune (2000); Mathiesen et al. (2000); Ihl and Klein (2001); Heggberget et al. (2002); Larter and Nagy (2004); Joly et al. (2007); Jung et al. (2015); Bjørkvoll et al. (2018)
Cervidae	*Rucervus*	*duvaucelii*	Variable Grazer	Kaiser et al. (2011)
Cervidae	*Rucervus*	*eldii*	Variable Grazer	McShea et al. (2001); Tripathi et al. (2019); Wong et al. (2021)
Cervidae	*Rusa*	*alfredi*	Generalist	Groves and Leslie (2011); Ali et al. (2021)
Cervidae	*Rusa*	*marianna*	Generalist	Groves and Leslie (2011); Ali et al. (2021)
Cervidae	*Rusa*	*unicolor*	Generalist	Kaiser et al. (2011); Leslie (2011); Bhattacharya et al. (2012); Zhang et al. (2020); Ali et al. (2021)
Giraffidae	*Giraffa*	*camelopardalis*	Browser	Tieszen and Imbamba (1980); Pellew (1984); Pérez-Barbería et al. (2004); Parker and Bernard (2006); Codron et al. (2007)
Giraffidae	*Okapia*	*johnstoni*	Browser	Hart and Hart (1988); Bodmer and Rabb (1992)
Hippopotamidae	*Hexaprotodon*	*liberiensis*	Generalist	Flacke and Decher (2019)
Hippopotamidae	*Hippopotamus*	*amphibius*	Obligate Grazer	Tieszen and Imbamba (1980); Pérez-Barbería and Gordon (2005); Codron et al. (2007)
Moschidae	*Moschus*	*berezovskii*	Browser	Zhang et al. (2008); Wang et al. (2015a, b); Su et al. (2020)
Moschidae	*Moschus*	*chrysogaster*	Browser	Green (1987); Bhattacharya et al. (2012); Syed and Ilyas (2012, 2014)
Moschidae	*Moschus*	*fuscus*	Browser	Groves and Leslie (2011); Wang et al. (2015b)
Moschidae	*Moschus*	*moschiferus*	Browser	Prikhod'ko (2015); Wang et al. (2015); Su et al. (2020)
Moschidae	*Moschus*	*sp.*	Browser	

Suidae	*Hylochoerus*	*meinertzhageni*	Omnivore	Groves and Leslie (2011)
Suidae	*Phacochoerus*	*aethiopicus*	Variable Grazer	Groves and Leslie (2011)
Suidae	*Phacochoerus*	*africanus*	Variable Grazer	Codron et al. (2007); Steuer et al. (2014)
Suidae	*Potamochoerus*	*larvatus*	Omnivore	Groves and Leslie (2011)
Suidae	*Potamochoerus*	*porcus*	Omnivore	Groves and Leslie (2011)
Suidae	*Sus*	*barbatus*	Omnivore	Groves and Leslie (2011)
Suidae	*Sus*	*scrofa*	Omnivore	Groves and Leslie (2011)
Suidae	*Sus*	*sp.*	Omnivore	Groves and Leslie (2011)
Tayassuidae	*Catagonus*	*wagneri*	Generalist	Groves and Leslie (2011)
Tayassuidae	*Pecari*	*tajacu*	Omnivore	Groves and Leslie (2011)
Tayassuidae	*Tayassu*	*pecari*	Omnivore	Groves and Leslie (2011)
Tragulidae	*Hyemoschus*	*aquaticus*	Frugivore	Dubost (1984)
Tragulidae	*Moschiola*	*meminna*	Frugivore	Phillips (1984); Kaiser et al. (2011)
Tragulidae	*Tragulus*	*javanicus*	Frugivore	Medway (1983); Clauss et al. (2008); Farida et al. (2006); Groves and Leslie (2011)
Tragulidae	*Tragulus*	*kanchil*	Frugivore	Groves and Leslie (2011)
Tragulidae	*Tragulus*	*napu*	Frugivore	Clauss et al. (2008); Groves and Leslie (2011)
Tragulidae	*Tragulus*	*nigricans*	Browser	Groves and Leslie (2011)

References

Acevedo P, Cassinello J, 2009. Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus. *Mammal Rev* **39**:17–32.

Adhikari P, Park S-M, Kim T-W, Lee J-W, Kim G-R, Han S-H, Oh S-H, 2016. Seasonal and altitudinal variation in roe deer (*Capreolus pygargus tianschanicus*) diet on Jeju Island, South Korea. *J Asia Pac Biodivers* **9**:422–428.

Ahrestani FS, 2018. *Bos frontalis* and *Bos gaurus* (Artiodactyla: Bovidae). *Mamm Species* **50**:34c50.

Al Majaini HM, 1999. Nutritional Ecology of the Arabian Tahr *Hemitragus jayakari* Thomas 1894 in Wadi Sareen Reserve area. M.Sc. thesis, Sultan Qaboos University, Oman.

Ali NANG, Abdullah ML, Nor SAM, Pau TM, Kulaimi NAM, Naim DM, 2021. A review of the genus *Rusa* in the Indo-Malayan archipelago and conservation efforts. *Saudi J Biol Sci* **28**:10–26.

Anthony RG, Smith NS, 1974. Comparison of rumen and fecal analysis to describe deer diets. *J Wildl Manag* **38**:535–540.

Arceo G, Mandujano S, Gallina S, Perez-Jimenez LA, 2005. Diet diversity of white-tailed deer (*Odocoileus virginianus*) in a tropical dry forest in Mexico. *Mammalia* **69**:159–168.

Ashraf N, Anwar M, Oli MK, Pine WE, Sarwar M, Hussain I, Awan MS, 2017. Seasonal variation in the diet of the grey goral (*Naemorhedus goral*) in Machiara National Park (MNP), Azad Jammu and Kashmir, Pakistan. *Mammalia* **81**: 235–244.

Baharav D, 1981. Food habits of the mountain gazelle in semi-arid habitats of eastern Lower Galilee, Israel. *J Arid Environ* **4**:63–69.

Barrio J, 2013. *Hippocamelus antisensis* (Artiodactyla: Cervidae). *Mamm Species* **45**:49–59.

Bashir M, Fazili MF, Ahmad F, Ahmad J, 2020. Dietary ecology of Markhor (*Capra falconeri cashmiriensis*) in winter range of Kazinag National Park, Kashmir, J&K, India. *Indian J Sci Technol* **13**:2463–2474.

Baskaran N, Ramkumaran K, Karthikeyan G, 2016. Spatial and dietary overlap between blackbuck (*Antilope cervicapra*) and feral horse (*Equus caballus*) at Point Calimere Wildlife Sanctuary, Southern India: Competition between native versus introduced species. *Mamm Biol* **81**:296–302.

Baskin L, Danell K, 2003. *Ecology of Ungulates*. Berlin, Heidelberg: Springer.

Benamor N, Bounaceur F, Baha M, Aulagnier S, 2019. First data on the seasonal diet of the vulnerable *Gazella cuvieri* (Mammalia: Bovidae) in the Djebel Messaâd forest, northern Algeria. *Folia Zool* **68**:253–260.

Bhattacharya T, Kittur S, Sathyakumar S, Rawat GS, 2012. Diet overlap between wild ungulates and domestic livestock in the Greater Himalaya: Implications for management of grazing practices. *Proc Zool Soc* **65**:11–21.

Bjørkvoll E, Pedersen B, Hytteborn H, Jónsdóttir IS, Langvatn R, 2009. Seasonal and interannual dietary variation during winter in female Svalbard reindeer (*Rangifer Tarandus Platyrhynchus*). *AAAR* **41**:88–96,

Bjune AE, 2000. Pollen analysis of faeces as a method of demonstrating seasonal variations in the diet of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Polar Res* **19**:183–192.

Bodmer RE, Rabb GB, 1992. *Okapia johnstoni*. *Mamm Species* **422**:1–8.

Borgnia M, Vilá BL, Cassini MH, 2010. Foraging ecology of Vicuña, *Vicugna vicugna*, in dry Puna of Argentina. *Small Rum Res* **88**:44–53.

Borowski S, Kransinski Z, Milkowski L, 1967. Food and role of European bison in forest ecosystems. *Acta Theriol* **12**:367–376.

Bowyer RT, Leslie DM Jr, 1992. *Ovis dalli*. *Mamm Species* **393**:1–7.

Branan WV, Werkhoven MCM, Marchinton RL, 1985. Food habits of brocket and white-tailed deer in Suriname. *J Wildl Manag* **49**:972–976.

Cassini GH, Toledo N, 2021. An ecomorphological approach to craniomandibular integration in neotropical deer. *J Mammal Evol* **28**:111–123.

Cerling TE, Harris JM, Passey BH, 2003. Diets of East African Bovidae based on stable isotope analysis. *J Mammal* **84**:456–470.

Chaiyarat R, Laohajinda W, Kutintara U, Nabhitabhata J, 1999. Ecology of the goral (*Naemorhedus goral*) in Om Koi Wildlife Sanctuary, Thailand. *Nat Hist Bull SIAM Soc* **47**:191–205.

Chen W, Hu J, Lu X, 2009. Habitat use and separation between the Chinese serow (*Capricornis milneedwardsi*) and the Chinese goral (*Naemorhedus griseus*) in winter. *Mammalia* **73**: 249–252.

Clauss M, Hofmann RR, Streich WJ, Fickel J, Hummel J, 2008. Higher masseter muscle mass in grazing than in browsing ruminants. *Oecologia* **157**:377–385.

Clauss M, Hummel J, Vercammen F, Streich WJ, 2005. Observations on the Macroscopic Digestive Anatomy of the Himalayan Tahr (*Hemitragus jemlahicus*). *Anat Histol Embryol* **34**:276–278.

Clauss M, Reese S, Eulenberger K, 2009. Macroscopic digestive anatomy of a captive lowland anoa (*Bubalus depressicornis*). In: Clauss Mm Fidgett A, Jean-Michel H, Huisman T, Hummel J, Janssen G, Nijboer J, Plowman A, editors. Zoo Animal Nutrition, Vol. IV. Fürth: Filander. Pp 255–263.

Clemente F, Holechek JL, Valdez R, Mendoza GD, 2009. Influence of range condition on pronghorn (*Antilocapra americana*) and cattle diets in southern New Mexico. *J Appl Anim Res* **36**:13–16.

Codron D, Codron J, Lee-Thorp JA, Sponheimer M, de Ruiter D, Sealy J, Grant R, Fourie N, 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *J Zool* **273**:21–29.

Coppedge BR, Leslie DM, Shaw JH, 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. *J Range Manag* **51**:379–382.

Cornelis J, Casaer J, Hermy M, 1999. Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): A review. *J Zool* **248**:195–207.

Cosse M, Gonzales S, Gimenez-Dixon M, 2009. Feeding ecology of *Ozotoceros bezoarticus*: Conservation implications in Uruguay. *Iheringia Sér Zool* **99**:158–64.

Craine J, Towne E, Miller M, Fierer N, 2015. Climatic warming and the future of bison as grazers. *Sci Rep* **5**:16738.

Cromsigt JPGM, Kemp YJM, Rodriguez E, Kivit H, 2017. Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? *Restor Ecol* **26**:891–899.

Cunningham PL, 2009. Observations of the seasonal dietary preference of male *Gazella subgutturosa marica* Thomas, 1897 (Cetartiodactyla: Bovidae) along foraging trails of central Saudi Arabia. *J Threat Taxa* **1**:445–449.

Daigle C, Crête M, Lesage L, Ouellet J-P, Huot J, 2004. Summer diet of two white-tailed deer, *Odocoileus virginianus*, populations living at low and high density in Southern Québec. *Can Field-Nat* **188**:360–367.

Dailey TV, Hobbs NT, Woodard TN, 1984. Experimental comparisons of diet selection by mountain goats and mountain sheep in Colorado. *J Wildl Manage* **48**: 799–806.

Danilkin AA, 1995. *Capreolus pygargus*. *Mamm Species* **512**:1–7.

Dar JA, Fazili MF, Bhat BA, Ahmad R, 2020. Winter diet composition of Himalayan goral (*Naemorhedus goral*) in Kazinag National Park, Jammu and Kashmir, India. *Int J Sci Technol Res* **9**:3048–3054.

Desbiez ALJ, Santos SA, Alvarez JM, Tomas WM, 2011. Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (Ozotoceros bezoarticus) in a seasonal Neotropical wetland. *Mammal Biol* **76**:351–357.

Dhungel SK, O'Gara BW, 1991. Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildl Monogr* **119**:3–40.

Djagoun CAMS, Codron D, Sealy J, Mensah GA, Sinsin B, 2013. Stable carbon isotope analysis of the diets of west African bovids in Pendjari Biosphere Reserve, northern Benin. *S Afr J Wildl Res* **43**:33–43.

Dubost G, 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. *J Mammal* **65**:298–316.

Dunbar RIM, 1978. Competition and niche separation in a high altitude herbivore community in Ethiopia. *Afr J Ecol* **16**:183–199.

Eldridge WD, Macnamara MM, Pacheco NV, 1987. Activity patterns and habitat utilization of pudus (*Pudu puda*) in south-central Chile. In: Wemmer CM (ed.) Biology and Management of the Cervidae. Washington, D.C.: Smithsonian Inst. Press. Pp 352-369.

Elliot HW, Barrett RH, 1985. Dietary overlap among axis, fallow, and black-tailed deer and cattle. *J Range Manag* **38**:435–439.

Farida WR, Semiadi G, Handayani TH, Harun, 2006. Habitat distribution and diversity of plants as feed resources for mouse deer (*Tragulus javanicus*) and barking deer (*Muntiacus muntjak*) in Gunung Halimun National Park. *Tropics* **15**:371–376.

Fedosenko AK, Blank DA, 2001. *Capra sibirica*. *Mamm Species* **675**: 1–13.

Fedosenko AK, Blank DA, 2005. *Ovis ammon*. *Mamm Species* **773**: 1–15.

Feldhamer GA, 1980. *Cervus nippon*. *Mamm Species* **128**:1–7.

Festa-Bianchet M, 1999. Bighorn sheep. In: Wilson D, Ruff S (eds.) The Smithsonian Book of North American Mammals. Washington, D.C.: The Smithsonian Institution Press. Pp 348–350.

Flacke GL, Decher J, 2019. *Choeropsis liberiensis* (Artiodactyla: Hippopotamidae). *Mamm Species* **51**:100–118.

Flores-Miyamoto K, Clauss M, Ortmann S, Sainsbury AW, 2005. Nutrition of captive lowland anoa (*Bubalus depressicornis*): a study on ingesta passage, intake, digestibility, and a diet survey. *Zoobiology* **24**:125 – 134.

Fortin D, Fryxell JM, Pilote R, 2002. The temporal scale of foraging decisions in bison. *Ecology* **83**:970–982.

Fox JL, Smith CA, 1988. Winter mountain goat diets in southeast Alaska. *J Wildl Manage* **83**:362–365.

Fukhar-I-Abbas F, Akhtar T, Mian A, 2008. Food and feeding preferences of Himalayan gray goral (*Naemorhedus goral bedfordi*) in Pakistan and Azad Jammu and Kashmir. *Zoo Biology* **27**:371–380.

Gagnon M, Chew AE, 2000. Dietary preferences in extant African Bovidae. *J Mammal* **81**:490–511.

Galende G, Ramilo E, Beati A, 2005. Diet of Huemul deer (*Hippocamelus bisulcus*) in Nahuel Huapi National Park, Argentina. *Stud Neotrop Fauna Environ* **40**:1–5.

Gallina-Tessaro S, Pérez-Solano LA, Reyna-Hurtado R, Escobedo-Morales LA, 2019. Brocket deer. In: Gallina-Tessaro S. (eds) Ecology and Conservation of Tropical Ungulates in Latin America. Springer, Cham.

García-Gonzalez R, Cuartas P, 1989. A comparison of the diets of the wild goat (*Capra pyrenaica*), domestic goat (*Capra hircus*), mouflon (*Ovis musimon*) and domestic sheep (*Ovis aries*) in the Cazorla mountain range. *Acta Biol Mont* **9**:123–132.

Garcia-Gonzalez R, Cuartas P, 1996. Trophic utilization of a montane/subalpine forest by chamois (*Rupicapra pyrenaica*) in the Central Pyrenees. *For Ecol Manag* **88**:15–23.

Gayot M, Henry O, Dubost G, and Sabatier D, 2004. Comparative diet of the two forest cervids of the genus *Mazama* in French Guiana. *J Trop Ecol* **20**:31–43.

Gazzolo C, Barrio J, 2016. Feeding ecology of taruca (*Hippocamelus antisensis*) populations during the rainy and dry seasons in central Peru. *Int J Zool* **2016**:5806472.

Gębczyńska Z, Gębczyński M, Martynowicz E, 1991. Food eaten by the free-living European bison in Białowieża Forest. *Acta Theriol* **36**:307–313.

Gebremedhin B, Flagstad Ø, Bekele A, Chala D, Bakkestuen V, Boessenkool S, Popp M, Gussarova G, Schrøder-Nielsen A, Nemomissa S, Brochmann C, Stenseth NC, Epp LS,

2016. DNA metabarcoding reveals diet overlap between the endangered walia ibex and domestic goats - implications for conservation. *PLoS ONE* **1**:e0159133.

Giotto N, Laurent A, Mohamed N, Prevot N, Gerard J-F, 2008. Observations on the behaviour and ecology of a threatened and poorly known dwarf antelope: the beira (*Dorcatragus megalotis*). *Eur J Wildl Res* **54**:539–547.

Giotto N, Picot D, Moussa E, Rech J, Maublanc M-L, Bideau E, Mohamed N, Gerard J-F, 2016. Compared diets of sympatric beira antelopes and domestic goats in the growing season. *Eur J Wildl Res* **62**:687–693.

Gray GG, Simpson CD, 1980. *Ammotragus lervia*. *Mamm Species* **144**:1–7.

Green MJB, 1978. The ecology and feeding behaviour of the Himalayan tahr (Hemitragus jemlahicus) in the Langtang Valley, Nepal. M. Sc. Thesis: University of Durham.

Green MJB, 1987. Ecological separation in Himalayan ungulates. *J Zool* **1**:693–719.

Groves CP, Leslie DM Jr, 2011. Family Bovidae (hollow-horned ruminants). In: Wilson DE, Mittermeier RA, editors. Handbook of the Mammals of the World. Vol. 2. Hoofed Mammals. Barcelona: Lynx Edicions. Pp 444–575.

Guo G, Zhang E, 2005. Diet of the Chinese water deer (*Hydropotes inermis*) in Zhoushan Archipelago, China. *Acta Theriol Sin* **25**:122–130.

Hakham E, Ritte U, 1993. Foraging pressure of the Nubian ibex *Capra ibex nubiana* and its effect on the indigenous vegetation of the En Gedi Nature Reserve, Israel. *Biol Conserv* **63**:9–21.

Han L, Blank D, Wang M, da Silva AA, Yang W, Ruckstuhl K, Alves J, 2020. Diet differences between males and females in sexually dimorphic ungulates: A case study on Siberian ibex. *Eur J Wildl Res* **66**:55.

Harris RB, Miller DJ, 1995. Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia* **59**:197–212.

Hart JA, Hart TB. 1988. A summary report on the behaviour,ecology and conservation of the okapi (*Okapia johnstoni*) in Zaire. *Acta Zool Pathol Antverpiensa* **80**:19–28.

Heggberget TM, Gaare E, Ball JP, 2002. Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. *Rangifer* **22**:13–31.

Hejcmanová P, Ortmann S, Stoklasová L, Clauss M, 2020. Digesta passage in common eland (*Taurotragus oryx*) on a monocot or a dicot diet. *Comp Biochem Physiol* **246**:110720.

Henke SE, Demarais E, Pfister JA, 1988. Digestive capacity and diets of white-tailed deer and exotic ruminants. *J Wildl Manag* **52**:595–598.

Heptner V, Nasimovish A, Bannikov A, 1988. Mammals of the Soviet Union, Vol. 1. New Deli: Amerind Publishing Co.

Hodder DP, Rea RV, Crowley SM, 2013. Diet content and overlap of sympatric mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*) during a deep snow winter in northcentral British Columbia, Canada. *Can Wildl Biol Manag* **2**:43–50.

Hoefs M, 1985. Wild Sheep: Distribution, Abundance, Management and Conservation of the Sheep of the World and Closely Related Mountain Ungulates. Whitehorse: Northern Wild Sheep and Goat Council.

Hofmann RR, Streich WJ, Fickel J, Hummel J, Clauss M, 2008. Convergent evolution in feeding types: Salivary gland mass differences in wild ruminant species. *J Morph* **269**:240–257.

Ihl C, Klein DR, 2001. Habitat and diet selection by muskoxen and reindeer in western Alaska. *J Wildl Manage* **65**:964–972.

Ilyas O, Khan J, 2003. Food habits of barking deer (*Muntiacus muntjak*) and goral (*Naemorhedus goral*) in Binsar Wildlife Sanctuary, India. *Mammalia* **67**:521–531.

Jackson JE, Chapman DI, 1977. A note on the food of Muntjac deer (*Muntiacus reevesi*). *J Zool* **183**:546–548.

Jackson JE, Giulietti JD, 1988. The food habits of Pampas deer *Ozotoceros bezoarticus celer* in relation to its conservation in a relict natural grassland in Argentina. *Biol Conserv* **45**:1–10.

Jacques CN, Sievers JD, Jenks JA, Sexton CL, Roddy DE, 2006. Evaluating diet composition of pronghorn in Wind Cave National Park, South Dakota. *Prairie Nat* **38**:239–250.

Jhala YV, Isvaran K, 2016. Behavioural ecology of a grassland antelope, the blackbuck *Antilope cervicapra*: Linking habitat, ecology and behaviour. In: Ahrestani F, Sankaran M (eds.) The Ecology of Large Herbivores in South and Southeast Asia. Springer: Dordrecht. Pp 151–176.

Jiang Z, Takatsuki S, Gao Z, Jin K, 1998. The present status, ecology and conservation of the Mongolian gazelle, *Procapra gutturosa*: A review. *Mammal Study* **23**:63–78.

Jiang Z, Takatsuki S, Li J, Wang W, Gao Z, Ma J, 2002. Seasonal variations in foods and digestion of Mongolian gazelles in China. *J Wildl Manage* **66**:40-47.

Joly K, Cole MJ, Jandt RR, 2007. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in arctic tundra vegetation. *Can Field-Nat* **121**:379–383.

Jung TS, Stotny SA, Czetwertynski SM, 2015. Dietary overlap and potential competition in a dynamic ungulate community in Northwestern Canada. *Wildl Manage* **79**:1277–1285.

Kaiser TM, DWH Müller, Fortelius M, Schulz E, Codron D, Clauss M, 2011. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Rev* **43**:34–46.

Kaya MA, Bunch TD, Konuk M, 2004. On Konya wild sheep, *Ovis orientalis anatolica*, in the Bozdag protected area. *Mammalia* **68**:229–232.

Khan JA, 1994. Food habits of ungulates in dry tropical forests of Gir Lion Sanctuary, Gujarat, India. *Acta Theriol* **39**:185–193.

Kim BJ, Lee NS, Lee SD, 2011. Feeding diets of the Korean water deer (*Hydropotes inermis argyropus*) based on a 202 bp rbcL sequence analysis. *Conserv Genet* **12**:851–856.

Klein DR, 1991. Comparative ecological and behavioral adaptations of *Ovibos moschatus* and *Rangifer tarandus*. *Rangifer* **12**:47–55.

Klein DR, Bay C, 1994. Resource partitioning by mammalian herbivores in the high Arctic. *Oecologia* **97**:439–450.

Kohl MT, Hebblewhite M, Cleveland SM, Callaway RM, 2012. Forage value of invasive species to the diet of Rocky Mountain elk. *Rangelands* **34**:24–28.

Krishna C, Clyne PJ, Krishnashwamy J, Kumar NS, 2009. Distributional and ecological review of the four horned antelope, *Tetracerus quadricornis*. *Mammalia* **73**:1–6.

La Morgia V, Bassano B, 2009. Feeding habits, forage selection, and diet overlap in Alpine chamois (*Rupicapra rupicapra* L.) and domestic sheep. *Ecol Res* **24**:1043–1050.

Larter NC, Gates CC, 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Can J Zool* **69**:2677–2685.

Larter NC, Nagy JA, 2006. Seasonal changes in the composition of the diets of Peary caribou and muskoxen on Banks Island. *Polar Res* **23**:131–140.

Lent PC, 1988. *Ovibos moschatus*. *Mamm Species* **302**:1–9.

Leslie DM Jr, 2008. *Boselaphus tragocamelus* (Artiodactyla: Bovidae). *Mamm Species* **813**:1–16.

Leslie DM Jr, 2010. *Procapra picticaudata* (Artiodactyla: Bovidae). *Mamm Species* **42**:138–148.

Leslie DM Jr, Lee DN, Dolman RW, 2013. *Elaphodus cephalophus* (Artiodactyla: Cervidae). *Mamm Species* **45**:80–91.

Leslie DM, 2011. *Rusa unicolor* (Artiodactyla: Cervidae). *Mamm Species* **43**:1–30.

Leslie DM, Schaller GB, 2008. *Pantholops hodgsonii* (Artiodactyla: Bovidae). *Mamm Species* **817**:1–13.

Leslie DM, Sharma K, 2009. *Tetracerus quadricornis* (Artiodactyla: Bovidae). *Mamm Species* **843**:1–11.

Li B, Xu W, Blank DA, Wang M, Yang W, 2018. Diet characteristics of wild sheep (*Ovis ammon darwini*) in the Mengluoke Mountains, Xinjiang, China. *J Arid Land* **10**:482–491.

Lizcano D, Alvarez SJ, 2008. *Mazama rufina*. *IUCN Red List Threatened Species* **2008**: e.T12914A3397972.

Macdonald, D. 2001. Wild Cattle and Spiral-Horned Antelope. In: G Bateman, T Allan, M Salad, eds. The New Encyclopedia of Mammals. New York: Oxford University Press. Pp. 530-539.

Martínez T, 2002. Summer feeding strategy of Spanish ibex *Capra pyrenaica* and domestic sheep *Ovis aries* in south-eastern Spain. *Acta Theriol* **47**:479–490.

Martínez T, Martínez E, 1987. Diet of Spanish wild goat, *Capra pyrenaica*, in spring and summer at the Sierra de Gredos, Spain. *Mammalia* **51**: 547–557.

Mathiesen SD, Haga ØE, Kaino T, Tyler NJC, 2000. Diet composition, rumen papillation and maintenance of carcass mass in female Norwegian reindeer (*Rangifer tarandus tarandus*) in winter. *J Zool* **251**:129–138.

Matsubayashi H, Lagan P, Sukor JRA, 2007. Herbal seed dispersal by the banteng in a Bornean tropical rainforest. *Malay Nat J* **59**:297–303.

McCracken JG, Hansen RM, 1981. Diets of domestic sheep and other large herbivores in southcentral Colorado. *J Range Manag* **34**:242–243.

McShea WJ, Aung M, Poszig D, Wemmer C, Monfort S, 2001. Forage, habitat use, and sexual segregation by a tropical deer (*Cervus Eldi Thamin*) in a dipterocarp forest. *J Mammal* **82**:848–857.

McShea WJ, Sukmasuang R, Erickson DL, Herrmann V, Ngoprasert D, Bhumpakphan N, Davies SJ, 2019. Metabarcoding reveals diet diversity in an ungulate community in Thailand. *Biotropica* **51**:923–937.

Mead JI, 1989. *Nemorhaedus goral*. *Mamm Species* **335**:1–5.

Meagher M, 1986. *Bison bison*. *Mamm Species* **266**:1–8.

Medway LD, 1983. The Wild Mammals of Malaya (Peninsular Malayjsiu) and Singapore (2nd edition). Oxford University Press, Kuahr Lumpur.

Melletti M, Hassanin A, Mirabile M, 2014. Kouprey Bos sauveli A. Urbain, 1937. In: Melletti M, Burton J (eds.) Ecology, Evolution and Behaviour of Wild Cattle: Implications for Conservation. Cambridge University Press: Cambridge.

Mendelsohn H, Yom-Tom Y, Groves C, 1995. *Gazella gazella*. *Mamm Species* **490**:1–7.

Mimoun JB, Nouira S, 2015. Food habits of the aoudad *Ammotragus lervia* in the Bou Hedma mountains, Tunisia. *S Afr J Sci* **111**:11–12.

Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA, Prins HHT, 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Appl Ecol* **41**:344 – 354.

Moço G, Serrano E, Guerreiro M, Ferreira AF, Petrucci-Fonseca F, Maia MJ, Soriguer RC, Pérez JM, 2013. Seasonal dietary shifts and selection of Iberian wild goat *Capra pyrenaica* Schinz, 1838 in Peneda-Gerês National Park (Portugal). *Galemys* **25**:13–27.

Mohamed SA, Abbas J, Saleh M, 1991. Natural diet of the Arabian Rheem gazelle, *Gazella subgutturosa marica*. *J Arid Environ* **20**:371–374.

Mosca Torres ME, Puig S, 2010. Seasonal diet of vicuñas in the Los Andes protected area (Salta, Argentina): Are they optimal foragers? *J Arid Environ* **74**:450–457.

Müller DWH, Lackey LB, Streich WJ, Fickel J, Hatt J-M, Clauss M, 2010. Mating system, feeding type and ex situ conservation effort determine life expectancy in captive ruminants. *Proc R Soc B* **278**:2076–2080.

Munton P 1985. The ecology of the Arabian Tahr (*Hemitragus jayakari* Thomas, 1894) and strategy for the conservation of the species. *J Oman Stud* **8**:11–48.

Nickols L, Bunnell FL, 1999. Natural history of the thinhorn sheep. In: Valdez R, Krausman PR, editors. Mountain sheep of North America. Tuscon: University of Arizona Press. 23–77.

Oka GM, 1998. Factors affecting the management of Muntjac Deer (*Muntiacus muntjak*) in Bali Barat National Park, Indonesia. University of Western Sydney PhD Thesis.

Olson KA, Murray MG, Fuller TK, 2010. Vegetation composition and nutritional quality of forage for gazelle in Eastern Mongolia. *Rangel Ecol Manag* **63**:593–598.

Parker DM, Bernard RTF, 2006. The diet and ecological role of giraffe (*Giraffa camelopardalis*) introduced to the Eastern Cape, South Africa. *J Zool* **267**:203–210.

Parrini F, Cain JW, Krausman PR, 2009. *Capra ibex* (Artiodactyla: Bovidae). *Mamm Species* **830**:1–12.

Payne J, Francis CM, 2005. A Field Guide to the Mammals of Borneo. The Sabah Society and WWF Malaysia: Kota Kinabalu and Kuala Lumpur, Malaysia.

Payne J, Francis CM, Phillipps K, 1985. A Field Guide to the Mammals of Borneo. The Sabah Society and WWF Malaysia: Kota Kinabalu and Kuala Lumpur, Malaysia.

Peden DG, Van Dyne GM, Rice RW, Hansen RM, 1974. The tropic ecology of *Bison bison* L. on shortgrass plains. *J Appl Ecol* **11**: 489–497.

Pellow RA, 1984. The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). *J Zool* **202**:57–81.

Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius AW, 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proc R Soc Lond B Biol Sci* **271**:1081–1090.

Pérez-Barbería FJ, Gordon IJ, 2005. Gregariousness increases brain size in ungulates. *Oecologia* **145**:41–52.

Peréz-Barberia FJ, Oliván M, Osoro K, Nores C, 1997. Sex, seasonal and spatial differences in the diet of Cantabrian chamois *Rupicapra pyrenaica parva*. *Acta Theriol* **42**:37–46.

Phillipps Q, 2016. Banteng and water buffalo. Phillipps' Field Guide to the Mammals of Borneo: Sabah, Sarawak, Brunei, and Kalimantan. Princeton: Princeton University Press. Pp 304–305.

Phillips W, 1984. *Manual of the Mammals of Sri Lanka*. Sri Lanka: Wildlife and Nature Protection Society of Sri Lanka.

Prado HM, 2013. Feeding ecology of five neotropical ungulates: A critial review. *Oecol Aust* **17**:459–473.

Prikhod'ko VI, 2015. Cranial features and feeding types of subspecies forms of *Moschus moschife*rus L. (Moschidae, Cetartiodactyla). *Biol Bull* **42**:54–60.

Pujaningsih R, Sutrisno CI, Supriondho Y, Malik A, Djuwantoko D, Pudyatmoko S, Amir MA, Aryanto S, 2009. Diet composition of anoa (*Buballus* sp.) studied using direct observation and dung analysis method in their habitat. *J Indones Trop Anim Agric* **34**:223–228.

Redford K, Eisenberg J, 1992. Mammals of the Neotropics (Vol. 2): the Southern Cone. Chicago, USA: The University of Chicago Press.

Rideout CB, Hoffmann RS, 1975. *Oreamnos americanus*. *Mamm Species* **63**:1–6.

Rumiz DI, Pardo E, 2010. Peruvian dwarf brocket deer *Mazama chunyi*. In: Duarte JMB, Gonzales S (eds.) Neotropical Cervidology: Biology and Medicine of Latin American Deer. Pp 185–189.

Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S, Fearn E, Fleener C, Forrest S, Gerlach C, Gates CC, Gross JE, Gogan P, Grassel S, Hilty JA, Jensen M, Kunkel K, Lammers D, List R, Minkowski K, Olson T, Pague C, Robertson PB, Stephenson B, 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conserv Biol* **22**: 252–266.

Santiapillai C, Ramono W, 1994. The serow (*Capricornis sumatraensis*) - its status, distribution and conservation in Sumatra. *Tigerpaper* **21**:15–19.

Schaller G, 1998. *Wildlife of the Tibetan Steppe*. Chicago: University of Chicago Press.

Schaller GB, 1973. Observations on Himalyan tahr (*Hemitragus jemlahicus*). *J Bombay Natl Hist Soc* **70**:1–24.

Schuette JR, Leslie DM Jr., Lochmiller RL, Jenks JA, 1998. Diets of hartebeest and Roan antelope in Burkina Faso: support of the long-faced hypothesis. *J Mammal* **79**:426–436.

Serbent MP, Periago ME, Leynaud GC, 2011. *Mazama gouazoubira* (Cervidae) diet during the dry season in the arid Chaco of Córdoba (Argentina). *J Arid Environ* **75**:87–90.

Shackleton DM, 1985. *Ovis canadensis*. *Mamm Species* **230**:1–9.

Shalmon B, 1989. The ecology of *Gazella gazella* spp. in the southern Arava Valley. *Isr J Zool* **35**:97.

Sheng H, Lu H, 1980. Current studies on the rare Chinese black muntjac. *J Nat Hist* **14**:803–807.

Sheng H, Lu H, 1982. Distribution, habits and resource status of the tufted deer ("*Elaphodus cephalophus*"). *Acta Zool Sin* **28**:307–311.

Sheng HL, Ohtaishi N, Lu HJ, 1999. *The Mammals of China*. China Forestry Publishing House: Beijing, China.

Shrestha R, Wegge P, Koirala RA, 2006. Summer diets of wild and domestic ungulates in Nepal Himalaya. *J Zool* **266**:111–119.

Smith C, Valdez R, Holechek JL, Zwank PJ, Cardenas M, 1998. Diets of native and non-native ungulates in southcentral New Mexico. *Southwest Nat* **43**:163–169.

Smith WP, 1991. *Odocoileus virginianus*. *Mamm Species* **388**:1–13.

Sokolov VE, 1974. *Saiga tatarica*. *Mamm Species* **38**:1–4.

Solanki GS, Naik RM, 1998. Grazing interactions between wild and domestic herbivores. *Small Ruminant Res* **27**:231–235.

Spinage, CA, Ryan C, Shedd M, 1980. Food selection by the Grant's gazelle. *Afr J Ecol* **18**:19–25.

Spitzer R, Felton A, Landman M, Singh NJ, Widemo F, Cromsigt JPGM, 2020. Fifty years of European ungulate dietary studies: A synthesis. *Oikos* **129**:1668–1680.

Sponheimer M, Lee-Thorp JA, DeRuiter DJ, Smith JM, van der Merwe NJ, Reed K, Grant CC, Ayliffe LK, Robinson TF, Heidelberger C, Marcus W, 2003. Diets of Southern African Bovidae: stable isotope evidence. *J Mammal* **84**:471–479.

Stallings JR, 1984. Notes on feeding habits of *Mazama gouazoubira* in the Chaco Boreal of Paraguay. *Biotropica* **16**:155–157.

Steuer P, Südekum K, Tütken T, Müller DWH, Kaandorp J, Bucher M, Clauss M, Humme J, 2014. Does body mass convey a digestive advantage for large herbivores? *Funct Ecol* **28**:1127–1134.

Suryawanshi KR, Bhatnagar YV, Mishra C, 2010. Why should a grazer browse? Livestock impact on winter resource use by bharal *Pseudois nayaur*. *Oecologia* **162**:453–462.

Syed Z, Ilyas O, 2012. Status, distribution and aspects of ecology of Alpine Musk Deer (*Moschus chrysogaster*) in Uttrakhand Himalayas, India. *DSG Newsletter* Nº24:4–12.

Syed Z, Ilyas O, 2014. Habitat preference and feeding ecology of alpine musk deer (*Moschus chrysogaster*) in Kedarnath Wildlife Sanctuary, Uttarakhand, India. *Anim Prod Sci* **56**:978–987.

Tieszen LL, Imbamba SK, 1980. Photosynthetic systems, carbon isotope discrimination and herbivore selectivity in Kenya. *Afr J Ecol* **18**:237–242.

Timmins R, Chan BP, 2016. *Muntiacus crinifrons*. *IUCN Red List Threatened Species* **2016**: e.T13924A22160753.

Tolcha A, Ayechew B, Shibru S, 2019. Feeding ecology of Swayne's hartebeest (*Alcelaphus buselaphus swaynei*, Sclater, 1892) in Maze National Park. *GSJ* **7**:1623–1639.

Tripathi S, Basumatary SK, Singh YR, McDonald HG, Tripathi D, Singh LJ, 2019. Multiproxy studies on dung of endangered Sangai (*Rucervus eldii eldii*) and Hog deer (*Axis porcinus*) from Manipur, India: Implications for paleoherbivory and paleoecology. *Rev Palaeobot Palynol* **263**:85–103.

Van Wieren SE, 1996. Browsers and grazers: foraging strategies in ruminants. In: Van Wieren SE (ed.) Digestive Strategies in Ruminants and Nonruminants. Thesis landbouw. University of Wageningen, Wageningen, pp 119–146.

Vasquez Y, Tarango L, López-Pérez E, Herrera J, Mendoza G, Mandujano S, 2015. Variation in the diet composition of the white tailed deer (*Odocoileus virginianus*) in the Tehuacán-Cuicatlán Biosphere Reserve. *Revista Chapingo Serie Ciencias Forestales y del Ambiente* **22**:00–00.

Vila AR, Galende GI, Pastore H, 2009. Feeding ecology of the endangered huemul (*Hippocamelus bisulcus*) in Los Alerces National Park, Argentina. *Mastozool Neotrop* **16**:423–431.

Wale M, 2016. The walia ibex (Capra walie). J Biodivers Endanger Species 4:161.

Wang W, He L, Liu B, Li L, Wei N, Zhou R, Qi L, Liu S, Hu D, 2015a. Feeding performance and preferences of captive forest musk deer while on a cafeteria diet. *Folia Zool* **64**:151–160.

Wang X, Hoffmann RS, 1987. *Pseudois nayaur* and *Pseudois schaeferi*. *Mamm Species* **278**:1–6.

Wang X, Zhou R, He L, Liu S, Zhou J, Qi L, Li L, Hu D, 2015b. The progress in nutrition research of musk deer: Implication for conservation. *Appl Anim Behav Sci* **172**:1–8.

Wangchuck TR, Wegge P, Sangay T, 2015. Habitat and diet of Bhutan takin *Budorcas taxicolor* whitei during summer in Jigme Dorji National Park, Bhutan. *J Nat Hist* **50**:759–770.

Weber M, Gonzales S, 2016. Latin American deer diversity and conservation: A review of status and distribution. *Ecoscience* **10**:443–454.

Wilhelmi FK, 2013. *Ammodorcas clarkei* Dibatag (Clarke's Gazelle). In: Kingdon J, Hoffmann M (eds.) Mammals of Africa Volume VI. London: Bloomsbury. Pp 387–390.

Wong MHG, Mo Y, Chan BPL, 2021. Past, present and future of the globally endangered Eld's deer (*Rucervus eldii*) on Hainan Island, China. *Glob Ecol Conserv* **26**:e01505.

Xu W, Xia C, Lin J, Yang W, Blank DA, Qiao J, Liu W, 2012. Diet of *Gazella subgutturosa* (Güldenstaedt, 1780) and food overlap with domestic sheep in Xinjiang, China. Fol*ia Zool* **61**:54–60.

Yin BF, Huai HY, Zhang YL, Le Z, Wei WH, 2007. Trophic niches of *Pantholops hodgsoni*, *Procapra picticaudata* and *Equus kiang* in Kekexili region. *J Appl Ecol* **18**:766-770.

Yokoyama M, Kaji K, Suzuki M, 2000. Food habits of sika deer and nutritional value of sika deer diets in eastern Hokkaido, Japan. *Ecol Res* **15**:345–355.

Zhang C, 1987. *Nemorhaedus cranbrookii* Hayman. In: Soma H (ed.), The Biology and Management of Capricornis and related Mountain Antelopes. Croom-Helm Ltd: New South Wales, Australia. Pp 213-220.

Zhang LB, Xu HF, Xue WJ, Jiang HR, Meng XX, 2008. Winter and spring diet composition of musk deer in Feng County, Shaanxi Province. *Sichuan J Zool* **27**:110-4.

Zhang Q, Yang B, Fu Q, Wang Y, Gong X, Zhang Y, 2020. The winter diet of sambar (*Rusa unicolor*) in the Qionglai Mountains. *Biodiv Sci* **28**:1190–1201.