Title

Evolutionary Response of Large Mammalian Predators to the Functional Biodiversity of Their Presumed Large Herbivore Prey

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A dissertation submitted in partial satisfaction

of the requirements for the degree Doctor of Philosophy

in Biology

by

Evan Michael Doughty

2024

ABSTRACT OF THE DISSERTATION

Evolutionary Response of Large Mammalian

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by

Evan Michael Doughty

Doctor of Philosophy in Biology

University of California, Los Angeles, 2024

Professor Blaire Van Valkenburgh, Chair

The evolution of life on this planet is influenced by many factors, key among them being the means in which predators and their prey interact. Direct morphological evidence for how large mammalian predators evolutionarily respond to their presumed herbivore prey is lacking, but predator richness positively correlates with that of extinct and extant herbivores. In my dissertation, I apply statistical methods to investigate how predators respond to the biodiversity of their presumed herbivore prey over the Cenozoic (66-1Ma).

Chapter 1 evaluates the strength of the correlation between North American predators and their presumed prey over the Cenozoic (66-1Ma). I quantify species richness of both the large mammalian predator and herbivore guilds relative to body mass and then apply statistical methods to determine to determine whether the species richness of predators tracks that of their

presumed herbivore prey. I observed notable correlations between large (>21kg) wolf-size predators and herbivores of roughly equal size (25kg) and larger.

Chapter 2 evaluates whether the predator guild exhibits an evolutionary response to changes in the distribution of herbivore body sizes over the Cenozoic. I quantify species richness of both guilds relative to body mass and then apply statistical methods to determine when either guild underwent statistically significant changes in their distribution of body mass. I then compare these significant shifts to determine if changes in predator guild structure coincide with, or follow, that of the herbivore guild. I observed multiple significant shifts within predator guild that followed shifts in the herbivores and were suggestive of an evolutionary response.

Chapter 3 evaluates whether the relative abundance of herbivores, specifically those antelope-size and larger, could be a plausible explanation for species richness trends within the predator guild over the Neogene (23-1Ma). I quantify the occupancy, a proxy of relative abundance, of herbivore genera in relation to body mass and compare that occupancy with predator richness. I observed relatively high (>0.25) and stable occupancy for larger (>25 kg) herbivores despite declining herbivore richness over Neogene, which could explain the unusually high ratio of predator to prey species in the Plio-Pleistocene.

Overall, this dissertation demonstrates that body mass, predator diet, and taxonomic diversity influences the evolution of both predator and herbivore guilds and underpins how the former responds to the latter over geologic time.

The dissertation of Evan Michael Doughty is approved.

David K Jacobs

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Jonathan David Marcot

Karen Elizabeth Sears

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University of California, Los Angeles

2024

This dissertation is dedicated to my late grandfather, Raymond DeVault.

“My dog has fleas.”

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

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CHAPTER I: CENOZOIC TRENDS IN FUNCTIONAL GROUP RICHNESS BETWEEN NORTH AMERICAN MAMMALIAN PREDATORS AND PREY

Abstract

The species richness of large mammalian predators increases with the richness of their large herbivore prey in extant African assemblages. Similarly, predator richness has been found to roughly track the richness of their presumed large herbivore prey over the later Paleogene and Neogene of North America; however, the scope and character of this posited coevolutionary relationship has remained relatively unexplored. Here we quantify species richness of both the large herbivore and predator guilds at the continental scale using estimated body mass and predator diet (e.g., hypercarnivore, mesocarnivores, and hypocarnivore). Following our initial expectations, we found significant positive correlations between lion-size (>100 kg) large predators and antelope- (25 to 150 kg) to rhino-size (>500 kg) large herbivores, correlations that increased in strength when the predator guild was restricted to hypercarnivores. Wild-cat size (1 to 7 kg) mesocarnivores were also observed to exhibit significant positive relationships with javelina- to horse-size herbivores and lion-size hypercarnivores. These results illuminate previously unknown trends between the predator and large herbivore guilds of the North American Cenozoic and demonstrate the importance of utilizing functional traits when investigating coevolutionary relationships.

Introduction:

Coevolution between predators and their prey has been used to explain parallel trends of evolution over a wide range of organisms (e.g., invertebrates, plants, fish, and birds) (Dawkins et al., 1979; Vermeij, 1987; Davies & Brooke, 1988; West, Cohen & Baron, 1991; Kelley, 1992). Both large mammalian predators and their presumed large herbivore prey are known to have undergone roughly coincidental and qualitatively similar changes in morphology and species

richness throughout the Cenozoic (Bakker, 1983; Van Valkenburgh & Janis, 1993). However, plausible, direct evidence for such a linkage existing between the trophic levels is limited, (see Janis & Wilhelm, 1993) and testing a direct coevolutionary relationship remains challenging as coevolution can occur at different organismal (e.g., allele, individual, population, species, lineage, community/assemblage, guild, etc.), temporal (e.g., microevolutionary versus macroevolutionary timescales) and spatial scales (Stanley, Van Valkenburgh & Steneck, 1983; Van Valen, 1983; Thompson, 1994, 2005; Abrams, 2000). Demonstrating coevolution between predator and prey is even more challenging among fossil taxa, where the nature of the fossil record limits the time-scale and available data (Futuyama & Slatkin, 1983; Stanley, Van Valkenburgh & Steneck, 1983; Jablonski, 2008). Nevertheless, within extant mammal assemblages, predator richness is related to prey richness at regional and global scales (Sandom et al., 2013). Van Valkenburgh and Janis (1993) documented this correlation of predator and prey taxonomic richness over geologic time, showing a roughly positive relationship between patterns of continental-scale species richness in large mammal predators (Orders Carnivora and Creodonta) and their presumed ungulate prey (Orders Artiodactyla, Perissodactyla, and Proboscidea) over the past 44 Ma of the North American fossil record (Figure 1). The observed correspondence of predator and prey taxonomic richness might suggest a causal evolutionary link between guilds, but there are several other possible explanations, and additional evidence is required to more completely demonstrate such a link. They proposed that a comparison of predator and prey functional traits (e.g., traits related to body mass, locomotion, or diet) over time might help reveal underlying mechanisms that drive their observed changes in species richness over the Cenozoic.

In this study, we expand on the work of Van Valkenburgh and Janis (1993) by exploring the coevolution of North American mammalian carnivores and ungulate-like herbivores by comparing their respective taxonomic richness throughout the Cenozoic. We extend their study by including functional traits in our analyses of species richness, namely body mass of both guilds and inferred predator diet, to determine when and if the species richness of specific functional groups are correlated.

We use body mass in this analysis because it influences many aspects of how predator and prey interact on ecological scales (Carbone et al., 1999; Sinclair, Mduma & Brashares, 2003; Radloff & Du Toit, 2004; Carbone, Teacher & Rowcliffe, 2007; Owen-Smith & Mills, 2008). For example, hunting success has been observed to increase alongside predator body size since larger predators tend to have greater strength and speed (MacNulty et al., 2009; Wilson et al., 2015). Mean and maximum mass of preferred prey is strongly related to predator mass in extant assemblages (Gittleman, 1985; Sinclair, Mduma & Brashares, 2003; Radloff & Du Toit, 2004; Owen-Smith & Mills, 2008), with carnivores over 21.5 kg tending to hunt prey of near equal or larger size due to metabolic requirements (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). On a larger scale, Sandom et al. (2013) observed that positive correlations between predator and prey species richness increased in strength when their analyses were restricted to large predators (> 21.5 kg) and large herbivores (> 10kg).

These previous observations suggest that the strength of correlations among various body mass categories of predators and ungulate prey will differ in strength and magnitude, and allow us to make three more specific predictions. First, we expect that a coevolutionary relationship will be most prominent between the species richness of large predators (> 21.5 kg) and the species richness of their potential large, bodied prey (>10 kg) due to the metabolic requirements

of those predators requiring them to take relevantly sized prey (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). Second, we expect a weaker relationship, or none at all, between the richness of predators and the richness of the largest herbivores (i.e., rhino-sized and larger, > 500 kg) due to their larger body sizes acting as a deterrent to predation. Specifically, large size has been suggested to reduce predation risk to ungulates and even confer relative immunity from predation at very large sizes, as exemplified by extant mammalian megaherbivores (> 800 kg) (Owen-Smith, 1988; Terborgh et al., 1999; Sinclair, Mduma & Brashares, 2003; Owen-Smith & Mills, 2008). Finally, we expect the richness of predators in the smallest size categories (<21.5 kg) to show weak, or nonexistent relationship with the richness of any ungulate herbivores, since these smaller predators tend to go after prey that is their size or smaller (e.g., rodents or lagomorphs which are not included within this study) and/or incorporate a greater proportion of non-vertebrate food (e.g., insects, plants, etc.) into their diets (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007).

Diet varies among mammalian predators, ranging from species that primarily consume meat (i.e., hypercarnivores) to those that also consume more plant matter and/or invertebrates in their diets (e.g., hypocarnivores). As among body size categories, we also expect that the strength of relationships between predators and their prey will differ among predator dietary groups. Specifically, we expect that the tracking of species richness between large predators and herbivores will be strongest for large hypercarnivores given their reliance on large prey as opposed to smaller and/or omnivorous predators that incorporate sources of non-vertebrate food (e.g., invertebrates, plants, etc.) (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). We assign fossil predators to dietary categories (hypercarnivore, mesocarnivore, and hypocarnivore) based on previous work on the association between dental morphology, body

mass, and diet in extant carnivorans (see Van Valkenburgh, 1989). By doing so, we are able to quantify the relationship between large herbivore richness and each of the predator dietary groups.

Alternatively, predator and herbivore species richness may not track each other closely if the predators are generalized in their choice of prey (Vermeij, 1982, 1987). For example, even though extant African carnivorans exhibit a positive relationship between their body mass and their mean and maximum size of preferred prey, their preferred size range of prey also includes smaller bodied herbivores (Sinclair, Mduma & Brashares, 2003; Owen-Smith & Mills, 2008). Similarly, some extant predators smaller than 21.5 kg (e.g., bobcats, coyotes, and wolverines) occasionally take adult herbivore prey that are larger than themselves (Burkholder, 1962; Haglund, 1966, 1974; Bjarvall, 1982; Labisky & Boulay, 1998; Lofroth et al., 2007; Inman & Packila, 2015; Mattisson et al., 2016; Magoun et al., 2018). We expect that correlations between predator and prey species richness would be nonexistent across the different body size and predator diet categories if predators are opportunistic and take a wide range of prey sizes.

A lack of a coevolutionary connection between predator and prey can also be demonstrated in the presence of significant correlations (Janzen, 1980; Nuismer, Gomulkiewicz & Ridenhour, 2010). Predator and herbivore richness could appear to be correlated due to both groups independently responding to similar environmental changes (e.g., opening habitats, aridification, changes in productivity, etc.) that have been inferred over the Cenozoic (Strömberg, 2002, 2004, 2011; Nuismer, Gomulkiewicz & Ridenhour, 2010). Extant large mammal prey (> 10kg) richness and ecomorphology (e.g., calcaneal gear ratio, hypsodonty, etc.) have been observed to be more strongly linked to climate and productivity than predator richness

at regional and continental scales (Eronen et al., 2010; Sandom et al., 2013; Lawing et al., 2017; Short & Lawing, 2021). Extant predator richness, as previously stated, corresponds more closely to prey richness than climate and productivity (Sandom et al., 2013); however, the locomotor morphology of extant carnivorans tracks aspects of climate and vegetation cover (Polly, 2010). Within the fossil record, Figueirido et al. (2012, 2019) observed that generic richness and ecomorphology (e.g., body mass, locomotion, and diet type) of North American large (> 1 kg) terrestrial mammals (orders Creodonta, Carnivora, Condylarthra, Dinocerata, Pantodonta, Taeniodonta, Tillodontia, Artiodactyla, Perissodactyla, Proboscidea, and Xenarthra) correlated with changes in climate and vegetation when those genera were aggregated into six chronofaunas at the continental scale. We expect that correlations will be similar between the different size and predator diet categories (e.g., hypercarnivores and hypocarnivores) if both guilds are reacting independently to similar environmental factors.

Our study encompasses a greater taxonomic and temporal scope of the North American fossil record than prior studies (see Van Valkenburgh & Janis (1993) and Janis (2000)) but retains a focus on North America due to the well-sampled and studied mammalian fossil record (Stanley, Van Valkenburgh & Steneck, 1983; Van Valkenburgh & Janis, 1993; Raja et al., 2021). By retaining the focus on the North American record, we are able to incorporate ~28 more years of paleontological discovery and bring to bear the repositories and databases (e.g., Paleobiological Database, https://paleobiodb.org/#/) that did not exist during the writing of the initial study. Moreover, Van Valkenburgh and Janis (1993) reported that the species richness of the predator guild roughly tracked that of the large herbivore guild, however, it was unclear if this relationship developed at the start of their time-series (the Late Uintan ~44 Ma) or if it

existed prior to that time. We explore this ambiguity by expanding our temporal scope to cover the entire Cenozoic (66 Ma to present).

This expansion necessitates that we increase the taxonomic scope to encompass many of the early members of the larger herbivore and predator guilds, which are not members of modern mammalian orders. We enlarged the predator guild sample to include Creodonta, Mesonychidae, and Paleogene Carnivoramorpha in addition to members of Carnivora. Likewise, we expand the large herbivore guild to include the ungulate to ungulate-like "Condylarthra", Dinocerata, Tillodontia, Taeniodonta, Pantodonta, and Proboscidea (Janis et al., 1998) in addition to Artiodactyla and Perissodactyla. Our use of the term guild within this study refers broadly to the continental assemblage (see Van Valkenburgh and Janis, 1993) of mammalian predators and large herbivores rather than the locality or community scale typically utilized in extant ecology (Root, 1967).

In sum, our goals are to 1) quantify the relationship between predators and prey, with respect to their body masses, over the Cenozoic and 2) determine how these relationships differ among predator dietary groups (e.g., hypercarnivore versus omnivore). In doing so, we hope to elucidate previously unrecognized trends between large mammalian predators and prey within the North American fossil record.

Methods and Materials

Our study involved these steps: 1) estimation of predator and prey body masses from dental measurements, 2) determination of stratigraphic ranges of species, and assignment to discrete time intervals, and 3) the correlation of taxonomic richness of predator and prey over the

Cenozoic. All data processing, replicate generation, and analysis was performed in R, version 4.3.1 (R Core Team, 2024). All datasets are located in Appendix A.

Taxonomic Sampling and Body Mass Estimation and Binning

We used linear measurements of teeth to estimate body masses of prey. We compiled linear dental measurements (e.g., lengths and widths) for North American large mammalian herbivores (Artiodactyla, Perissodactyla, “Condylarthra”, Dinocerata, Taeniodonta, Tillodontia, and Pantodonta; n=1087 species). Our category “Condylarthra" follows Halliday, Upchurch & Goswami (2017) and Scott et al. (2013) in that it includes the North American families Arctocyonidae, Chriacidae, Hyopsodontidae, Periptychidae, and Phenacodontidae. We compiled measurements of most species from the literature (n=~11,488 entries of 1058 species) and supplemented these with our own measurements from museum specimens (n=~542 specimens of 92 species).

Specifically, we used the length and width of the upper and lower cheek teeth (i.e., second premolar to third molar), individually and in aggregate (e.g., upper or lower first molar to third molar, etc.), to estimate herbivore body mass. We excluded the upper and lower first premolar as these teeth are absent in many large herbivore species. We assigned each herbivore the median values for all measurements over all specimens. Specimens represented by teeth with uncertain identity (e.g. M1 or M2, M?, etc.), as indicated by the author(s), were excluded from analysis unless the specimen(s) in question was (were) the only representative(s) of the species (e.g. *Crustulus fontanus* (Clemens, 2018)). Similarly, obviously redundant measurements, such as those directly cited from another source, were also excluded unless the primary source was unavailable.

We estimated body masses for almost all herbivore species using a maximum likelihood approach that incorporates all available measurements simultaneously. Damuth (1990) published univariate regression equation parameters (e.g., slope and intercept) and associated percent standard error of the estimate (%SEE) for univariate regression of each of our individual cheek tooth measurements (see Damuth, 1990; Appendix, Table 16.8). Using these equations, we calculated the log-likelihood of a particular body mass estimate of a species for any one particular measurement using the normal probability density, with a mean set to the body mass predicted from that measurement's published regression equation based on the measurement value, and the standard deviation calculated directly from the published %SEE. We then calculated the log-likelihood of a particular body mass estimate over all measurements for a particular species as the sum of the log-likelihoods of that estimate over all available measurements. We determined a maximum likelihood estimate of the body mass of a species via numerical optimization (e.g., function optim in R). In essence, this procedure determines the maximum likelihood estimate of body mass using all measurements, with the contribution of each measurement proportional to the previously published strength of its relationship to body mass. This procedure is similar in principle to multivariate regression, in that it simultaneously uses data from multiple measurements, but differs mathematically, because the available published regression equation parameter estimates were all generated using univariate regression.

The exact relationship between body mass and our dental measurements varies among subgroups of mammalian herbivores with different general tooth crown morphologies (e.g., selenodont vs. nonselenodont), and between diets (e.g., browsers vs. grazers). Accordingly, in addition to separate regression equation parameters for each particular measurement, Damuth

(1990) also published separate sets of equation parameters for each of these subgroups (e.g., nonselenodonts, selenodont browsers, and selenodont grazers, etc.). We assigned each species to one of these subgroups (see Supplementary Table 5, Appendix A) and used the corresponding set of regression equation parameters to estimate body mass.

Herbivore species were binned into five biologically informed size categories following Janis (Janis, 2000) as shown in Table 1: < 5 kg (chevrotain-size), 5-25 kg (javelina-size), 25-150 kg (antelope-size), 150-500 kg (horse-size), and > 500 kg (rhino-size). All proboscideans (n= 42 species) were assigned to our largest herbivore size category given that the smallest North American species, *Mammuthus exilis*, was estimated by Larramendi (2016) to have an adult wight of 1350 kg.

We used body mass estimates for Creodonta and Carnivoramorpha (n= 385 species) from Juhn (2023) and estimates for mesonychid and hapalodectid species (n =15) were taken from Gunnell and Gingerich (1996), Solé et al. (2021), and Zhou (1995). Predators were binned into five categories following the ecological "breaks" of Juhn (2023) as shown in Table 1: <1 kg (weasel-size), 1-7 kg (wildcat-size), 7-21 kg (coyote-size), 21-100 kg (wolf-size), and >100 kg (lion-size).

Predator Diet

We assigned each predator species into one of three primary dietary categories (Van Valkenburgh, 1989): hypercarnivore (>70% meat consumed), mesocarnivore (50-70% meat consumed), and hypocarnivore (<50% meat consumed) following Jacquemetton (2024), with the adjustment that we included the "meat and bone consumers" within the hypercarnivore category.

Combinations of these categories were also considered (e.g., hypercarnivores and mesocarnivores, mesocarnivores and hypocarnivores, etc.), but yielded results consistent with those of the dietary categories considered separately.

Species Occurrences and Replicate Setup

We utilized species occurrence data from the Paleobiology Database (PBDB) to determine the duration of each species. We downloaded occurrences for all North American mammals on 9/27/2023 (http://paleobiodb.org/data1.2/occs/list.csv?base_name=Mammalia &continent=NOA&show=full&limit=all). We observed that most collections contained a single occurrence for each taxon but there were cases where multiple occurrences of the same species existed within the same collection, usually due to taxonomic synonymization. We randomly selected one of these "duplicate" occurrences to represent the taxon for that collection. Occurrences for predominantly aquatic taxa of Carnivora (e.g., *Kolponomos*) and exclusively marine clades (e.g., Cetacea, Desmostylia, Pinnipedimorpha, Sirenia, etc.) were also removed prior to analysis.

The exact ages of fossil collections are subject to some degree of uncertainty, and have been assigned maximum and minimum age estimates. To incorporate into our results the variance due to this uncertainty, we performed ten thousand pseudoreplicates analyses. Within each pseudoreplicate, we assigned to all collections a random date drawn from a uniform distribution between its maximum and minimum age estimates, and all constituent occurrences were assigned that randomly drawn collection date.

We then binned species occurrences into intervals of uniform 2 My spanning 66 to 1 Ma. For the subset of analyses for which we subdivided the predators by diet, we constrained the

temporal scope of our to the Oligocene onward (~34 Ma to present). We assumed species durations ranged through all intervals between their first and last occurrences, even if they were not sampled during all intervening intervals. For example, if a taxon occurred in intervals 2 and 5, but not 3 or 4, then it was then also assigned to intervals 3 and 4.

To minimize the influence of uneven sampling among time intervals, we subsampled species occurrences within each interval to a quota set equal to the fewest occurrences observed within any interval during a particular pseudoreplicate analysis (Sanders, 1968; Alroy, 1996; Miller & Foote, 1996; Schloss, 2023). Once assigned to intervals, we removed the occurrences of species that lacked a body mass estimate due to a lack of usable dental measurements and/or being in non-target clades (e.g. rodents).

Correlation Analyses

We assessed potential coevolutionary relationships between predators and herbivores by modifying the methodology of Huntley and Kowalewski (2007) and Key and Schweitzer (2019). Following them, we inferred temporal coupling between guilds using the strength and statistical significance of the correlations of first-differences of taxonomic richness. We first determined median richness of predators within each size and dietary category, and the median richness of herbivores within each size category, over all pseudoreplicate analyses. We calculated first-differences as the difference of species richness between successive intervals, to reduce potential biases related to temporal autocorrelation (McKinney & Oyen, 1989; Huntley & Kowalewski, 2007; Key Jr. & Schweitzer, 2019). We excluded temporal intervals with zero values within median species richness data to avoid biases associated with whether those zero values truly represented unchanged richness between intervals or were rather an artifact of our methodology

(e.g., subsampling) or the preservational nature of fossil record (e.g., uncertainty of a given species first and last occurrence). Finally, we performed Spearman rank correlations for the first-differences of median richness. We also calculated correlations within each guild (e.g., between predator species or between herbivore species) since intraguild competition, predation, and/or facilitation could theoretically contribute to the evolutionary dynamics of either guild (Table 3, Appendix B).

Sensitivity Analyses

Throughout our analyses, we made decisions regarding the analytical design and parameters that have the potential to influence our results, including our choice of the number of pseudoreplicate analyses, taxonomic scope, the body size categories used, our method of subsampling taxonomic occurrences, our assumption of taxa "range through" across their observed stratigraphic range, and temporal interval length. Accordingly, we conducted a series of sensitivity analyses to determine the degree to which our results were dependent upon these decisions. All methods and results for these analyses can be found within Appendix C.

Results:

Total Median Species Richness

Total species richness of both the large herbivore and predator guilds varied substantially over the Cenozoic (Figure 2). Predator and herbivores exhibited notably different patterns of total species richness for the Paleocene (~66 to 56 Ma) and Eocene (~56 to 34 Ma) but then broadly tracked each other through the Oligocene and Neogene (~33.9 Ma to 1 Ma). During the late Paleocene and early Eocene, predators show a marked expansion in richness followed by a

sharp decline in the mid- to late Eocene. By contrast, herbivore richness remains relatively stable throughout this interval. Subsequently, the two guilds move more in tandem with both guilds showing pronounced increases in total species richness throughout the Oligocene and into the early Miocene (~33.9 to 16 Ma). Peak absolute species richness was attained for both guilds during this time, but the timing differed between predators (25 to 23 Ma) and herbivores (21 to 19 Ma). Both guilds then show a gradual net decline in total richness over the remainder of the Neogene (~16 to 1 Ma) in both guilds following their respective peak richness's. Overall, herbivore richness was greater than predator richness for much of Cenozoic, except during the Plio-Pleistocene when overall species richness for both guilds declined to their Neogene minima (Figure 2a & c; note the y-axis scale differences) and specie richness of herbivores and predators became nearly equal.

Category Specific Median Species Richness

Median species richness of each body size and predator diet category also varied substantially through the Cenozoic (Figures 2 and 3). Body size of both herbivores and predators during the Paleocene and early Eocene (~56 to 49 Ma) initially was small, with richness concentrated in the chevrotain-size herbivores and weasel- to wildcat-size predators, respectively (Figure 2). Larger size categories, such as the horse and rhino-sized herbivores and coyote and wolf-sized predators, first appeared during this interval but remained a minor component of their guild assemblages until the Oligocene. Increasing species richness through the Oligocene and early Miocene was largely driven by expansions within the antelope-, horse-, and rhino-size herbivores and the wildcat-, coyote-, wolf-, and lion-size predators across all dietary categories. The declining richness observed through the middle Miocene and Pliocene

affected the size categories of each guild differently. This decline left the large herbivore guild restricted to the antelope, horse, and rhino size categories by the Pliocene whereas predator richness was more evenly distributed across each of the body size categories. However, the distribution of predators by dietary category did shift substantially over the Cenozoic (Figure 3). The declines in predator richness in both the middle and late Miocene were dominated by the loss of large (>21 kg) hypercarnivores and medium to small bodied (<21 kg) mesocarnivores (Figure 3a-f). Hypocarnivorous taxa were still present in the Plio-Pleistocene, but very limited in number after their deterioration over much of the Neogene (Figure 3g-i).

Correlations

Because shifts in species richness of coeval predator and herbivore guilds, respectively, appear unrelated prior to the Oligocene and then track each other more closely for the remainder of the Cenozoic, we explored correlations in species richness over two time periods, the entire Cenozoic (67 Ma- 1Ma) and the Oligocene onward (35 Ma- 1Ma).

All Cenozoic (67 Ma- 1Ma). Species richness within body size categories for coeval herbivores and predators was significantly correlated in some cases (Figure 4; Table 2). For example, positive relationships were strongest between the antelope and rhino-sized large herbivores and predators exceeding 100 kg for the "All Cenozoic" (67-1 Ma) analysis. We observed that the weak correlation between wolf-size predators and horse-size herbivores was marginally significant.

Dietary Subdivisions (35 Ma- 1Ma). Subdividing predators into dietary categories showed that correlations within the hypercarnivore analysis were broadly similar to the "All Cenozoic" analysis while the correlations within the mesocarnivores and hypocarnivore analyses

differed. Specifically, we observed significant and marginally significant positive correlations of moderate strength between lion-size hypercarnivores and herbivores that are antelope-size and larger. Mesocarnivores showed moderately to strongly positive and negative correlations that were not evident within the "All Cenozoic" predator analysis. A single weak marginally significant negative correlation was observed between wildcat-size hypocarnivores and horse-size herbivores.

Correlations could not be calculated for some predator size categories when the guild was subdivided by diet. We observed that predator categories that were either nonexistent (e.g., lion-size hypocarnivores) or exhibited a richness that had a very limited temporal extent (e.g., weasel-size hypercarnivores, weasel- and wolf-size hypocarnivores, etc.) failed to generate a correlation since they lacked two or more intervals where they were coeval with a given herbivore category. Additionally, correlations involving wolf- and lion-size mesocarnivores could not be performed as those predator categories had a standard deviation of zero.

Intraguild Correlations. Intraguild correlations were limited in strength and significance for the predator guild (e.g., lion-size hypercarnivores and wild-cat size mesocarnivores) (Table 4 and Table 5, Appendix B) whereas the herbivore guild showed significant weak to moderate positive correlations between intermediate categories (e.g., chevrotain and javelina, javelina and antelope, antelope, horse, and rhino, etc.) (Table 6, Appendix B). Correlations involving combinations of predator diets (e.g., hypercarnivores plus mesocarnivores) yielded results consistent with those of the dietary categories considered separately.

Discussion:

Van Valkenburgh and Janis (1993) demonstrated that the species richness of the mammalian North American predator guild broadly tracked that of the large herbivore guild but their study had limited data and did not attempt to correct for sampling bias inherent in fossil data. Moreover, these authors felt that the incorporation of functional traits was required to truly determine if this pattern represented a coevolutionary relationship. We sought to reevaluate and build on their work by subdividing herbivore and predator richness into ecologically relevant body size classes (Janis, 2000; Juhn, 2023) to determine if, when, and how these categories were correlated over the Cenozoic. We also further separated predator richness by dietary categories since hypercarnivorous predators are more reliant on relatively large vertebrate prey (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007) than mesocarnivores and hypocarnivores. We identified significant positive correlations between median species richness of North American predator and herbivore guilds in some size and dietary categories that are suggestive of diffuse coevolutionary relationships.

Significant, or nearly significant, positive correlations between predator and herbivore guilds largely matched our initial expectations (Figure 4). For example, we expected that the richness of large (>21 kg) hypercarnivores would track that of the large (antelope-size and larger) prey. Within the "All Cenozoic" analysis, in which predator diet is ignored, we identified positive correlations between both wolf- and lion-size carnivores and the herbivores categories of equal or larger size (e.g., antelope, horse, and rhino). Focusing on hypercarnivorous predators, most of which were over 21 kg, strengthened the correlation between the antelope- and horse-size herbivores. These correlations are consistent with patterns of extant predator species richness, which are more strongly related to the richness of their prey than aspects of climate and

productivity; a relationship that strengthens with increasing predator size (Sandom et al., 2013). Linkage between the species richness of the largest, generally hypercarnivorous, predators and herbivores of similar or larger size is understandable as metabolic constraints require extant predators larger than 21 kg to take prey of similar or larger sizes to sustain themselves (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007; Mukherjee & Heithaus, 2013). Similar metabolic constraints likely existed throughout the Cenozoic given that the nutritional value of the material components (e.g., meat, bone, fat, etc.) of large herbivores has changed little over the Cenozoic (Van Valkenburgh, 1995).

We initially expected no strong correlations between the largest (i.e., rhino-size) herbivores and predators of any of the size classes due to reduced predation risk conveyed by very large body mass. However, we found relatively moderate positive correlations between herbivores in the rhino-size class and lion-size predators when predators diets were analyzed together (i.e., the All Cenozoic analysis). Estimates of the threshold body mass of potential prey species, above which predation risk diminishes, has varied in the literature from 150kg (Sinclair, Mduma & Brashares, 2003) to 800kg and above (Owen-Smith, 1988; Owen-Smith & Mills, 2008). However, attaining absolute predation immunity is unlikely as larger predators or those employing group hunting strategies can and will take adult prey of this size given the opportunity. For example, extant African lions (~162 kg body mass (Smith et al., 2003)) have been reported to, on rare occasions, predate herbivores in this class, including adult elephants (Joubert, 2006), hippopotami (Bourliere, 1963; Pienaar, 1969), and white rhinoceroses (Pienaar, 1969; Radloff & Du Toit, 2004). Moreover, prey size estimates for some very large Pleistocene mammalian predators, such as the American Lion (*Panthera leo atrox*) and the dire wolf (*Aenocyon dirus*), found that maximum prey size extended into the lower margins of the

megaherbivore size range (Van Valkenburgh et al., 2016), suggesting that the size threshold for reduced predation risk may have been higher in the past.

In any case, even if adults in the rhino-size category exhibited reduced predation risk, smaller juveniles probably remained vulnerable (Van Valkenburgh et al., 2016), as is the case today for hippos, rhinos, and elephants (see Bourliere, 1963; Pienaar, 1969; Joubert, 2006; Loveridge et al., 2006; Power & Compion, 2009). In both extant and Pleistocene large mammal assemblages the taking of juvenile prey tends to increase proportionally with adult prey size (Palmqvist, Martínez-Navarro & Arribas, 1996; Gervasi, Nilsen & Linnell, 2015). Predation of juvenile African elephants, for example, occurs at a much higher frequency than adults (Joubert, 2006; Loveridge et al., 2006; Power & Compion, 2009; Juhn, 2023). Large predators have been documented to cause substantial decreases (33-40%) in the annual juvenile populations of their large herbivore prey species (Carbyn, Oosenbrug & Anions., 1993; Barber-Meyer, Mech & White, 2008). Significant predation of juveniles by predators has likely occurred throughout the Cenozoic, and thus it is not surprising to find a positive correlation between the species richness of large (> 21kg) predators and megaherbivores despite the difficulty of killing adults.

Predators below 21kg generally exhibited limited correlation strength and significance when considering either the entire predator guild or dietary subgroups. Specifically, we observed that species richness of weasel-, wildcat-, and coyote-size predators generally lacked significant positive correlations with herbivores of any size class, except for one group, the wild-cat size mesocarnivores, which were positively associated with three herbivore size categories (5-500kg) (Figure 4; Table 2). Given that extant carnivores below 21kg usually take prey smaller than themselves (e.g., rodents, lagomorphs, lizards, etc.), and may, incorporate

nonvertebrate foods in their diets (e.g., insects, fruits, etc.) (Carbone et al., 1999), we expected to find little or no correlation between the species richness of predators<21kg and herbivores larger than 15-20kg. Large herbivores (e.g., deer) are known to be consumed by coyote-size predators (e.g., bobcats, coyotes, etc.), but smaller prey (e.g., rodents, lagomorphs, etc.) are typically the primary source of meat (Newbury & Hodges, 2018). Overall, predators of these smaller size categories likely consumed similar diets of smaller-bodied prey over the Cenozoic and rarely hunted larger herbivores while foraging.

The significant, moderate to strong correlations between the wildcat-sized mesocarnivores and antelope- and horse-size herbivores are both interesting and perplexing. The decreased amount of meat (relative to hypercarnivores) in mesocarnivore diets and the fact that the antelope and horse size categories were one order of magnitude (or more) larger suggests these correlations are being driven by factors other than a strict predator-prey relationship. Even though wild-cat-size mesocarnivores may not be actively killing larger prey, outside of rare occurrences (e.g., wolverines, a wildcat- to coyote-size mesocarnivore, prey on juvenile to adult caribou and elk (Gustine et al., 2006; Inman & Packila, 2015; Mattisson et al., 2016; Magoun et al., 2018)), they could be opportunistically scavenging carcasses of large prey species. For example, extant wolverines have been observed to facultatively scavenge the carcasses of much larger herbivores (e.g., caribou, elk, and moose) during winter months (Lofroth et al., 2007; Van Dijk et al., 2008; Inman & Packila, 2015). If antelope- to horse-size herbivores were sufficiently abundant in the past they could have been an important source of carrion for wild-cat-size mesocarnivores, especially if larger, “top” predators were producing carcasses year round (Pereira, Owen-Smith & Moleón, 2014). Moreover, such a relationship could explain the positive linkage between lion-size predators and the wild-cat-size mesocarnivores we observed

within our intraguild correlations. An increase in lion-size hypercarnivore richness could result in a rise in the availability of carcasses on the landscape (Prugh & Sivy, 2020).

Significant intraguild correlations among the size classes of herbivores were limited in number but suggest that each responded to similar environmental factors. Shifts in the distribution of large herbivore guild body mass coincide with large scale climatic and vegetative transitions, namely the opening of habitat and spread of grasslands (Strömberg, 2004, 2011). We found that the chevrotain- and javelina-size large herbivores began to decline at a time coincident with the earliest reported development and expansion of open habitats (~42-40 Ma, Figure 2) (Webb, 1977; Dillhoff et al., 2009; Townsend et al., 2010). Likewise, the proliferation and peak richness of antelope and horse-size large herbivores was largely coincidental with the spread of open habitats and grasslands in the Great Plains regions (~25 to 20 Ma, Figure 2) (Strömberg, 2004, 2005, 2011), an interval that has been suggested to have elevated productivity (Janis, Damuth & Theodor, 2000). This makes sense; species richness and body size of large mammalian herbivores have been strongly associated with climate and vegetation in both extant (Sandom et al., 2013) and fossil (Huang et al., 2022) assemblages.

Unlike the large herbivores, the changing body mass distribution within the predator guild seem to be relatively independent of large-scale transitions in habitat (Juhn, 2023), and instead seems to have tracked roughly the absolute and category specific species richness (e.g., antelope-, horse-, and rhino-size) of the large herbivore guild throughout the late Paleogene and most of the Neogene. Specifically, the early Oligocene expansion of the largely hypercarnivorous coyote- and wolf-size predators and the appearance of the lion-size predators was mostly coincident with, or slightly lagged behind, the gradual increases in the species richness of the antelope and horse-size large herbivores during the Oligocene and early Miocene

(Figure 2). Extant large predators, and particularly the hypercarnivores, typically require their preferred size prey to be plentiful on the landscape (Carbone, Teacher & Rowcliffe, 2007). The Oligocene to early Miocene expansions in large herbivore richness likely facilitated increases in coyote- to lion-size predator richness due to energetically profitable prey becoming more common. However, exploitation of larger prey, especially those with cranial weaponry such as horns or antlers, comes with a greater risk of injury or death (Edmunds, 1974; Creel & Creel, 2002; Berger-Tal et al., 2009; Mukherjee & Heithaus, 2013). Members of the predator guild likely would have undergone broad selection for larger body size to improve hunting success (MacNulty et al., 2009) and to mitigate the risk of injury or death while tackling larger prey (Mukherjee & Heithaus, 2013).

Diffuse coevolution is a likely explanation for the linkage between the species richness of the largest predators and herbivores that are antelope-size and larger. The strength and symmetry of selection between the two guilds and how that selection varies spatiotemporally remains poorly understood and requires further study. Nevertheless, selection was likely asymmetrical, with the herbivores imparting a greater selective pressure for larger predator body size rather than vice versa, because changes in the distribution of species richness within these predator size categories track the richness of relevantly sized prey whereas changes in herbivore species richness coincided with environmental transitions. Selection could also be suggested to be spatiotemporally heterogenous because we only observe the predator guild to broadly tracks the herbivore guild during the Oligocene and Neogene. The absence of tracking of the herbivore guild by predator guild prior to the Oligocene and early Miocene suggests that selection between the two guilds was limited or nonexistent for much of the Paleogene.

Even though our analysis has shown that tracking of the herbivore guild by the predators guild was restricted to the Oligocene and Neogene our understanding of predator-prey dynamics within the Paleocene and Eocene remains uncertain. Most of the predator guild during the Paleocene and Eocene were small-bodied (<21 kg; Figure 2A) and would have likely predated on smaller bodied prey (e.g., multituberculates, rodents, etc.) and/or incorporated plants and other foodstuffs into their diet (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). Wolf- to lion-size predators existed during this same interval, but their species richness remained relatively stable despite fluctuations in the species richness of antelope-to rhino-size herbivores. This was perplexing as the wolf- and lion-size categories during the Paleocene and Eocene are comprised of mesonychids and creodotids, which have been inferred to trend towards carnivory, specifically hypercarnivory, based on their dentition (Van Valkenburgh, 1988; Archibald, 1998). Based solely on the data included in our study, it is difficult to discern why these wolf- to lion-size predators fail to track the species richness of relevantly sized prey during this interval, but it may lie in a misunderstanding of their ecology. For example, the determination of mesonychids and creodonts as strictly hypercarnivorous could be inaccurate since these inferences were based on comparisons with extant taxa that are not directly analogous (e.g., canids, felids, suids, etc.). Alternatively, predator-prey relationships between the predator and large herbivore guild may have been present prior to the Oligocene but went undetected within our analyses because morphological traits (e.g., locomotion, diet, etc.) other than body mass were mediating those predator-prey interactions.

Predator species richness has been broadly shown to exhibit a positive relationship with herbivore richness in both extant communities (Sandom et al., 2013) and within the fossil record (Van Valkenburgh & Janis, 1993), but this relationship appears to breakdown over the course of

the latter half of the Neogene. Like Van Valkenburgh and Janis (1993), we found that predator species richness did not decline to the same degree as that of the large herbivore guild over the Neogene. Van Valkenburgh and Janis (1993) suggested that an increase in the proportion of omnivores and generalist predators within the late Neogene predator guild might explain this disjunction. However, we found that the Plio-Pleistocene were largely comprised of large bodied hypercarnivores (>21 kg) (~40% of the guild) and smaller bodied mesocarnivores (<21 kg) (~40% of guild). If this is the case, then how were so many large bodied species of hypercarnivores able to coexist? The answers to this question are likely complex, however, Carbone et al. (2007) indicates that the abundance of large prey is critical in supporting large predators. Prey abundance, measured by population size or biomass, has a positive relationship with predator population density (Carbone & Gittleman, 2002; Cohen, Jonsson & Carpenter, 2003; Hayward, O'Brien & Kerley, 2007) and predator body mass (Cohen, Jonsson & Carpenter, 2003; Carbone, Pettorelli & Stephens, 2011) in both marine and terrestrial systems. For extant large mammalian carnivores such as lions and spotted hyenas, their ability to coexist likely is more determined by total herbivore abundance than the presence of multiple herbivore species (Périquet, Fritz & Revilla, 2015). In general, coexisting lions and hyenas do not specialize on different herbivore species; they both focus on whatever prey species are easiest to acquire (e.g., wildebeest, zebra) (Hayward, 2006; Owen-Smith & Mills, 2008; Hayward et al., 2011; Barnardo et al., 2020). If this is true for most or all large carnivores, then a decline in herbivore species richness would not affect them negatively if the remaining species of similar size expanded their abundance to replace them. Declining species richness of the large herbivores could have been compensated by increases of the relative abundance of remaining large-bodied prey species over the course of the Miocene and later and facilitated the coexistence of multiple large bodied

hypercarnivores. A small number of large-bodied prey species (e.g., *Bison, Equus,* etc.) at high relative abundance on landscape then their biomass might offer sufficient biomass to support the coexistence of multiple species of large hypercarnivores (e.g., *Aenocyon dirus*, *Smilodon*, *Panthera leo atrox*, etc.).

Conclusion

In conclusion, total and body-size-specific species richness of mammalian predators and prey has changed substantially over the North American Cenozoic. Total species richness of the predator guild roughly tracked that of the large herbivore guild over a large portion of the North American Cenozoic. Body-size-specific richness trends within the herbivore guild appear to broadly coincide with continental-scale climatic and vegetative events (e.g., the opening of habitats, spread of grasslands, etc.) whereas body-size- and diet-specific trends of coyote- to lion-size predators appear to broadly follow changes in species richness of the herbivore guild during the Oligocene and onward. Despite the apparent tracking between total and size specific species richness, significant positive correlations between the two guilds are limited to only a few size categories. Correlations between lion-size predators and antelope- and rhino-size herbivores suggest a coupled predator-prey relationship wherein the predators of this size category must take prey of near equal or larger size (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). We also found positive correlations between the richness of wild-cat-size mesocarnivores and that of javelina- to horse-size herbivores, but these are unlikely to represent a strict predator-prey relationship. Wild-cat-size mesocarnivores have been observed to scavenge the carcasses larger herbivores, a behavior that could be prevalent in the presence of apex predators that produce carcasses via their own predation (Pereira, Owen-Smith & Moleón, 2014). Overall, these significant positive correlations are suggestive of coevolutionary

relationships, but the exact nature of these linkages and their underlying drivers remains unclear. The analysis of how the mammalian predator guild responds to the large herbivore guild would be bolstered by incorporating measures of relative herbivore abundance (e.g., relative occupancy) and by substantiating existing ecological interpretations of Paleocene and Eocene taxa through the inclusion of other morphological traits related to diet and locomotion or by the application of isotopic analyses (e.g., N^{15} or Zn^{66}).

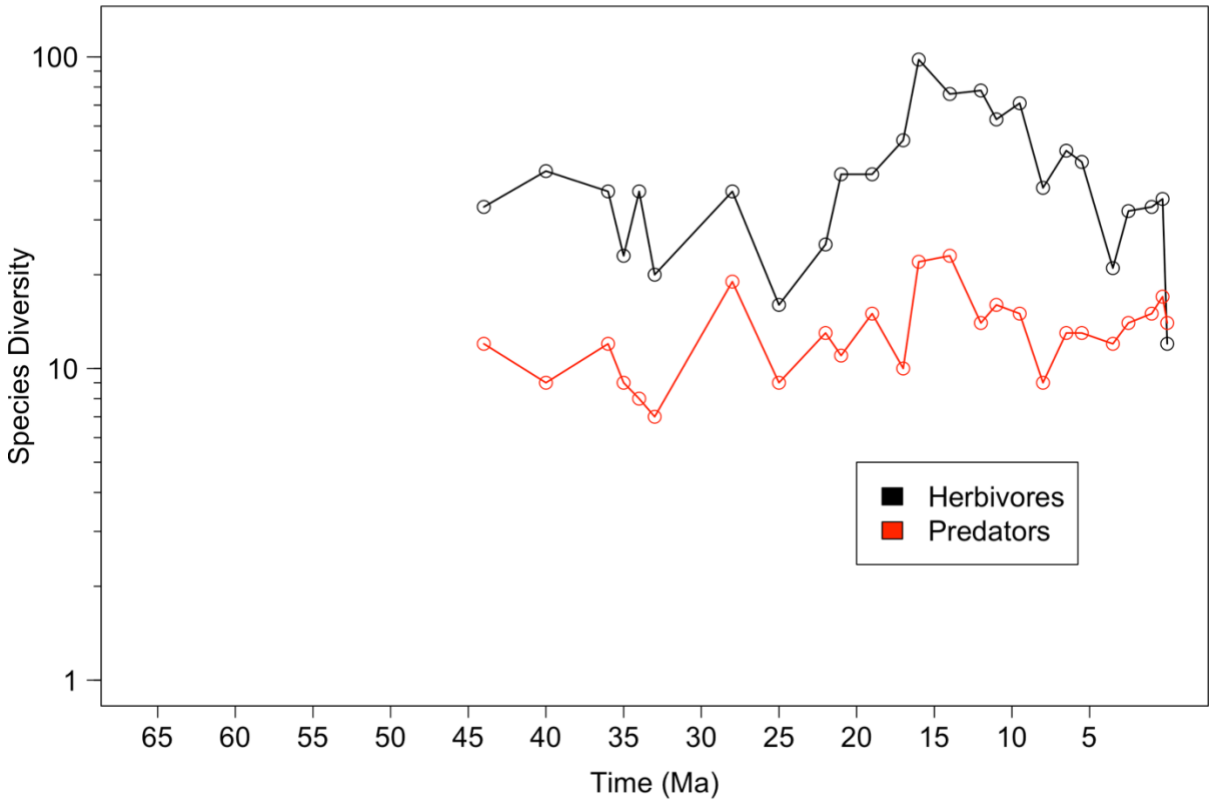

Figure 1. Total species richness of large mammalian herbivores and predators for the Late Uintan to Holocene (~44 Ma to present). Data was taken from Table 28.1 of Van Valkenburgh and Janis (1993). Points represent the midpoint of each NALMA or Sub-NALMA.

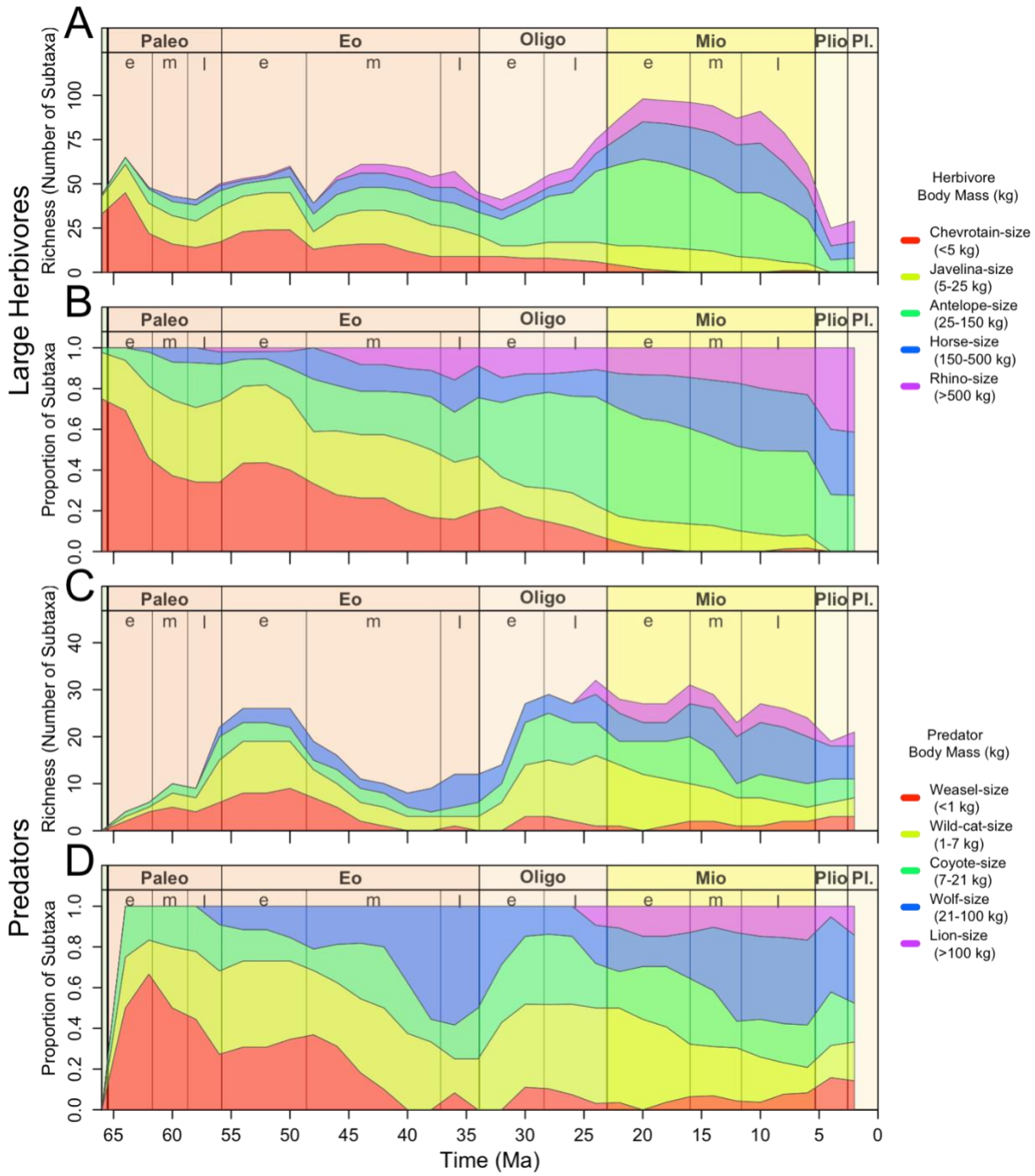
A
B
C
D
Large Herbivores
Predators
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Proportion of Subtaxa
Herbivore Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)
Predator Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)
Time (Ma)

Figure 2. Total (A and C) and proportional (B and D) median species richness of both the large mammalian herbivore and predator guilds through the Cenozoic. Median species richness values are compiled across all 10,000 subsampled pseudoreplicates and are plotted at the midpoints of each 2Ma long interval. Median species richness values are representative and not exact due to this subsampling. Each guild is subset into distinct size categories following Janis (2000) for the large herbivores and by the author for the predator guild (Table 1).

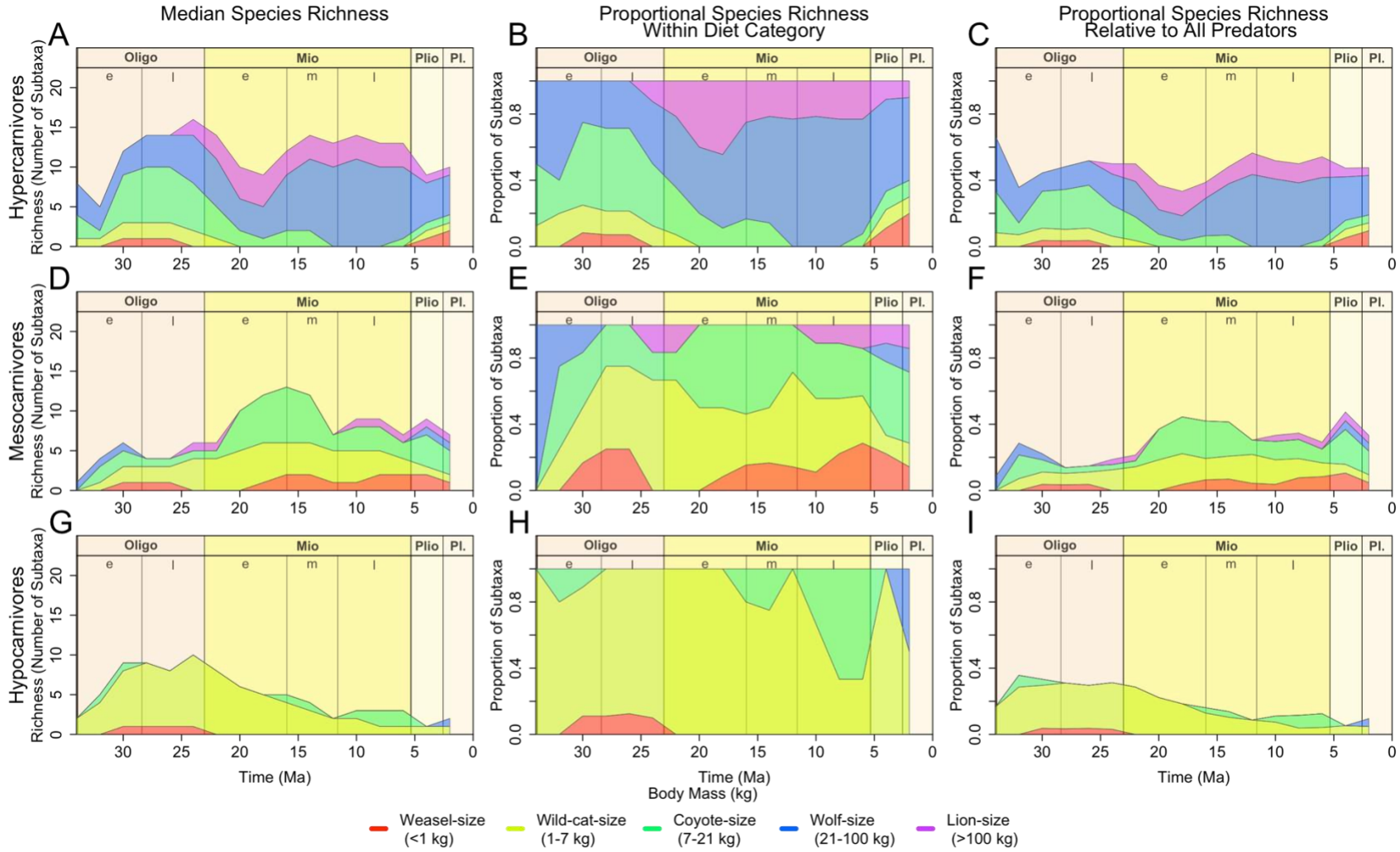
Median Species Richness
Proportional Species Richness Within Diet Category
Proportional Species Richness Relative to All Predators
A
B
C
D
E
F
G
H
I
Hypercarnivores
Mesocarnivores
Hypocarnivores
Richness (Number of Subtaxa)
Proportion of Subtaxa
Oligo
Mio
Plio
Pl.
e
l
m
Time (Ma)
Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)

Figure 3. Total (A, D, and G) and proportional (B, C, E, F, H, and I) median species richness of the hypercarnivores (A-C), mesocarnivores (D-F), and hypocarnivores (G-I) of the predator guild through the Oligocene and Neogene (34 Ma to present). Proportional richness is calculated for both the within dietary category species richness (B, E, and H) and against the total predator species richness (C, F, and I). Median species richness values are compiled across all 10,000 subsampled pseudoreplicates and are plotted at the midpoints of each 2 Ma long interval. Median species richness values are representative and not exact due to this subsampling. Predator body size categories are the same as Figure 2 and Table 1.

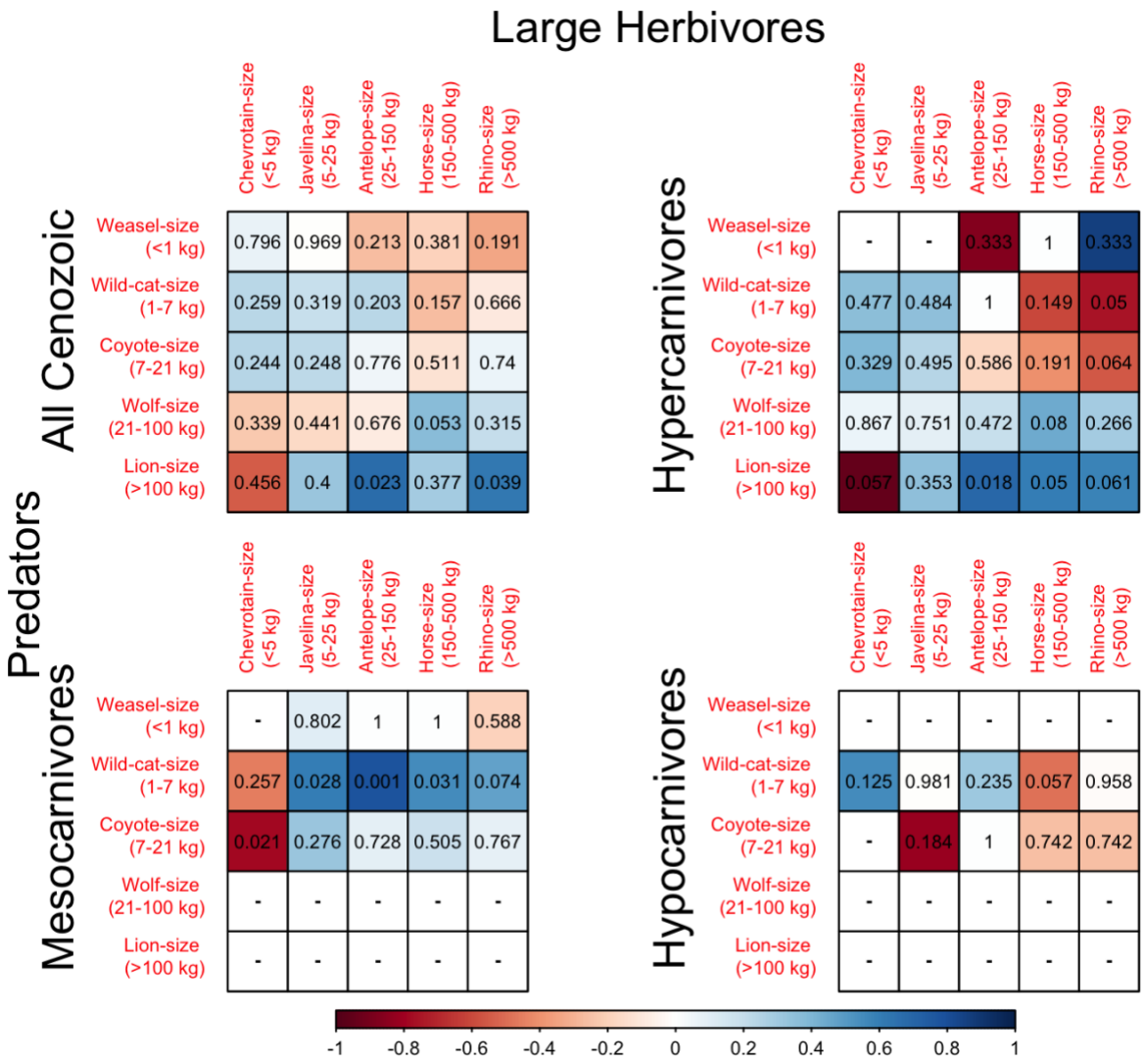

Figure 4. Spearman correlation matrices for the first-differenced median species richness within each size category of the large herbivore and predator guilds. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 0 Ma) while the analyses utilizing the dietary subdivisions of the predator guild (e.g., hypercarnivore, mesocarnivores, and hypocarnivore) cover the Oligocene to present (~35 Ma to 0 Ma). Size categories are the same as Table 1. Color scale represents how strongly negative (red) or positive (blue) the correlations were estimated to be. Numbers within the correlogram denote the p-value for a given correlation whereas dashes denote correlations that could not be performed.

Table 1. Size Categories for the large herbivore and predator guilds. We labeled the "rabbit" and "dog" categories of Janis (2000) with the names of species within the large herbivore guild to prevent confusion when making comparisons between the predator and prey guilds.

		Category Name				
Guild	Size Range	Prior Studies	This Study	#Species	#Genera	Author(s)
Predator						
	<1 kg	Weasel-sized	Weasel-sized	64	25	(Juhn, 2023)
	1-7 kg	Wildcat-sized	Wildcat-sized	119	48	(Juhn, 2023)
	7-21 kg	Coyote-sized	Coyote-sized	93	44	(Juhn, 2023)
	21-100 kg	Wolf-sized	Wolf-sized	89	45	(Juhn, 2023)
	>100 kg	Lion-sized	Lion-sized	35	20	(Juhn, 2023)
			Total	400	182	
Large Herbivore						
	<5 kg	Rabbit-sized	Chevrotain-sized	220	77	(Janis, 2000)
	5-25 kg	Dog-sized	Javelina-sized	220	96	(Janis, 2000)
	25-150 kg	Antelope-sized	Antelope-sized	338	139	(Janis, 2000)
	150-500 kg	Horse-sized	Horse-sized	197	66	(Janis, 2000)
	>500 kg	Rhino-sized	Rhino-sized	154	63	(Janis, 2000)
			Total	1129	441	

Table 2. Spearman correlation matrix for the detrended (via first-differences) median species richness within each size category for the large mammalian herbivore and predator guilds. First-difference corrections were calculated by performing a first-difference correction on the median species richness of 10,000 subsampled pseudoreplicates. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 1 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (All Cenozoic)	<1 kg	0.07	-0.009	-0.27	-0.197	-0.333
	1 to 7gk	0.24	0.192	0.235	-0.265	-0.091
	7 to 21 kg	0.247	0.222	0.053	-0.125	0.07
	21 to 100 kg	-0.225	-0.161	-0.084	0.377	0.21
	>100 kg	-0.544	0.321	**0.674***	0.296	**0.627***
Predators 34 Ma-1Ma (Hypercarnivores)	<1 kg	--	--	-0.866	0	0.866
	1 to 7gk	0.365	0.359	0	-0.607	**-0.755***
	7 to 21 kg	0.398	0.245	-0.175	-0.406	-0.55
	21 to 100 kg	0.065	0.094	0.194	0.45	0.296
	>100 kg	-0.943	0.352	**0.695***	0.601	0.581
Predators 34 Ma-1Ma (Mesocarnivores)	<1 kg	--	0.106	0	0	-0.196
	1to 7 kg	-0.455	**0.606***	**0.782*****	**0.556***	0.475
	7 to 21 kg	**-0.786***	0.327	0.098	0.187	0.084
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Predators 34 Ma-1Ma (Hypocarnivores)	<1 kg	--	--	--	--	--
	1 to 7gk	0.551	-0.007	0.315	-0.484	-0.014
	7 to 21 kg	--	-0.816	0	-0.258	-0.258
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

CHAPTER II: EVOLUTIONARY RESPONSE OF PREDATORS TO THEIR LARGE HERBIVORE PREY WITHIN THE NORTH AMERICAN CENOZOIC

Abstract

Large mammalian herbivore and predator species richness (both overall and size- and diet-specific) are correlated over the North American Cenozoic (66Ma to present). However, it remains unclear whether the correlation is a result of the predator guild responding to changes in herbivore guild richness and/or structure, a byproduct of other drivers, or stochasticity. To explore this, we tested for statistically significant changes within the functional (as measured by body size) and taxonomic distribution of both the predator (i.e. Carnivoramorpha, Creodonta, Mesonychidae) and large herbivore (i.e. Artiodactyla, Perissodactyla, "Condylarthra", Dinocerata, Taeniodonta, Tillodontia, and Pantodonta) guilds. We evaluated these significant shifts in functional and taxonomic distribution to determine if they were consistent with an evolutionary response of the predator guild to the herbivore guild (e.g., coincidental with, or slightly lagged behind shifts in guild structure). Each guild underwent multiple shifts in their respective functional and taxonomic distributions over the course of the Cenozoic, and three of these shifts (circa 46Ma, 32 Ma, and 18Ma) coincided between the guilds. We argue that these concomitant shifts were representative of evolutionary responses by the predator guild to the herbivore guild based on their timing and the character of the underlying changes in guild structure. In addition, we explored the relationship between climatic events and shifts in the herbivore guild. We found that shifts in the functional and taxonomic structure of the herbivore guild were largely coincident with, or lagged behind, major climatic events (e.g., Early Eocene Climatic Optimum, Eocene-Oligocene Boundary) and vegetation transitions (e.g., spread of grass dominated habitats, C_3/C_4 transition) throughout the Cenozoic. We also argue that these shifts were representative of evolutionary responses by the herbivore guild to environmental factors (e.g., temperature, precipitation, vegetation structure, etc.).

Introduction

The evolutionary response of predators to their prey has been used to explain evolutionary trends across a wide array of fauna and flora (Dawkins et al., 1979; Vermeij, 1987; Davies & Brooke, 1988; West, Cohen & Baron, 1991; Kelley, 1992). At broad scales, large (>7kg) mammalian predator species richness is correlated positively with that of their presumed large (>10kg) herbivore prey in both extant (Sandom et al., 2013) and fossil (Van Valkenburgh & Janis, 1993) assemblages. Morphological traits (e.g., limb morphology) of large mammalian predators also appear to exhibit evidence of evolutionary responses of predators to their presumed large herbivore prey. For example, Bakker (1983) suggested the evolution of longer limbs in carnivorans over the Cenozoic was an "arms-race"-style coevolutionary response to increased limb length (and therefore increased running speed) observed within their presumed ungulate prey. This coevolutionary 'arms-race" hypothesis was challenged by Janis & Wilhelm (1993) who showed that limb evolution in herbivores occurred much earlier than it did within the carnivorans. Nevertheless, the inclusion of trait-based ecomorphological analyses within the exploration of diversification patterns (e.g., species richness) should help determine the underlying evolutionary and ecological dynamics that drive changes over time (Van Valkenburgh & Janis, 1993).

In Chapter 1, we observed that the richness of the predator guild, specifically the wolf- (21-100kg) and lion-size (>100kg) hypercarnivorous predators, roughly tracked that of their presumed prey within the herbivore guild, the antelope- (25-150kg) and horse-size (150-500kg) herbivores, during the Oligocene and Neogene (Figures 2 and 4). These parallel shifts in predator and prey richness appear to support the hypothesis that the predator guild responded to changes in the distribution of herbivore richness among different body mass categories.

Nevertheless, it remains unclear if these changes in predator and herbivore guild structure were truly coincident as correlations between predators and their presumed prey were documented over large timescales (e.g., most of the Cenozoic [67-1Ma] or the Oligocene and Neogene [35-1Ma]) in both Van Valkenburgh and Janis (1993) and our prior chapter. Determining the timing of statistically significant changes of the richness within body mass categories within both guilds would reveal if changes in the underlying distribution of body mass in herbivores led to changes within the structure of the predator guild. Juhn (2023) identified statistically significant changes in the distribution of functional traits (relative blade length of lower carnassial and body mass) and taxonomic composition of the predator guild over the Cenozoic, but did not consider herbivore body mass distributions, nor their influence on large predator richness.

In this study, we expand on the previous chapter and Juhn (2023) by characterizing the continental assemblage of both the predator and large herbivore guilds using body mass and taxonomic identity to determine which functional and taxonomic groups drove significant changes within each guild. We then empirically test 1) the degree to which changes in the functional and taxonomic composition of the herbivore guild was coincidental with major environmental transitions (e.g., climatic warming or cooling, vegetative transitions) and 2) the degree to which changes in the composition of the predator guild were coincidental with changes within the herbivore guild.

We consider a shift in the functional structure of the predator guild to be an evolutionary response to their prey if the shift meets two criteria. First, a given shift in the distribution of predator body mass must be coeval with or lag slightly behind (≤2Myr) a shift of the herbivores. Second, the observed shift must be the result of changes within one or more size categories that include the likely predators of herbivores in the size categories that expanded or declined. For

example, extant predators over 21kg tend to take prey of near equal size (>45% predator mass) or larger to meet metabolic requirements, whereas predators less than 21kg tend to kill prey that are smaller than themselves (e.g., rodents, lagomorphs) and/or consume a greater degree of non-vertebrate foods (e.g., plants, invertebrates) (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). We would consider a shift characterized by a greater proportion of wolf- and/or lion-size predators to be an evolutionary response, if it were simultaneous with or followed soon after a concomitant increase in the richness of their likely prey, namely antelope-size and horse-size herbivores. However, we would not expect a shift of similar magnitude and timing among smaller carnivores (e.g., weasel- [<1kg] and/or wild-cat-size [1-7kg]) to be representative of an evolutionary response to this same increase in large herbivores, as the size mismatch precludes a direct predator-prey relationship.

The North American fossil record provides a chronicle of the response of the herbivore guild to changes in climate and vegetation that occurred over the Cenozoic (66Ma to present) (Zachos et al., 2001; Strömberg, 2011). Broadly, environments throughout North America shift from a wet, "hothouse" climate with closed, forested habitats to a much cooler, arid climate, and open, grass-dominated ecosystems (e.g., prairies and savannas) (Zachos et al., 2001; Strömberg, 2011). Coupling these environmental trends with observations of how extant herbivore richness and functional anatomy are influenced by their environment allows us to make predictions concerning the timing of significant shifts. We expect shifts in the distribution of body mass within the herbivore guild to coincide with or slightly lag behind major climatic (e.g., Paleocene-Eocene Thermal Maximum [PETM, ~56Ma], Eocene-Oligocene Transition [~34Ma], Mid Miocene Climatic Optimum [MMCO, 17-15Ma], etc.) and vegetative transition events (e.g., opening of habitats [starting ~42Ma], spread of grasslands [starting ~26Ma (Strömberg, 2011)],

the C3/C4 grassland transition [~8-6Ma]). Notably, the spread of grasslands and the MMCO were roughly coincident with early Miocene regime shifts (22.2, 18.5 and 16Ma) among large carnivorans ((Juhn, 2023). Here we use a likelihood approach (Handley, Sheets & Mitchell, 2009) to explore in greater detail possible parallels in species richness between predators and prey, and their associations with major climatic events over the Cenozoic.

In sum, our goals are to 1) empirically test for significant changes in guild structure (species richness of body size and clades) in both predators and herbivore (ungulate or ungulate-like) prey over the Cenozoic, 2) examine the possible role of major climatic events in determining major shifts in the body mass and taxonomic distribution of herbivores over the Cenozoic, and 3) determine if the identified shifts in body mass distribution in the predator guild are coincident and plausibly related to those of the herbivore guild.

Methods and Materials

Our study involved these steps: 1) estimation of predator and prey body mass from dental measurements, 2) determination of stratigraphic ranges of species, and assignment to discrete time intervals, 3) identification of the timing and character of statistically significant changes in function and taxonomic structure of the herbivore and predator guilds, 4) comparison of the timing of significant shifts within the herbivore guild to major climatic and vegetative events over the Cenozoic, and 5) comparison of the timing of shifts within the predator guild and the herbivore guild, respectively. All data processing, pseudoreplicate generation, and analyses were performed in R, version 4.3.1 (R Core Team, 2024) All data sets are available in Appendix A.

Taxonomic Sampling and Body Mass Estimation and Binning. Our data sampling and body mass categorization methods were the same as those detailed within the previous chapter. In summary, we compiled an extensive dataset of linear dental measurements of

ungulate and ungulate-like mammals (e.g., Artiodactyla, Perissodactyla, “Condylarthra”, Dinocerata, Taeniodonta, Tillodontia, and Pantodonta) from the literature and our own measurements of museum specimens. We sued these measurements to estimate body mass using a maximum likelihood approach based on the subgroup regressions of Damuth (1990). Herbivores were partitioned into five biologically informed size classes following Janis (2000) (Chap. 1, Table 1). Proboscideans were also included within the herbivore guild and were assigned to the largest, rhino-size category because the smallest known North American species (*Mammuthus exilis*) was estimated to have a body mass (1350kg) above the 500kg threshold (Larramendi, 2016). We drew predator body masses from multiple sources: Carnivoramorpha and Creodonta were taken from Juhn (2023) whereas the body masses for Mesonychidae were taken from Zhou (1995), Gunnell and Gingerich (1996), Solè et al., (2021). As we did for the herbivores, we partitioned predators into five biologically informed size classes following Juhn (2023) (Table 1).

We recognize that our body mass estimates are subject to error. Specifically, the regressions equations used by our study and others (e.g., Zhou (1995), Gunnell and Gingerich (1996), Solè et al., (2021)) are derived using data from extant taxa that may or may not be a good analog for fossil taxa (e.g., different allometric relationships), even for species within the same family (Gingerich, Smith & Rosenberg, 1982; Conroy, 1987; Damuth & MacFadden, 1990). Body mass regressions rely on measurements of dental and skeletal elements whose allometric relationships vary not only across different taxonomic groups of mammals, but also over time (Conroy, 1987; Damuth, 1990). For example, carnivoran regressions are, in part, informed by extant canids within Caninae that are more gracile and cursorial than many of their extinct counterparts within Hesperocyoninae and Borophaginae (Van Valkenburgh, Sacco & Wang,

2003; Figueirido et al., 2015). A regression equation based on extant species may therefore under- or overestimate body mass when applied to extinct species; a source of error that might be particularly acute for taxa that completely lack extant representatives (e.g., creodonts, Mesonychidae, "Condylarthra") (Conroy, 1987; Damuth, 1990). Nevertheless, these regressions represent our best, and in many cases only, opportunity to estimate the body mass of extinct fauna.

Species Occurrences and Replicate Setup. To account for uncertainty in the dating of fossil collections, we followed the same protocols as in Chapter 1, with the exception that we used more constrained minimum and maximum age estimates for many of the collections within the Paleobiology Database (PBDB) by matching collections to the New and Old-World (NOW) Database of Fossil Mammals (The NOW Community, 2023) (Figure 5). Specifically, we downloaded occurrences for all North American mammals from the PBDB on 11/6/2023. We manually matched the PBDB collections to localities of similar names and/or stratigraphy within NOW database (downloaded on 10/2/2023). If a match was possible, we replaced the maximum and minimum age estimates for the PBDB collection with those of the corresponding NOW locality (n=6031). However, some PBDB collections (n=3300) could not be easily matched to a corresponding NOW database locality, and in these cases, we retained the PBDB minimum and maximum age estimates of those collections. NOW database localities assigned to the Puercan-2 and Puercan-3 were found to have an incorrect lower or upper bound of 64.1Ma. We reassigned the lower and upper bounds for these localities, so they were equivalent to the accepted Puercan2/3 category (65.84Ma and 64.81Ma, respectively) (Sprain et al., 2015; Ogg, Ogg & Gradstein, 2016).

We binned collections into uniform 2Myr intervals that spanned 67 to 1Ma, and assumed that species durations ranged through all intervals between those of their first and last occurrence, and generated subsampled pseudoreplicate analyses using the same methodology as the prior chapter.

Identifying Significant Shifts. We investigated whether significant changes, or shifts, in the functional structure, or separately, the taxonomic structure of the predator and herbivore guilds were coeval using the likelihood approach of Handley, Sheets, and Mitchell (2009) following the methodology of Juhn (2023). We first calculated the median (over 10,000 pseudoreplicates) richness of herbivore and predator richness within each size category within 2Myr intervals. Following Handley, Sheets, and Mitchell (2009), we assumed that the number of species within body mass categories were drawn randomly from a multinomial distribution. Like Juhn (2023), we refer to a series of consecutive intervals with a common distribution as a single regime, and the boundaries between distinct regimes as regime shifts. For example, a model with a single hypothetical regime shift at 53Ma creates two regimes: one containing all intervals between 67 to 53Ma and another containing all intervals younger than 53Ma. Given a specified number of shifts, we identified their optimal timing using the sample-size corrected Akaike Information Criterion (AIC_c). To determine the optimal number of regime shifts, we used a stepwise AIC approach in which we sequentially added more shifts until additional shifts offered no improvement in AIC_c value.

Taxonomic turnover theoretically could cause shifts in the distribution of functional traits simply due to the appearance (i.e., origination or immigration) or loss (i.e., extinction or emigration) of particular taxonomic groups rather than some evolutionary response (Juhn, 2023). For example, the loss of Nimravidae at the onset of the "cat gap" and the appearance of Felidae

at its end (Martin, 1998) resulted in significant shifts in the distribution of a key indicator of carnivore diet, carnassial (lower first molar) relative blade length (rbl), within the predator guild (Juhn, 2023). We therefore also tested for shifts in taxonomic structure of each guild to explore the potentially confounding role of taxonomic turnover.

Like Juhn (2023), we characterized regimes using the number of constituent species within families (e.g., Equidae, Felidae, etc.). We aggregated the few taxa that were not assigned at the family level (e.g., *Azygonyx*, *Desmatoclaenus*, *Heptodon*, *Onychodectes*, *etc.*) into their own "No Family" category. We understand that this could be problematic since this creates a polyphyletic group that aggregates taxa from distantly related higher-level clades. However, the number of taxa without a familial identification within a given interval was limited (upwards of 5 species) for the herbivores whereas the majority of taxa without familial identification within the predator guild were historically assigned to "Miacidae" and thus our use of a single "No Family" category would have a limited effect on our results.

We then tested for shifts in taxonomic distribution in the same manner as our functional analyses (Handley, Sheets & Mitchell, 2009). We considered any functional shift that was coincident with a taxonomic shift to not be an evolutionary response to the environment (e.g., predator richness changing in response their presumed prey) when the origination or extinction of one or more families (e.g., taxonomic turnover) was largely responsible for change in the functional distribution. For example, a shift in the functional structure of a guild due to the extinction of a family that dominated a particular size category (e.g., wolf-size predators) would be attributed to taxonomic turnover, rather than an evolutionary response to changes in the herbivore guild. Nevertheless, a functional shift that was coincident with a taxonomic shift could still be representative of an evolutionary response to the environment if the taxonomic shift in

question was driven by a change in species richness of endemic families (i.e., families that are already present in the assemblage) and/or was the result of the origination or extinction of one or more families that had minimal influence on the functional distribution of body mass (e.g., families that were species poor or evenly distributed among multiple size categories).

Sensitivity Analyses. As in Chapter 1, we conducted a series of sensitivity analyses to determine whether our choices of taxonomic level (species, genera), methods of subsampling, or the handling of range-through taxa impacted our results. We also investigated differences between our result and those of Juhn (2023) to determine that observed disparities were caused by methodological differences. We found that methodological differences (e.g., temporal interval length and the use of PBDB versus NOW occurrences) between our studies drove the observed dissimilarity in species richness patterns and the apparent timing of regime shifts in our respective results. An in-depth discussion of the results of our methodological evaluations can be found in Appendix D.

Results

Herbivore Guild. Our best performing models for the distribution of body mass among herbivores identified six distinct regimes separated by five regime shifts at 61Ma, 47Ma, 33Ma, 19Ma, and 9Ma (Figure 6). These shifts were broadly characterized by a long-term, gradual transition toward antelope- and horse-size body sizes throughout the Cenozoic.

Our best performing models for taxonomic composition identified five distinct regimes for the herbivore guild (Figure 7). Three of the four regime shifts in herbivore taxonomic composition corresponded with shifts in the distribution of body mass (47Ma, 35Ma, and 19Ma). These three shifts were driven by the sequential appearance, proliferation, decline, and extinction of dominant families within each taxonomic assemblage. Specifically, the taxonomic regime

shift at 47Ma was driven, in part, by the notable appearance and proliferation of Agriochoeridae. The subsequent regime shift at 35Ma was driven by the decline of the Agriochoeridae and the expansion of Merycoidodontidae. Likewise, the regime shift at 19Ma saw Merycoidontidae supplanted by Equidae as the dominant family within the North American herbivore assemblage.

As expected, most herbivore regime shifts, both functional and taxonomic, occurred in proximity to major climatic events (e.g., Early Eocene Thermal Optimum [~53-49 Ma] and Eocene-Oligocene boundary [~33.9 Ma]) (Zachos, Dickens & Zeebe, 2008; Westerhold et al., 2020) and vegetative transitions (e.g., origin and spread of grasslands [~26-19Ma], C3/C4 transition [~8-5Ma]) (Strömberg, 2011; Strömberg & McInerney, 2011) (Figure 6). This makes sense as climate and vegetation influence the functional and taxonomic composition of extant herbivore assemblages (du Toit & Owen-Smith, 1989; Eronen et al., 2010; Sandom et al., 2013; Short, Pinson & Lawing, 2021; Short & Lawing, 2021). Nonetheless, some of the regime shifts we observed (e.g., 47Ma, 33Ma, and 19Ma) tended to occur after these climatic and vegetative transitions suggesting a lag in the evolutionary response.

Predator Guild. Our best performing models for the distribution of body mass identified five distinct regimes for the predator guild with regime shifts identified at 45Ma, 31Ma, 23Ma, and 17Ma (Figure 6). Like the herbivore guild, the predator guild trended toward a greater representation of larger bodied species (wolf-size and larger) over the Cenozoic but this gradual change was less monotonic when compared to the herbivore guild (Figure 6B and D). We identified three regime shifts that were roughly concurrent (± one interval) between the guilds (circa 46Ma, 32Ma, and 18Ma, Figure 6A and C) with the predator guild shifts lagging behind those of the herbivore guild by no more than 2Myr in all cases. The 23Ma regime shift had no parallel among the herbivores and reflected the loss of the smallest predator size category (<1

kg) and the expansion of the largest (>100 kg). Additionally, this shift was roughly coincident with the onset of the "cat-gap" (Van Valkenburgh, 1999).

Our best performing models for shifts in taxonomic composition identified four distinct taxonomic regimes for the predator guild with regime shifts identified at 39Ma, 31Ma, and 9Ma (Figure 8). Only one of the four shifts in predator taxonomic composition (31Ma) coincided with a shift in predator body mass. This shift was characterized by the extinction of Hyaenodontidae (21-100kg) and the notable expansion of Canidae (1kg-21kg) that persists into the Miocene, and results in canids comprising most of the guild in the following regimes (Figure 8).

Discussion

Van Valkenburgh & Janis (1993) found that the species richness of large mammalian predators broadly tracked that of their presumed large herbivore prey over much of the North American Cenozoic and suggested that this might reflect predator-prey relationships. In our prior chapter, we observed that the richness of wolf- and lion-size predators was positively correlated with that of ungulates of antelope-size and larger, but whether these correlations represented an evolutionary link remained uncertain. This was because these correlations, and those of Van Valkenburgh and Janis (1993), were estimated across the Cenozoic, either in its entirety (67-1Ma; Chapter 1) or restricted intervals (e.g., Oligocene to Neogene [35-1Ma] (Chapter 1), Uintan to Holocene [~46Ma-present] (Van Valkenburgh & Janis, 1993)), and did not identify when and how the body mass distribution of either guild changed in relation to one another over shorter timescales. To remedy this, we tested for changes in the underlying distribution of body mass and taxonomic composition in both guilds to determine whether the timing of these changes was consistent with an evolutionary response of the predator guild to the

herbivore guild (e.g., coincidental, or slightly lagged shifts in herbivore guild structure). We observed multiple (3-5) regime shifts in the taxonomic composition and functional distribution within both the herbivore and predator guilds. Ultimately, we identified three corresponding regime shifts between the guilds (circa 46Ma, 32Ma, and 18Ma) (Figure 6) that could be considered as representing evolutionary responses. Below we discuss each of the regime shifts in the two guilds.

Large Herbivore Guild.

61Ma Regime Shift. The body mass regime shift identified at 61Ma did not coincide with an obvious climatic or environmental transition. This regime shift was driven by a loss of chevrotain-size (< 5kg) species, an increase in antelope-size (25-150kg) species, and the origination of horse-size category (150-500kg). The proximity of this shift to the Cretaceous-Paleogene (K/Pg) boundary (~66Ma) suggests that this shift may be a consequence of the K/Pg extinction event and its immediate aftermath. Specifically, North American herbivore assemblages were predominantly small-bodied following the extinction (~66Ma), but antelope-sized herbivores increased in prevalence near 63Ma while horse- sized herbivores eventually appeared by 61Ma. Exploring other functional traits (e.g., dental and locomotory morphology) in conjunction with body mass could better characterize the niches occupied by the early Paleocene large herbivores and provide a better understanding of the environmental pressures driving these changes.

47Ma Regime Shift. The 47Ma regime shift lagged behind the Early Eocene Climatic Optimum (EECO) (~53-49Ma (Zachos, Dickens & Zeebe, 2008; Westerhold et al., 2020)) and separates the herbivore assemblage into two distinct regimes that experienced very different climatic settings. The regime occurring between 61Ma and 47Ma inhabited an interval of high

global temperatures, encompassing not only the EECO but also the Paleocene-Eocene Thermal Maximum (PETM) (~56Ma). The subsequent regime (47-33Ma) encountered a period of declining global temperatures, increasing aridity, and the development and spread of the earliest open habitats (~42Ma) (Zachos, Dickens & Zeebe, 2008; Townsend et al., 2010; Westerhold et al., 2020). Elevated temperatures and pCO_2 levels, particularly those during the PETM and EECO, coincided with the dwarfing of herbivore genera from multiple clades (e.g., Artiodactyla, "Condylarthra", Perissodactyla, and Tillodontia) (Gingerich, 2003; Secord et al., 2012; D'Ambrosia et al., 2017). Bergmann's Rule and reduced nutritional availability (e.g., limited plant growth and/or lower nutritional quality of vegetation due to high pCO_2 and/or reduced precipitation) have been invoked as explanations for the observed declines in body mass amongst these herbivore congeners over these hyperthermal events (see Gingerich, 2003, 2006; Secord et al., 2012; D'Ambrosia et al., 2017). "Hot house" conditions of the 61-47Ma regime may have induced broad constraints on the evolution of body size amongst herbivores over the duration of the regime and resulted in an assemblage dominated by smaller-bodied (e.g., chevrotain- and javelina-sized) taxa. The removal of these constraints during the 47-33Ma regime led to the observed decline in the number of chevrotain-size species and expansions in herbivores that were javelina-size and larger.

33Ma Regime Shift. A regime shift at 33Ma was roughly coincident with the climatic transitions that occurred near the Eocene-Oligocene (E/O) Boundary (~33.9Ma). Global temperatures underwent a sharp decline near the E/O boundary and remained relatively low (compared to the rest of the Paleogene) until the late Oligocene and early Miocene (Zachos, Dickens & Zeebe, 2008; Westerhold et al., 2020). This decline in temperatures, coupled with increased aridity, accelerated the spread of open, and eventually grass-dominated habitats (e.g.,

woodland savanna) that were dominated by low-quality, high-cellulose forage (~26Ma and onward) (Jacobs, Kingston & Jacobs, 1999; Strömberg, 2005, 2011). Our observed changes in the underlying distribution of body mass within the herbivore guild across the 33Ma regime shift (e.g., expansion of antelope- and horse-size herbivores and the decline of the javelina- and chevrotain-sized herbivores) were likely an evolutionary response to these vegetative transitions. Larger body sizes entail lower mass-specific energy requirements which, when coupled with evolutionary increases in locomotory efficiency that occurred over the Oligocene, allowed larger herbivores to traverse open habitats more effectively (e.g., larger movement ranges, faster movement, decrease in transport costs) relative to their smaller counterparts (Taylor, Schmidt-Nielsen & Raab, 1970; Schmidt-Nielsen, 1972; Altmann, 1987; Janis & Wilhelm, 1993).

19Ma Regime Shift. The decline and loss of chevrotain-size herbivores and the increased richness of horse- and rhino-size herbivores within the 19-9Ma regime were likely evolutionary response to the continued spread of open, grass-dominated habitats (e.g. woodland savanna, open grasslands). Within ungulates, larger body size has been related to improved digestive efficiency (e.g., slower passage rates increasing digestion time) because gut capacity scales linearly with body size (Parra, 1978; Demment & Van Soest, 1985; Owen-Smith, 1988). This increase in digestive efficiency allows larger ungulates to tolerate lower quality forage (e.g., grasses) compared to their smaller-bodied contemporaries (Bell, 1971; Jarman, 1974). Grass-dominated ecosystems first appear within the Late Oligocene (~26Ma and onward) but were initially limited in their geographic distribution (Strömberg, 2005, 2011). These novel habitats gradually expanded geograpically throughout the Great Plains region and temporally throughout the remaining Cenozoic (Strömberg, 2005, 2011). Therefore, these changes initially were geographically restricted, and would have affected only the regional, or even local herbivore

assemblages, but their effect on the continental herbivore assemblage only became evident as these events became more geographically widespread, and habitats became more homogenous.

9Ma Regime Shift. The decline in herbivore richness notably accelerates following the 9Ma regime shift (Figure 6). This decline is evident across all remaining size categories, but its magnitude was not uniform among the categories. Following the 9Ma shift, antelope- and horse-size herbivore median richness declined to that of rhino-size herbivores while javelina-size herbivores were lost altogether from the continent. The mechanisms driving the regime shift at 9Ma are unclear because a number of environmental factors (e.g., vegetative transition, increased seasonality) could be influencing herbivore richness during the Late Neogene. Nevertheless, proximity to the C_3/C_4 transition (8-5Ma) (Strömberg & McInerney, 2011) suggests that this vegetative transition may have influenced the timing of this regime shift. Extant C_3 grasses have a higher nutritional quality (e.g., high levels of nonstructural carbohydrates and proteins) relative to their toughness (e.g., lower fiber and silica content) than C_4 grasses (Bernays & Hamai, 1987; Barbehenn & Bernays, 1992; Van Soest, 1994). Declining species richness within the <9 Ma regime could be driven, at least in part, by the extinction of species that lacked the ability to effectively process and digest the nutritionally poor C_4 grasses.

Predator Guild

45Ma Regime Shift. We consider the regime shift at 45Ma to represent an evolutionary response of carnivores to corresponding changes within the herbivore guild. This shift reflects the diversification of wolf-size predators, and immediately follows an upturn in richness of antelope-size and larger herbivores (Figure 6). The increase in wolf-size predators also accompanied a notable shift toward greater relative blade lengths of the carnassial teeth (0.9-1.0) during the 45-31Ma regime (Juhn, 2023). This makes sense as extant carnivorans, especially

hypercarnivores, over 21kg usually kill prey of near equal size or larger due to energetic demands (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). The increased diversity of antelope-size and larger herbivores likely provided a more abundant food source and expanded ecological opportunities for predators to evolve larger body sizes and specialize for a more hypercarnivorous diet.

31Ma Regime Shift. The 31Ma regime shift among predators is characterized by a contraction of wolf-size predators and an expansion of the smaller weasel-, wild-cat-, and coyote-size predators. These changes in guild structure directly coincided with a taxonomic regime shift that was driven by the extinction of hyaenodontid creodonts (mostly wolf-size predators), the appearance of Mustelidae (mostly weasel-size predators), and a massive expansion of Canidae (chiefly wild-cat- to coyote-size predators) over the Oligocene (Figure 8). The coincidental timing of the taxonomic and functional regime shifts suggests that changes in predator guild structure occurred due to significant taxonomic turnover, and cannot be seen solely as an evolutionary response to the herbivore guild. For example, we might have expected wolf-size predators to have diversified alongside the antelope-size and larger herbivores during the Oligocene. Instead, wolf-sized Hyaenodontidae declined and became extinct, and were not replaced. However, ruling out any role for an evolutionary response would be premature. Significant changes in taxonomic composition could be a byproduct of selective pressures not directly related to predator-prey interactions, such as changes in vegetation structure, climate, or interspecific competition.

Comparing the diversity patterns of the creodonts (Hyaenodonta and Oxyaenodonta) with the timing of environmental events and parallel trends with coeval predators could offer explanations for the decline of the wolf-size predators near the 31Ma regime shift. First, the

decline in the richness of Hyaenodontidae, and the wolf-size predators as a whole, followed the E/O boundary (~33.9Ma), suggesting the decline and subsequent extinction of Hyaenodontidae may have been related to the environmental transitions (e.g., spread of open habitats, increased aridity) that followed the global cooling event at the E/O boundary. The large-bodied and hypercarnivorous hyaenodontids may have been unable to effectively adapt to these rapidly changing habitats in comparison to contemporary carnivoran clades (e.g., Canidae, Nimravidae) (Friscia & Van Valkenburgh, 2010). Second, the decline of creodont (Hyaenodonta and Oxyaenodonta) richness over the Eocene and Oligocene roughly coincided with the diversification of carnivorans (Van Valkenburgh, 1999; Friscia & Van Valkenburgh, 2010). These concurrent richness trends, alongside similarities in dentition (e.g., specialized slicing carnassial or carnassial-like cheekteeth) suggest that competition between the creodonts and carnivorans contributed to the extinction of the former (Flynn, 1998; Van Valkenburgh, 1999; Friscia & Van Valkenburgh, 2010, but see Christison et al., (2022)). Ultimately, the mechanisms that drove the decline of the wolf-size creodonts near the 31Ma regime shift remain poorly understood. Future studies should look to incorporate locomotory morphology into their analyses alongside body mass and dental morphology to better refine our understanding of how these predators hunted and the possible implications of habitat transitions.

Despite the apparent lack of a response among wolf-size predators to the increase in richness among their presumed prey, the antelope-sized herbivore, there does appear to be a positive response among the weasel-, wild-cat- and coyote-size predators within the 31- 23 Ma interval. This is surprising as we do not expect them to have been taking antelope-size and larger prey. Moreover, the wild-cat size species were mostly hypocarnivores (<50% meat in diet (Van Valkenburgh, 1989); n =11 of 17 wild-cat-size species) and thus their increased richness more

likely reflects environmental changes in plant matter, rather than of any vertebrate prey. The coyote-size species were mostly hypercarnivores (>70% meat in diet (Van Valkenburgh, 1989); *n*=13 of 19 coyote-size species), (Figure 3) and therefore might have preyed upon the diversifying antelope-size herbivores as well as smaller prey. Notably, extant wild-cat- to coyote-size predators, specifically mesocarnivores and hypercarnivores, have been observed to take antelope-size, and larger herbivores (Labisky & Boulay, 1998; Gustine et al., 2006; Lofroth et al., 2007; Van Dijk et al., 2008; Inman & Packila, 2015; Mattisson et al., 2016; Magoun et al., 2018; Newbury & Hodges, 2018). However, among extant species of this size, solitary predators rarely take adult prey, and instead favor more vulnerable subadults (Labisky & Boulay, 1998; Jarnemo et al., 2004; Gustine et al., 2006; Inman & Packila, 2015; Mattisson et al., 2016).

In addition, both the wild-cat- and coyote-size predators may have indirectly responded to the antelope-size herbivores via scavenging. Opportunistic scavenging of large ungulate carcasses (e.g., caribou (*Rangifer tarandus*), elk (*Cervus canadensis*), and moose (*Alces alces*)) provides a notable proportion of the meat consumed by some extant wild-cat- to coyote-size predators (e.g., coyote (*Canis latrans*), wolverine (*Gulo gulo*)) (Nellis & Keith, 1976; Bekoff & Wells, 1981; Crabtree & Sheldon, 1999; Lofroth et al., 2007; Van Dijk et al., 2008; Inman & Packila, 2015). Antelope-size herbivores may have been an important source of carrion if they were sufficiently abundant on the landscape during the Oligocene. This is a distinct possibility because the expansion of the antelope-size category over the 33-19Ma regime was largely driven by the expansion of Merycoidontidae (*n*=17 of 60 species) (Figure 7), a group that is exceptionally common in the fossil record throughout the middle Eocene to early Miocene (Clark, Beerbower & Kietzke, 1967; Cleaveland, Prothero & Welsh, 2022). Additionally, the limited presence of wolf- and lion-size predators (2-3 species) during this regime could have

further facilitated scavenging through the year-round production of carcasses from their own kills (Wilmers & Getz, 2004, 2005; Van Dijk et al., 2008; Pereira, Owen-Smith & Moleón, 2014).

The taking of antelope-size and larger prey may have been facilitated through changes in predator behavior. Coyote-size predators during the 31-23Ma body mass regime were chiefly canids (*n* = 11 of 19 species) (Figures 3 and 6). Extant coyote- to wolf-size pack-hunting canids (e.g., dhole (*Cuon alpinus*), African wild dog (*Lycaon pictus*)) have been observed to take adult antelope- and even horse-sized herbivores if the pack is sufficiently large (Hayward, Lyngdoh & Habib, 2014). Creel (2001) also observed that pack size was positively correlated with hunting success in African wild dogs. If hypercarnivorous canids during the Oligocene also hunted in packs, they could have hunted prey within the antelope-size category, which might partially explain their response to the increased antelope-size herbivore richness. Determining whether extinct taxa engaged in pack hunting is difficult because evidence for such behaviors are rarely preserved, and skeletal traits do not definitively indicate pack hunting. Nevertheless, pack hunting has been suggested for some genera of Borophaginae on the basis of their inferred hypercarnivory, less flexible limb posture, and abundance (Van Valkenburgh, Sacco & Wang, 2003). Likewise, pack hunting has been suggested for amphicyonids due to some morphological similarities to extant pack hunting canids (Hunt Jr., 2009). Figueirido et al., (2011) determined that some amphicyonids, the daphoenines in particular, occupied similar craniodental morphospace as extant hypercarnivorous pack hunting canids, but they did not use this overlap to directly suggest pack hunting behaviors.

Coincident expansion of the weasel-, wild-cat-, and coyote-size predators could represent a broad response to the availability of antelope-size herbivores, but the influence of smaller prey

that are not included in our study must also be considered. Small vertebrate prey (e.g., rodents, lagomorphs, lizards, birds, etc.) comprise an important component of the diets of extant predators below the 21kg threshold (Nellis & Keith, 1976; Inman & Packila, 2015; Newbury & Hodges, 2018). For example, the biomass consumed by *Lynx rufus* is heavily dominated by rodents and lagomorphs (e.g., red squirrels, cricetids, hares). The utilization of small prey by weasel-, wild-cat-, and coyote-size predators likely extended into the past. Samuels and Hopkins (2017) observed relatively high species richness in Rodentia and Lagomorpha over this regime (31-23Ma). Futures studies should evaluate, concurrently, small and large herbivores in order to determine how the relative influence of each affected the evolution of the predator guild over the Cenozoic.

23Ma Regime Shift. The regime shift at 23Ma was not coincident with a herbivore regime shift. We observed expansions within the wild-cat-, wolf-, and lion-size predators over the 23-17Ma regime that followed a marked increase in the richness of antelope-size herbivores in the late Oligocene (Figure 6). As within the previous regime, the wild-cat-size species within the 23-17Ma regime were predominantly hypocarnivorous (n = 14 out of 24 species) with a minor component having been mesocarnivores (50-70% meat in diet (Van Valkenburgh, 1989); n = 8 of 24 species) (Figure 3). Their smaller size (<7kg) and limited meat consumption suggests that this category was more likely responding to environmental factors (climate, vegetation) or shifts in small prey (e.g., lagomorphs, rodents) richness over this interval. By contrast, wolf- and lion-size predators were primarily hypercarnivorous (n = 11 of 11 species and n = 6 of 7 species, respectively) and likely preferred prey near their size or larger, and their increased richness might represent a response to a rise in prey abundance and richness. Although we did not detect a regime shift at 23Ma among the herbivores, it is clear that peak richness of

the antelope-sized herbivores occurred around 23Ma (Figure 6). Nevertheless, because there is not a coincidental body mass shift in the herbivores, we hesitate to classify the 23Ma surge in large hypercarnivores as representative of an evolutionary response by the predator guild to the herbivore guild.

17Ma Regime Shift. A regime shift at 17Ma closely follows a shift within the herbivore guild (19Ma). The 17Ma regime shift was driven by a notable decline in the richness of wild-cat-size predators and an expansion in wolf-size predators that coincided with elevated antelope- and horse-size herbivore richness (Figure 6). Decline of wild-cat-size richness was initially the result of a contraction of hypocarnivorous taxa, which was then followed by gradual declines in mesocarnivores (Figure 3). The limited amount of meat consumed by these two dietary categories and the smaller size of the wild-cat-size predators relative to the antelope- and horse-size herbivores, suggests that these predators were responding to other environmental stimuli (e.g., vegetation, other prey) rather than the large herbivore guild. However, wolf-size predators likely were responding to the expansion in the richness of horse-size herbivores. Expansion of horse-size herbivores over the 19-9Ma herbivore regime and already elevated antelope-size herbivore richness could have provided ecological opportunities for these wolf-size predators to increase in richness.

Predator Response to Herbivore Taxonomic Shifts

We observed significant changes in the taxonomic structure of the herbivore guild concurrent with body mass regime shifts, including the three shifts (47Ma, 33Ma, 19Ma) that occurred nearly simultaneously in both the predator and herbivore guilds. Changes in the richness of Agriochoeridae, Merycoidontidae, and Equidae drove taxonomic shifts at 47Ma, 33Ma, and 19Ma, respectively, and as discussed above, contributed to the shifts in the

distribution of body mass in each case (Figure 7). It is unlikely that the predator guild was responding to these taxonomic shifts rather than the shifts in body mass. Extant predators, despite having preferences for particular prey species, generally utilize a wide range of prey (Sinclair, Mduma & Brashares, 2003; Radloff & Du Toit, 2004; Hayward & Kerley, 2005). For example, lions have a noted preference for gemsbock (*Oryx gazella*), Cape buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*), and zebra (*Equus burchelli*), but they will take other prey (e.g., warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*)) based on their abundance, albeit at a lower frequency (Hayward & Kerley, 2005; Hayward et al., 2011). The abundance of prey and its spatiotemporal distribution on extant landscapes plays an important role in determining which prey are utilized by predators (Sunquist & Sunquist, 1989).

It seems likely that the positive association between prey abundance and prey choice held throughout the Cenozoic and would have contributed to how and when predators responded to their herbivore prey. For example, the prevalence of horse-size herbivores on the landscape could explain why wolf-size predators expand alongside the horse-size herbivores following the regime shifts circa 18Ma. Large predators (>21kg) require their large prey to be abundant so that metabolic requirements can be sustained (Carbone, Teacher & Rowcliffe, 2007). Equids dominated the horse-size category over the regimes spanning 19-9Ma (n = 49 of 87 species) and <9Ma (n = 40 of 69 species), and were both geographically widespread across the North American continent and numerically abundant within local assemblages (MacFadden, 1992). The relative abundance of these horse-size equids, in addition to their taxonomic richness throughout the Neogene likely made them frequent prey.

Scavenging Behaviors

We briefly discussed that scavenging behavior may have driven an evolutionary response among the wild-cat- and coyote-size predators to an increase in larger-bodied (antelope-size and larger) herbivores over the 31-23Ma regime. Even though our earlier focus was restricted to these two body-size categories, scavenging and its potential influence on evolutionary responses is relevant to all predator body size categories and during all time intervals. Facultative scavenging has been observed across all predator size categories in extant assemblages (Selva et al., 2003; Bell et al., 2023), but its frequency varies among predator species. Scavenging by extant predators ranges from those species that rarely consume carrion (e.g., cheetah (*Acinonyx jubatus*)) to those that are prolific consumers of carrion (e.g., brown hyaena (*Hyaena brunnea*)) (Skinner & Chimimba, 2005). The mechanisms underlying scavenging behaviors are complex, but the prevalence of scavenging is related to the availability of carrion relative to exploitable prey (e.g., prey within preferred prey ranges, subadult prey, or prey with reduced body condition due to old age, injury, or disease) on the landscape (DeVault, Rhodes & Shivik, 2003). The relative importance of non-predator and predator induced prey mortality varies substantially across, and within, mammal communities (Bergerud, 1980; Leader-Williams, 1988; Jędrzejewski et al., 1993; Oksanen & Oksanen, 2000), especially in ecosystems where seasonal trends (e.g., resource scarcity, population increases, migrations) are prevalent (see review by Pereira, Owen-Smith & Moleón, 2014 and references therein). Nonetheless, the presence of multiple predators within the same spatial area can further impact scavenging behaviors through facilitation (e.g., year-round creation of large herbivore carcasses via predation by large-bodied predators) or suppression (competition for prey, kleptoparatism, intraguild predation) (Pereira, Owen-Smith & Moleón, 2014; Moleón et al., 2014; Prugh & Sivy, 2020; Bell et al., 2023). Despite the clear

importance of scavenging in the diets of extant predators, determining the frequency of scavenging behaviors in an extinct species is very difficult, unless they exhibit extreme craniodental morphology for bone consumption (e.g., bulbous premolars and massive jaw muscles of hyaenas (Wang et al., 2018), specialized enamel microstructure (Rensberger & Wang, 2005; Tseng, Antón & Salesa, 2011), complex dental microwear indicative of durophagy (DeSantis et al., 2012, 2017), and/or heavy tooth wear suggestive of frequent bone consumption (e.g., broken teeth (Van Valkenburgh & Hertel, 1993). Nonetheless, scavenging remains an important aspect of predator ecology and should be considered, at least theoretically, in the interpretation of predator evolutionary responses, even if direct evidence was lacking.

Hunting of Subadult Prey

The taking of subadult prey is another behavior observed among extant predators that could have influenced our observed results. We previously discussed the taking of subadult prey (e.g., neonatal and juvenile) as being an important behavior that could explain the evolutionary response of the wild-cat- and coyote-size predators following the 31Ma regime shift. However, predation of subadults likely occurred throughout the Cenozoic and was not restricted to the 31-23Ma regime. Additionally, this behavior would not have been restricted to just the wild-cat- and coyote-size predators as extant wolf- and lion-size predators also employ this behavior in regards to the hunting of large herbivore prey (Gervasi, Nilsen & Linnell, 2015). For example, African lions (*Panthera leo*) have been observed to take subadult hippos, rhinos, and elephants (Bourliere, 1963; Pienaar, 1969b; Joubert, 2006; Loveridge et al., 2006; Power & Compion, 2009b). The taking of subadult prey increases proportionally with adult prey size in extant and Pleistocene large mammal assemblages (Palmqvist, Martínez-Navarro & Arribas, 1996; Gervasi, Nilsen & Linnell, 2015) and allows predators to utilize larger species that normally would be

outside of their preferred prey ranges (e.g., wild-cat- and coyote-size predators predating antelope-size and larger herbivores). Nonetheless, while the fossil record offers little evidence to determine the degree to which subadults were utilized as prey, modeling how subadult body sizes overlap with the preferred prey range of coeval predators could reveal the relative susceptibility of these subadults to predation (see Van Valkenburgh et al., (2016)).

Conclusion

In summary, we identified multiple significant shifts in the structure (species richness of body size and clades) of both the herbivore and predator guilds over the Cenozoic. Shifts in the distribution of body mass of the herbivore guild were roughly coincident with or followed major climatic events (e.g., Early Eocene Climatic Optimum, Eocene-Oligocene Boundary) and vegetation transitions (e.g., spread of grass dominated habitats, C_3/C_4 transition). Three of the shifts identified within the structure of the predator guild slightly lagged ($\leq$2Myr) behind those of the herbivore guild. We argue that the timing and nature of these body mass shifts are representative of evolutionary responses of the herbivore and predator guilds to environmental factors, and responses by the predator guild to the herbivore guild. Our inclusion of a functional trait (body mass) allowed us to begin to evaluate the mechanisms underlying parallel trends of herbivore and predator species richness originally observed by Van Valkenburgh & Janis (1993). Going forward, evaluation of richness patterns using dietary (e.g., hypsodont, relative blade length) and locomotory (e.g., calcaneal gear ratio, metatarsal to femur ratio) traits could further improve our understanding of how both guilds evolved relative to their environment and one another.

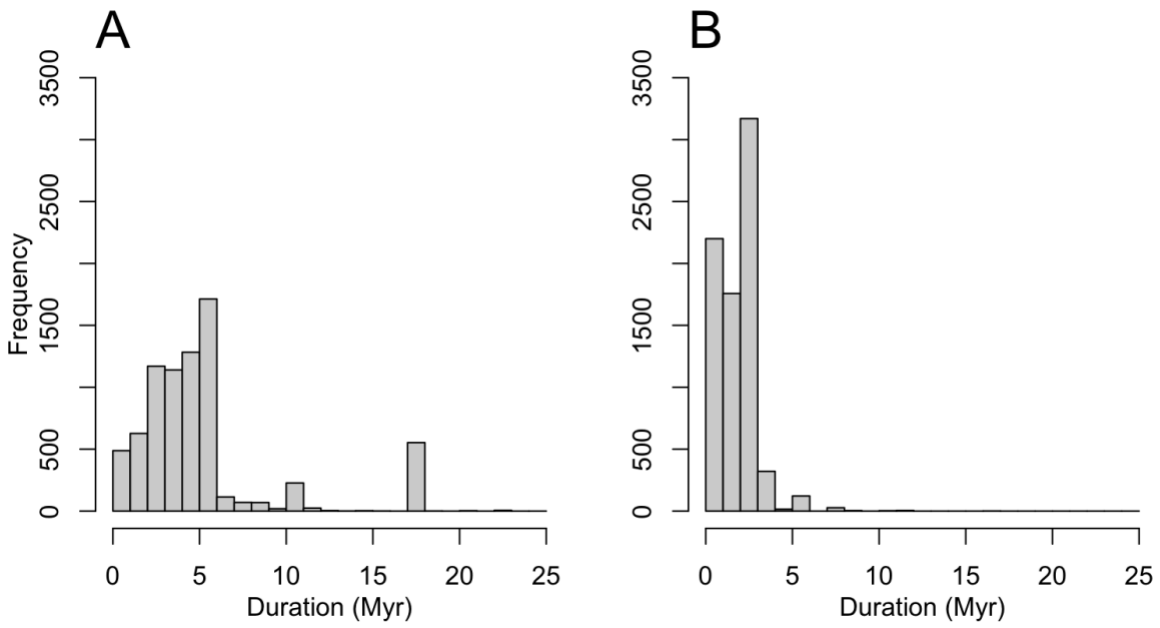

Figure 5. Stratigraphic uncertainty of Paleobiology Database (PBDB) collections. Stratigraphic uncertainty is the difference between the maximum and minimum date estimates for a given collection and are calculated using dates (A) provided by the PBDB, or (B) from localities within the New and Old-World (NOW) Database of Fossil Mammals that have been matched to PBDB collections. PBDB collections that could not be matched to NOW localities retained their dates assigned within the PBDB.

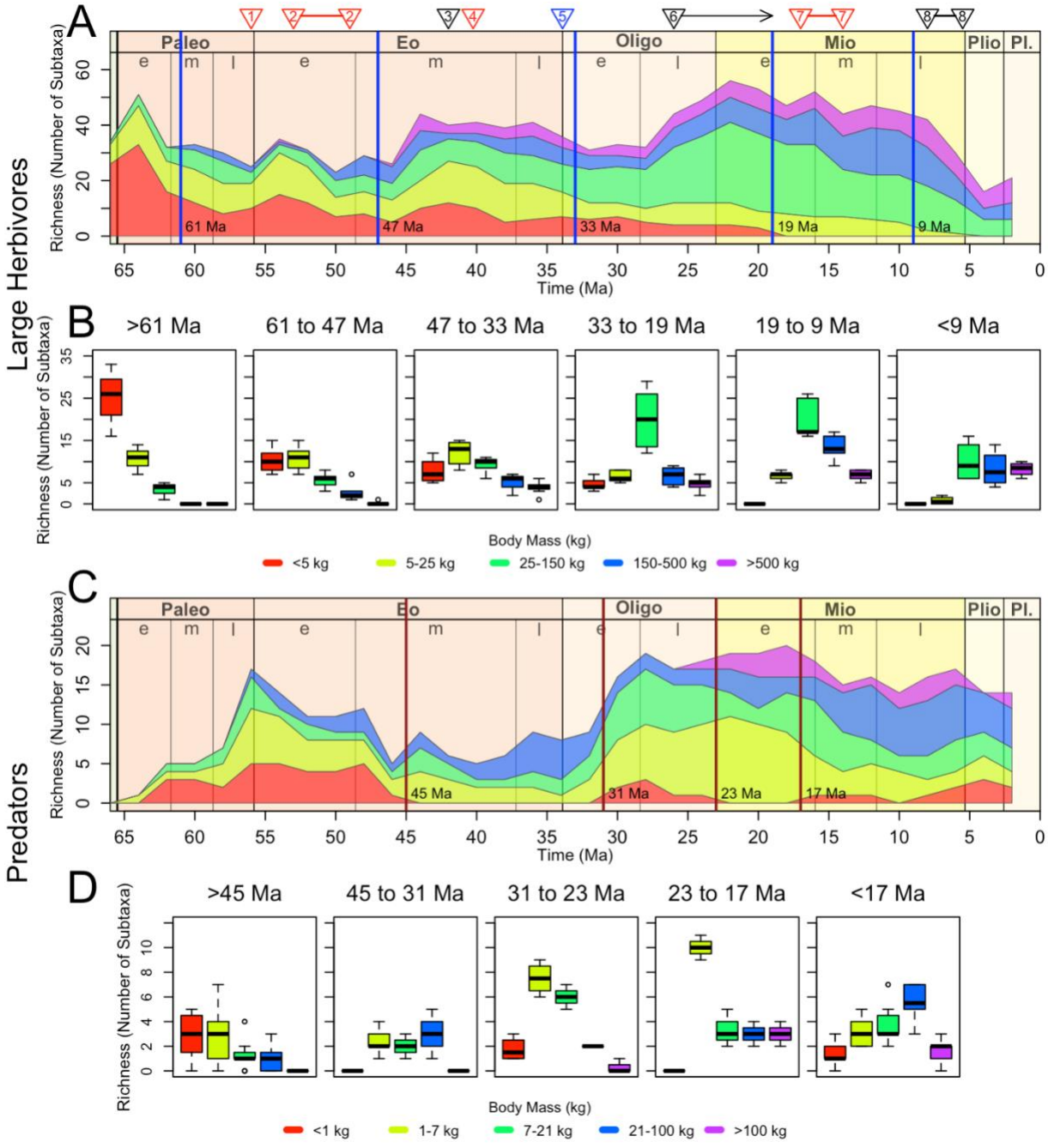
Large Herbivores
A
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Time (Ma)
61 Ma
47 Ma
33 Ma
19 Ma
9 Ma
B
>61 Ma
61 to 47 Ma
47 to 33 Ma
33 to 19 Ma
19 to 9 Ma
<9 Ma
Body Mass (kg)
<5 kg
5-25 kg
25-150 kg
150-500 kg
>500 kg
Predators
C
45 Ma
31 Ma
23 Ma
17 Ma
D
>45 Ma
45 to 31 Ma
31 to 23 Ma
23 to 17 Ma
<17 Ma
<1 kg
1-7 kg
7-21 kg
21-100 kg
>100 kg

Figure 6. Distribution of North American herbivore (A and B) and predator (C and D) species richness and body mass throughout the Cenozoic. Solid, vertical blue and red lines represent temporal boundaries between body mass regimes – distinct assemblages of body mass for herbivores and predators, respectively. Inverted triangles at the top mark the occurrence of major climatic warming (red) and cooling (blue) events and vegetation transitions (black). Inverted triangles correspond to the Paleocene-Eocene Thermal Maximum (1), Early Eocene Climatic Optimum (2), earliest inferred open habitats within North America (3), Middle Eocene Climatic Optimum (4), Eocene-Oligocene Boundary (5), onset and spread of grass dominated habitats within North America (6), Middle Miocene Climatic Optimum (7), and C3/C4 transition (8) (Zachos, Dickens & Zeebe, 2008; Townsend et al., 2010; Strömberg, 2011; Strömberg & McInerney, 2011; Westerhold et al., 2020). Boxplots (B and D) display the distribution of species richness within size categories within each regime.

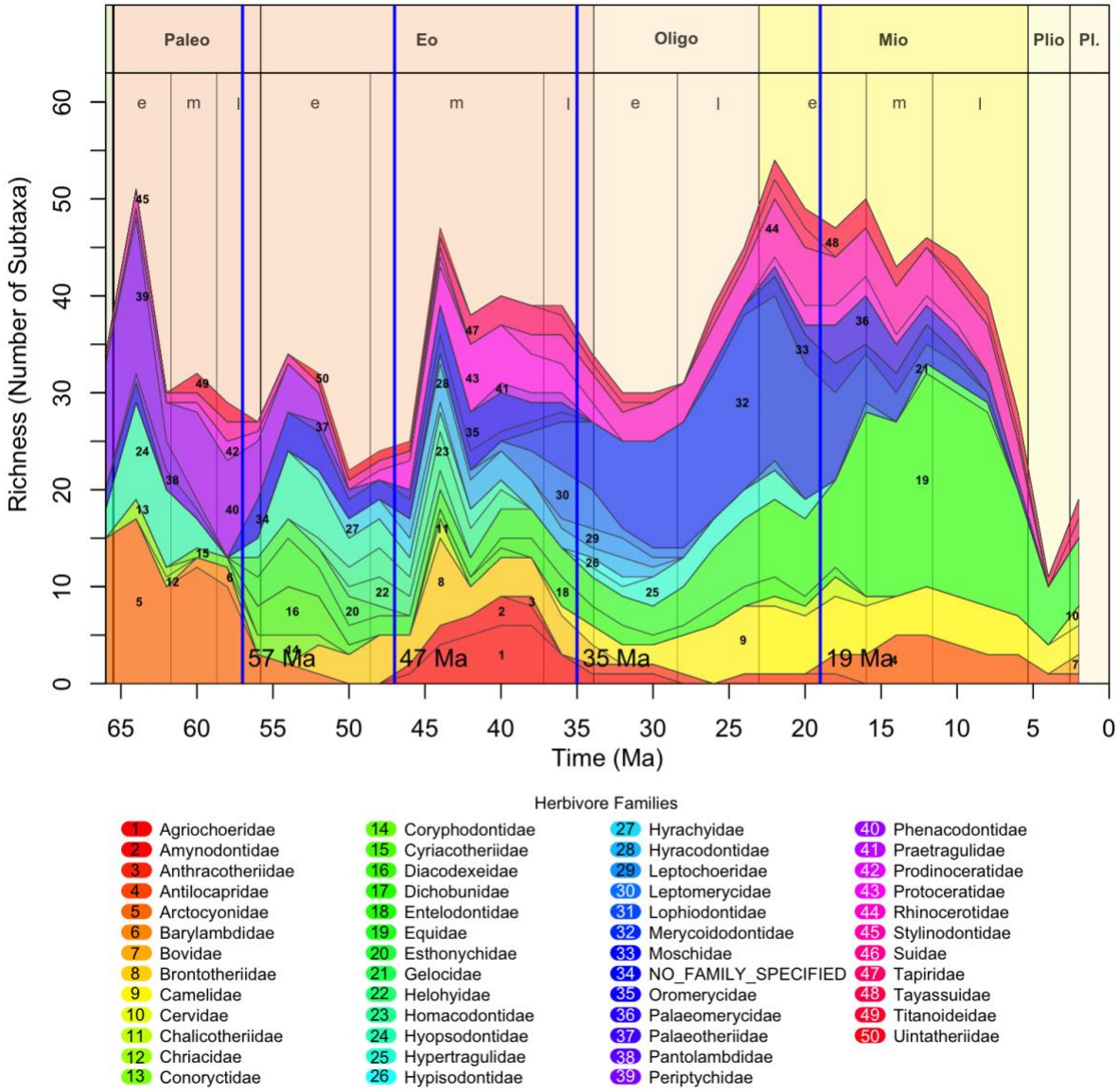

Figure 7. Species richness of the herbivore guild throughout the Cenozoic as partitioned by taxonomic family. Solid, vertical blue lines represent locations temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

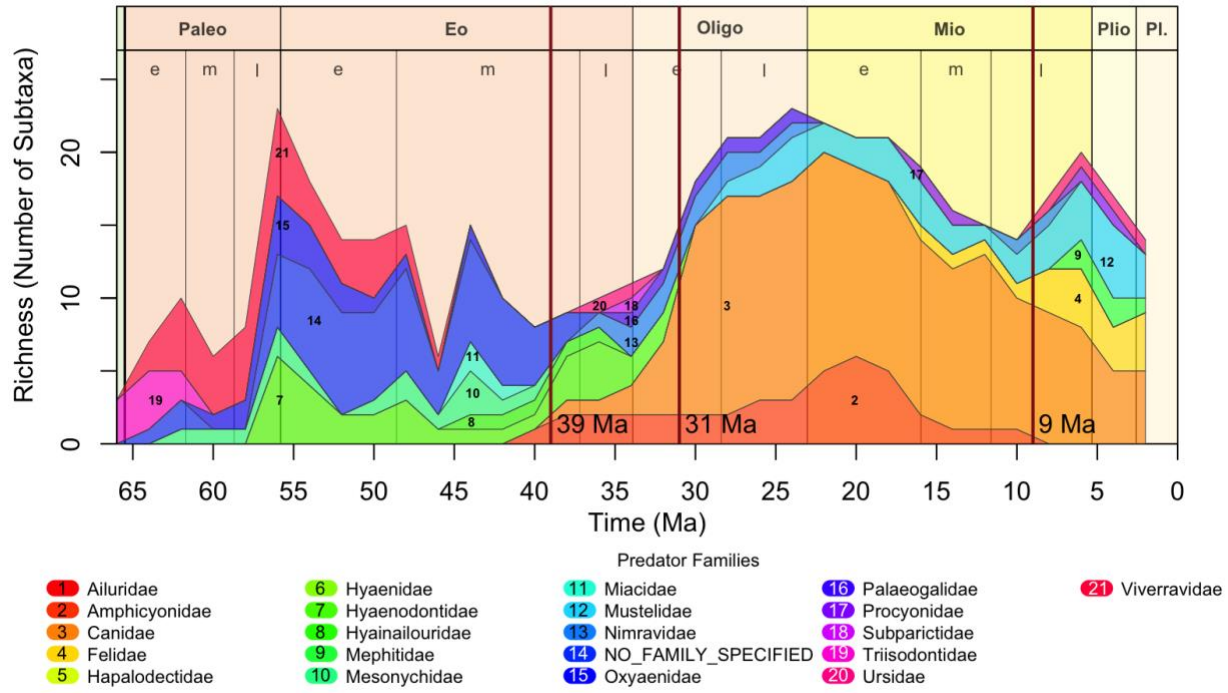

Figure 8. Species richness of the predator guild across the Cenozoic as partitioned by taxonomic family. Solid, vertical red lines represent temporal boundaries between taxonomic regimes– distinct assemblages of taxonomic composition.

CHAPTER III: SIZE-SPECIFIC TRENDS OF LARGE HERBIVORE ABUNDANCE RELATIVE TO PREDATOR RICHNESS WITHIN THE NORTH AMERICAN NEOGENE

Abstract

The species richness of large mammalian predators is positively correlated with that of their presumed herbivore prey in extant and extinct assemblages. Nonetheless, predator richness declined at a slower rate than that of the herbivores over the middle to late Miocene, resulting in uncharacteristically high predator/prey ratios over the Plio-Pleistocene. In this study, we evaluate whether the relative abundance of herbivores over the North American Neogene could explain this high predator-prey ratio despite declining herbivore richness. We estimated occupancy, a proxy of relative abundance, aggregated by size class (chevrotain-size [<5kg], javelina-size [5-25kg], antelope-size [25-150kg], horse-size [150-500kg], rhino-size [>500kg]) and for individual genera. We observed that occupancy remained high (>0.25) and stable throughout the Neogene if the guild is considered in its entirety. Similarly, antelope-size and larger herbivores exhibited high occupancies over the Neogene, but chevrotain- and javelina-size herbivores exhibited relatively low occupancies that steadily declined over the same interval. Changes in the occupancy of each size category paralleled the spread of open, grass-dominated habitats. Individual genera were mostly rare (occupancy less than 0.25) throughout the Neogene but genera that survived typically had a relatively higher occupancy and body-size than those genera that went extinct.

Introduction:

The species richness of large mammalian predators correlates positively with that of their large herbivore prey at regional and continental scales in extant (Sandom et al., 2013) and fossil assemblages (Figure 4) (Van Valkenburgh & Janis, 1993). Despite the strength of these correlations, predator richness declined at a slower rate than herbivore richness over the North American Miocene (~23 - 5 Ma); a phenomenon that resulted in higher predator-prey ratios during the Plio-Pleistocene (~5.3 - 0.012Ma) (Figures 1 and 2) (Van Valkenburgh & Janis, 1993). At face value, this disjunction in predator and prey richness suggests that the linkage between the guilds became decoupled, albeit not fully, over this interval (Van Valkenburgh & Janis, 1993). However, the mechanisms facilitating this change in the relationship between predator and prey richness remains unclear (Van Valkenburgh & Janis, 1993).

Van Valkenburgh and Janis (1993) suggested that the high predator/prey ratio near the end of Neogene (~23 Ma to present) might reflect a shift toward more mesocarnivorous (50-70% meat in diet) and hypocarnivorous (< 50% meat in diet) diets within the predator guild (Van Valkenburgh, 1989), but they did not explore this idea in their paper. We did so in Chapter 1 and observed that the Plio-Pleistocene predator guild was comprised of large-bodied (>21 kg) hypercarnivores (~40% of the guild; >70% meat in diet (Van Valkenburgh, 1989)) and smaller (<21 kg) mesocarnivores (~40% of guild) (Figure 3). Large predators, especially hypercarnivores, must take prey of near equal size or larger to remain energetically profitable (Carbone et al., 1999). These metabolic requirements coupled with the relatively high number of coexisting large (>21 kg) hypercarnivores suggests that a shift away from meat-eating was not the cause of the unusual predator-prey ratios and that another aspect of the predator-prey

relationship probably prevented predators from declining to the same extent as the herbivores over the Neogene.

Changes in, or lack thereof, the relative abundance of antelope-size (25-150kg) or larger prey over the North American Neogene could have facilitated the observed disjunction in predator richness and the coexistence of large-bodied hypercarnivores. Even though extant predators (e.g., lions) may prefer specific prey species (e.g., *Oryx gazella* (gemsbock), *Syncerus caffer* (Cape buffalo), *Connochaetes taurinus* (wildebeest), *Giraffa camelopardalis* (giraffe), and *Equus burchelli* (zebra)), they will often select ungulate prey based on their relative abundance within local assemblages (Hayward & Kerley, 2005; Hayward et al., 2011). The relative abundance of medium-size (120-400 kg) prey can also facilitate the coexistence of multiple large predator species (e.g., lions and hyaenas) within the same assemblage by either reducing competition pressure (e.g., more available biomass to exploit) and/or by improving a predator's ability to compete for resources (e.g., larger hyaena clans are better at both committing and defending against kleptoparasitism) (Périquet, Fritz & Revilla, 2015).

Some herbivore taxa, such as horses (Equidae) and rhinos (Rhinocerotidae), are known to have been numerically abundant in local assemblages, and geographically widespread across North America (MacFadden, 1992; Wang & Secord, 2020), but the relative abundances of herbivore taxa throughout the North American Neogene has not been quantified. Previous work on the European Neogene (23-2.6 Ma) found that the large mammalian herbivore trophic group (e.g., Artiodactyla, Perissodactyla, Proboscidea) as a whole exhibited relatively stable locality coverage (Jernvall & Fortelius, 2004). Whether North American herbivores exhibited similar patterns of stability over the same interval remains unclear.

In this study, we evaluate 1) the stability of large herbivore relative abundance over the North American Neogene (23-1Ma), 2) whether the relative abundances of functional groups varied, and 3) whether herbivore abundance could have plausibly sustained multiple large (>21.5kg), hypercarnivorous predators despite severe reductions in richness. We characterize both the predator and herbivore guilds using body mass and taxonomic identity. Then, we determine the occupancy, or relative site coverage (Gaston & Blackburn, 2000; Jernvall & Fortelius, 2002, 2004; Raia et al., 2006; Oksanen, 2019), of the herbivore guild as whole, and separately for size-specific and taxonomic groupings, as a proxy for their relative abundance on the continent. Finally, we compare patterns of functional and taxonomic herbivore occupancy with patterns of size-specific predator richness to determine if herbivore occupancy is a plausible explanation for observed spatiotemporal trends in predator richness.

Directly measuring relative abundance within extinct communities is difficult due to the incompleteness of the fossil record and spatiotemporally non-random sampling (Jernvall & Fortelius, 2004). Theoretical models have been developed (see Damuth, 1982) to estimate the relative abundance of species directly within the fossil record, but these methods are restricted in their applicability to single sites or local assemblages (Meloro, Raia & Barbera, 2007). Occupancy can be easily quantified as the proportion of collections within an interval in which a taxon occurs, and can be determined for individual taxa, guilds, or functional groups (e.g., hypsodont, mesodont, and brachydont herbivores) within the fossil record (see Jernvall & Fortelius, 2002, 2004; Raia et al., 2006; Meloro, Raia & Barbera, 2007; Liow, 2013; Oksanen, 2019). Occupancy is positively correlated with abundance (e.g., local density) and spatial distribution within extant assemblages (Brown, 1984; Hanski, Kouki & Halkka, 1993; Gaston &

Blackburn, 2000), suggesting that occupancy is a reasonable proxy for abundance in the fossil record.

The relatively high richness of wolf- to lion-size predators over the Neogene suggests that herbivores, specifically those antelope-size and larger, were relatively common. Prey must be of a minimum size and abundance to be metabolically profitable for large-bodied predators (Carbone et al., 1999; Carbone, Teacher & Rowcliffe, 2007). We hypothesize that large mammalian predators are more likely to evolutionarily respond to common prey as opposed to rare prey. If so, we expect that the relative occupancy (percent occurrence) of antelope-size and larger herbivores will remain high over the Neogene despite declines in herbivore richness. Additionally, we expect that declines in herbivore richness were driven by the loss of taxa that were rare since taxa tend to decline in relative abundance, and thus occupancy, prior to their extinction (Jernvall & Fortelius, 2004; Raia et al., 2006; Foote et al., 2007).

Methods and Materials

Our study builds on the previous chapters and involves: 1) characterization of the predator and prey guilds using body mass and taxonomic identity, 2) determination of stratigraphic ranges of genera, and assignment to discrete time intervals, 3) modeling the occupancy for herbivore body size categories and genera, 4) comparison of herbivore occupancy estimates with size-specific patterns of predator richness. All data processing, replicate generation, and analysis were performed in R, version 4.3.3 (R Core Team, 2024). All data sets are available in Appendix A.

Taxonomic Sampling and Body Mass Estimation and Binning. We followed the same methods of body mass estimation and binning used in prior chapters with the exception that

we sampled taxa at the generic level. Approximately 23% (125 out of 546 species) of Neogene herbivore species within our analyses were known from only a single collection. We performed analyses at the genus level on the recommendations of Jernvall & Fortelius (2002), who warned that the high number of single-collection species may bias inferences. Additionally, the aggregation of multiple congeners has been shown to have limited effect on occupancy trajectories (Foote et al., 2007). We used mean body mass across all congenerics to bin genera into body mass categories according to the methods of prior chapters.

Generic Occurrences and Temporal Binning. We determined the duration of genera using occurrence data from the Paleobiology Database (PBDB) following the same protocols as chapter 2. Like the previous chapter, we manually matched PBDB collections to localities within the New and Old World (NOW) Database of Fossil Mammals (The NOW Community, 2023) and replaced the maximum and minimum age estimates for PBDB collections that corresponded with a NOW locality (n = 6148 out of 9358). We downloaded occurrences for all North American mammals from the PBDB on 7/23/2024 while the list of NOW localities and their date estimates was downloaded on 10/2/2023. We removed PBDB collections (18518, 190543, 230906, 205394) that have been or should be split into multiple smaller collections due to poor spatiotemporal resolution (e.g., occurrences within a collection are aggregated across multiple horizons, beds, and/or formations of different ages).

Paleontological data, PBDB collections included, are nonrandomly distributed in space and time due to the nature of preservation and sampling intensities (Jernvall & Fortelius, 2004). To be more conservative in our inferences, we first divided North America into 0.125-degree (7.5 minute) latitude/longitude grid squares. Then, within each temporal interval, we merged all

collections (and their constituent occurrences) contained within a grid cell into a single composite collection following the methods of Jernvall and Fortelius (2002, 2004).

We generated 2500 pseudoreplicates using much of the same methodology as chapter 2 with some exceptions. Unlike the prior chapter, we binned collections into uniform 2Myr intervals that spanned 25 to 1Ma, we did not perform subsampling, and we did not assume that species durations ranged through all intervals between those of their first and last occurrence.

Estimating Occupancy We used the raw proportion of collections occupied within an interval to estimate the continental-scale occupancy of the herbivore guild within each 2Myr interval. Liow (2013) refers to these as "naïve" occupancy values because this methodology does not distinguish whether an absence from a collection of a taxon or functional group of interest represents a true absence or instead, a failure to be preserved, detected, or sampled (false absence). Like Jernvall and Fortelius (2004), we assume that abundance and occupancy are positively correlated, regardless of the underlying mechanisms driving that relationship.

We evaluated the stability of herbivore occupancy over the Neogene in two ways. First, we evaluated the overall stability of the herbivore guild and individual size categories following Jernvall and Fortelius (2004; Figure 6). This involved estimating occupancy by taking the proportion of sites that contained any member of the herbivore guild or a size category within an interval regardless of the generic identity. We repeated this process for each pseudoreplicate and then calculated the median occupancy of the guild or individual size categories across all pseudoreplicates.

Second, we evaluated how the stability of each size category was influenced by the "commonness" (occupancy greater than 0.25) of their constituent genera. Namely, we were

interested in determining whether larger, more "common" genera were more likely to persist into subsequent intervals compared to rarer genera. To do this, we categorized genera within a pseudoreplicate into one of the four fundamental classes of taxa following the methods of Foote (2000; Figure 1). We then calculated the median occupancy of each size category for each fundamental class of taxa from across all pseudoreplicates and compared the distribution of median occupancies for taxa that persisted through an interval (bt) and the taxa that went extinct within an interval (bL).

Sensitivity Analyses. We made decisions regarding the design of our analyses that have the potential to influence our results and, ultimately, our inferences. This includes our choice of taxonomic scope and grid square size. For this reason, we conducted a series of sensitivity analyses to evaluate the degree to which these choices affected our results. All methods and results of these sensitivity analyses can be found in Appendix E.

Results:

Overall Occupancy of the Herbivore Guild and Size-categories. We observed occupancy estimates that were not only relatively high (~0.54-0.82) but also relatively stable for much of the Neogene when we consider the herbivore guild in its entirety (occupancy was estimated without regard to generic identity) (Figure 9). Similarly, we observed that the occupancy estimates for the antelope-, horse-, and rhino-size herbivores remained elevated over the Neogene when each size category was observed in its entirety. Antelope- and horse-size herbivores were the most common herbivores throughout the Neogene, albeit not at the same time. Antelope-size herbivores dominated the continental assemblage until their decline during the Middle Miocene Climatic Optimum (MMCO). Horse-sized herbivores rose to dominate the

guild for the remainder of the Miocene following increases in occupancy over the MMCO. Rhino-size herbivores exhibited a more gradual net increase in occupancy over the Miocene but to a lesser extent that either of the prior categories. Overall and size-specific occupancies underwent notable declines over the Plio-Pleistocene, but the antelope-size and larger categories remain relatively common (>0.25). Meanwhile, chevrotain- and javelina-size herbivores exhibited occupancy estimates that gradually declined over the Neogene, with the former disappearing from the continent during the early Pliocene.

Occupancy as Informed by Generic Identity. We observed that most herbivore genera within an interval, regardless of size category, were rare (occupancy estimates <0.25) (Figure 10). Common genera (occupancy > 0.25) were limited in number ($n \leq 3$) within an interval and were restricted to antelope- to rhino-sized members of Equidae (e.g., *Equus*, *Dinohippus*, *Merychippus*, *Neohipparion*, and/or *Pliohippus*), Rhinocerotidae (e.g., *Teleoceras*), and/or Merycoidodontidae (e.g., *Merychyus*). Nonetheless, we observed that herbivore genera that persisted through an interval (bt) (Figure 11) typically exhibited relatively elevated occupancies compared to genera that were going extinct (bL). Persistent genera were roughly equally distributed across all size categories in Early Miocene but become restricted to antelope-, horse-, and rhino-size herbivores by the end of the Miocene. This was largely driven by the gradual net loss of relatively rare chevrotain- and javelina-size herbivores over much of the Miocene. Antelope-size and larger herbivores underwent a relatively steady rate of extinction throughout the Neogene, but this was initially offset by relatively high number of genera originating (Ft) in the early to middle Miocene. We must note that the notable extinction (bL and FL) of large-bodied genera within the 2Ma interval was due, in part, to analytical artifacts. The methods of

Foote (2000) assumes that the final interval that contains a taxon is its last occurrence whether this is a legitimate extinction or caused by reaching the end of the time series.

Discussion:

The species richness of large mammalian predators is positively correlated with that of their herbivore prey at regional to continental scales in both extant (Sandom et al., 2013) and fossil (Van Valkenburgh & Janis, 1993) ecosystems. Nonetheless, predator richness fails to decline to the same extent as that of their presumed herbivore prey over the North American Neogene. Van Valkenburgh and Janis (1993) suggested that the elevated predator-prey ratios of the Plio-Pleistocene could have been the result of a greater proportion of smaller-bodied omnivores and hypocarnivores within the predator guild over that interval. However, we observed in our first chapter that the predator guild was actually dominated by large hypercarnivores during this interval (Figure 3).

In the present study, we evaluated whether a change in the relative abundance of herbivores in North America could explain the relatively high number of large hypercarnivorous predators despite declining herbivore richness over the Middle to Late Miocene. We estimated the occupancy of the herbivore guild as a proxy for relative abundance. We observed that occupancy remained relatively high (>0.25) and stable over the Neogene when herbivores were considered as a whole or aggregated by body mass. As predicted, we observed high occupancy estimates within the three largest size-classes of herbivores throughout the Neogene. Conversely, occupancy estimates for the two smallest size classes, chevrotain- and javelina-size herbivores, were relatively low in comparison and declined throughout the Neogene. Changes in occupancy of each size category broadly paralleled the spread of open, grass-dominated habitats

over the Neogene. Through our investigation of individual genera, we observed that most genera were rare (<0.25) over the Neogene. Nonetheless, genera that persisted through an interval tended to have a relatively higher occupancy and body-size than those that went extinct.

Relative Abundance (Occupancy) of Herbivores as a Driver of Predator Evolutionary Response. Large terrestrial predators (e.g., wolf- and lion-size hypercarnivores) must take prey of near equal size (e.g., antelope-size) or larger to remain energetically profitable (Carbone et al., 1999). These relevantly-sized prey must be abundant on the landscape for these large predators to maintain the necessary rates of energy intake while minimizing energy expenditure (e.g., transport costs) (Carbone, Teacher & Rowcliffe, 2007). In extant ecosystems, large predator densities are broadly a reflection of the abundance of relevantly-sized prey (Orsdol, Hanby & Bygott, 1985; Laurenson, 1995; Stander et al., 1997; Fuller & Sievert, 2001; Karanth et al., 2004) wherein 10,000kg of prey supports approximately 90 kg of carnivoran biomass (Carbone & Gittleman, 2002). Nevertheless, the effect of prey abundance on predator richness is complex as mammalian predators often compete with one another for resources (Eaton, 1979; Van Valkenburgh, 1985, 1995). For example, the relative scarcity of *Lycaon pictus* (African wild dogs) within African ecosystems has been attributed to competitive limitation imposed by larger predators (e.g., *Panthera leo* [lion]and *Crocuta crocuta* [hyaena]) (Creel & Creel, 1996). Generally, lower prey abundances can lead to increased competition, and even competitive exclusion, amongst predator taxa, whereas high prey abundances can facilitate predator coexistence despite increases in predator densities (Périquet, Fritz & Revilla, 2015). Using first principles, we suggest that the elevated relative abundance (occupancy greater than 0.25) that we observed for the antelope-, horse-, and rhino-size herbivores could have plausibly facilitated the

coexistence of multiple wolf- to lion-size hypercarnivores despite declines in herbivore richness throughout the middle to late Miocene (Figures 1, 2, and 6, chapter 1 and 2).

Herbivore Commonness.

Overall Guild and Size-category Occupancy. Our observation that herbivores, as a whole or as size-specific groupings, were exceptionally common (occupancy greater than 0.25) throughout the Neogene appears to be broadly concordant with extant ecosystems (Elton, 1927; East, 1984; Robinson & Redford, 1986). Large (>10kg) mammalian herbivores (i.e., Artiodactyla, Perissodactyla, Proboscidea) comprise upwards of 58% of the total global biomass of wild terrestrial mammals (Greenspoon et al., 2023). Moreover, herbivore biomass is more heavily concentrated within antelope-size and larger taxa at both global and regional (southern and eastern Africa) scales (East, 1984; Greenspoon et al., 2023).

Occupancy of Individual Genera. Alternatively, we observed that individual genera, regardless of size class, were mostly rare (occupancy < 0.25), with the exception of a few (upwards of three) "common" genera, within an interval. Raia et al., (2006) similarly observed that large mammal species (e.g., artiodactyls, canids, felids, hyaenids, perissodactyls, proboscideans, and ursids) were generally rare in a paleocommuntity (PCOM) throughout the Plio-Pleistocene of Italy. Specifically, they observed that most PCOM's exhibited predominantly right-skewed occupancy-frequency distributions. Occupancy frequency distributions are scale-sensitive and tend to be unimodal and right-skewed at large spatial scales (e.g., entire geographic range of species, countries, continents) but bimodal at smaller, more local scales (e.g., cities, single habitats) (Gaston, 1996; McGeoch & Gaston, 2002; Suhonen et al., 2022). The underlying causes (e.g., habitat heterogeneity, spatial extent of taxa, etc.) for this

scale-sensitive pattern remain uncertain (McGeoch & Gaston, 2002; Gaston & He, 2011; White et al., 2023) but the skewed rarity observed within Raia et al., (2006) and this study was likely influenced, at least in part, by the spatial scale over which our analyses were performed.

The fact that the few common genera we observed were restricted to Merycoidodontidae, Equidae, and Rhinocerotidae was not surprising. These families have been reported to be geographically widespread and abundant at both continental, regional, and local scales (MacFadden, 1992; Wang & Secord, 2020; Cleaveland, Prothero & Welsh, 2022).

Herbivore Commonness and Persistence. Even though most genera within the Neogene were rare, we observed that genera that persisted through an interval tended to exhibit relatively higher occupancies than genera that went extinct which is consistent with comparable data from Neogene of Europe (Jernvall & Fortelius, 2004; Raia et al., 2006). A wide range of taxa (e.g., invertebrates, mammals, etc.) exhibited relatively low occupancies prior to extinction at both the species- and generic-level (Jernvall & Fortelius, 2004; Raia et al., 2006; Foote et al., 2007). The underlying mechanisms for this pattern are likely complex, but occupancy also exhibits a positive relationship with abundance and geographical range size (Brown, 1984; Hanski, Kouki & Halkka, 1993; Gaston & Blackburn, 2000), both predictors of extinction risk in extinct and extant invertebrates (Stanley, 1986; Jablonski, 1986; Payne & Finnegan, 2007; Payne et al., 2011; Harnik, Simpson & Payne, 2012; Saupe et al., 2015), mammals (Laurance, 1994), and flora (Turner et al., 1996). Typically, taxa that go extinct exhibit smaller geographical range sizes and/or lower abundances relative to those taxa that persist (Jablonski, 1986; Laurance, 1994; Turner et al., 1996; Payne & Finnegan, 2007; Payne et al., 2011; Harnik, Simpson & Payne, 2012; Saupe et al., 2015) because wider geographical range and higher abundances allow

taxa to be more resilient to short- and long-term environmental perturbations (e.g., natural or anthropogenic habitat fragmentation or loss) (Laurance, 1994; Harnik, Simpson & Payne, 2012). For example, taxa with wider geographical ranges have a greater chance of encompassing habitat that can act as refugia during adverse environmental conditions (Stewart & Lister, 2001; Saupe et al., 2015). It stands to reason that similar mechanisms were present over the North American Neogene and influenced the structure of the continental herbivore assemblage. Nevertheless, a thorough evaluation of how geographic range relates to occupancy and survival within the North American herbivore guild would be required to verify the influence of geographical range size, a task outside the scope of our current study.

Drivers of Herbivore Occupancy. Like Jernvall and Fortelius (2004), we observed that herbivores were not only common throughout the Neogene but also exhibited relatively stable occupancy estimates when considered as a whole. Pinpointing the underlying mechanism(s) facilitating this pattern is difficult when looking at the guild as a whole. Guild occupancy remained relatively stable despite declining herbivore richness (Figures 1, 2, and 6, chapter 1 and 2), taxonomic turnover (Figure 7, chapter 2) and changes in the herbivore niche (e.g., increased prevalence of hypsodonty) (Jernvall & Fortelius, 2004). However, subdividing the herbivore guild by body mass reveals that changes in size-specific occupancy broadly paralleled climatic (e.g., Middle Miocene climatic Optimum (MMCO; 17-14Ma) (Zachos, Dickens & Zeebe, 2008; Westerhold et al., 2020)) and vegetative events (e.g., spread of open, grass-dominated habitats, C_3/C_4 transition) (Strömberg, 2005, 2011; Strömberg & McInerney, 2011).

The decline in the occupancy of chevrotain- and javelina-size herbivores, much like their

decline in richness (Figures 2 and 6, chapter 1 and 2, respectively), roughly coincided with the continued spread of open, grass-dominated habitats over the Neogene (Janis, 2000; Strömberg, 2005, 2011). Chevrotain- and javelina-size herbivores are usually associated with, if not restricted to, habitats (e.g., shrublands, dense thickets) that contain higher quality forage (e.g., browse) due, in part, to their more restricted dietary tolerances (Bell, 1970; Jarman, 1974; Demment & Van Soest, 1985; du Toit & Owen-Smith, 1989; Bro-Jørgensen, 2008). Extant herbivores within these size classes are more constrained in their geographic distribution, and therefore occupancy, within African savanna ecosystems due to sharp declines in forage quality at habitat edges relative to more homogenous forest ecosystems (du Toit & Cumming, 1999). The occupancy of chevrotain- and javelina-size herbivores likely declined as they became rare within communities in response to the middle to late Miocene expansion of habitats dominated by low-quality forage (e.g., C_3 and then C_4 grasses) at the expense of higher-quality forage (Janis, Gordon & Illius, 1994; Strömberg & McInerney, 2011).

Concurrently, the continued spread of grass-dominated habitats likely contributed to the high, and broadly sustained, occupancy of the antelope-size and larger herbivores. Extant antelope-size and larger herbivores utilize a greater range of habitats and have larger geographic distributions than smaller herbivores within savanna ecosystems due to their wider dietary tolerances (du Toit & Owen-Smith, 1989; du Toit & Cumming, 1999). These larger-bodied herbivores can subsist on lower quality forage (e.g., grasses) since digestive capacity and passage rates increase with body size, relative to energy requirements (Parra, 1978; Demment & Van Soest, 1985; Illius & Gordon, 1992). These dietary tolerances would have allowed antelope-size or larger herbivores to remain at relatively high abundance compared to smaller herbivores as the

quality of their forage declined over the Miocene (Janis, Gordon & Illius, 1994; Strömberg & McInerney, 2011).

Interestingly, the occupancy of antelope- and horse-size herbivores broadly parallels the generic richness of brachydont and higher-crowned (mesodont and hypsodont) herbivores, respectively, over the Miocene (see Janis, Damuth & Theodor, 2000, 2002, 2004). Janis et al., (2002) inferred the diets of these herbivore genera, proposing that brachydont genera were browsers, mesodont genera were mixed-feeders, and hypsodont genera were either grazers or open-habitat mixed feeders. Following their dietary inferences, the decline in the occupancy antelope-size herbivores within the middle Miocene and subsequent stability of horse-size herbivore occupancy over the middle to late Miocene is not surprising because browse was becoming less plentiful as habitats became more open and dominated by grasses. (Strömberg, 2005, 2011).

All large-bodied (antelope-size and larger) herbivores show a notable reduction in occupancy within the Plio-Pleistocene, with the rhino-size herbivores being the only group to show a recovery. The cause of these reductions is not readily apparent, but these reductions do follow the C_3/C_4 transition. Reductions in occupancy could theoretically have been influenced, at least in part, by the continued decline in forage quality as grasslands transitioned from being dominated by C_3 grasses to more nutritionally poor C_4 grasses (Bernays & Hamai, 1987; Barbehenn & Bernays, 1992; Van Soest, 1994). Specifically, the expansion of C_4-dominated grasslands may have restricted habitats that could sustain antelope-size and horse-size herbivores, despite their dietary tolerances, leading to reduced geographic ranges. Rhino-size herbivores, despite an initial decline in occupancy, may have exhibited or developed sufficient

dietary tolerances to subsist on these nutritionally poor grasses due, in part, to their larger body sizes. Alternatively, the Plio-Pleistocene occupancy declines we observed also may have been a statistical artifact related to how occupancy is estimated. Occupancy will generally decline as the number of sites increases because the number of unoccupied sites will grow faster than the number of occupied sites (Foote, 2016). The number of sites within this study underwent a notable and sustained increase during the Plio-Pleistocene (Figure 50, Appendix E) which suggests that the declining occupancy we observed may be influenced, at least in part, by this statistical phenomenon.

Conclusion

In summary, we observed that occupancy of the herbivore guild remained relatively high (>0.25) throughout the North American Neogene, when we estimated occupancy for the entire guild, but each size category displayed different occupancy trends. The occupancy of smaller chevrotain- and javelina-size herbivores declined over the Neogene whereas antelope-size and larger herbivores remained at high occupancies, despite fluctuations. Changes in each size category broadly parallelled the spread of open, grass-dominated habitats and changes in the generic richness of browsing, mixed-feeding, and open feeding herbivores (Janis, Damuth & Theodor, 2000, 2002). Meanwhile, we observed that most genera were rare (occupancy less than 0.25) within an interval but genera that persisted exhibited relatively higher occupancies than genera that went extinct. We argue that the relative abundance of large (antelope-size and larger) herbivores on the North American continent could have buffered large mammalian predator richness from declining to the same degree as the herbivore richness over the middle to late Miocene and facilitated the coexistence of multiple large (>21 kg) hypercarnivores. Our

quantification of occupancy by body mass allowed us to begin to evaluate parallel trends of relative herbivore abundance in relation to parallel trend of predator and herbivore richness and major environmental transitions. Evaluation of these parallel trends and the mechanisms that underly these potential relationships could be further improved through the incorporation of dietary (e.g., hypsodonty indices) and locomotory (e.g., calcaneal gear ratio, metatarsal to femur ratio) traits. Additionally, our estimation of occupancy was simple and did not account for the influence of "false" absences or spatiotemporal differences in habitat (e.g., open versus closed). Going forward, evaluation of Neogene herbivore occupancy using modeling approaches (see MacKenzie and Kendall, 2002)) that incorporate detection probabilities in their estimation of occupancy and information regarding habitat and habitat heterogeneity (White et al., 2023) could improve our understanding of the drivers of herbivore abundance as well as the evolutionary response of the predator guild to changes in herbivore abundance.

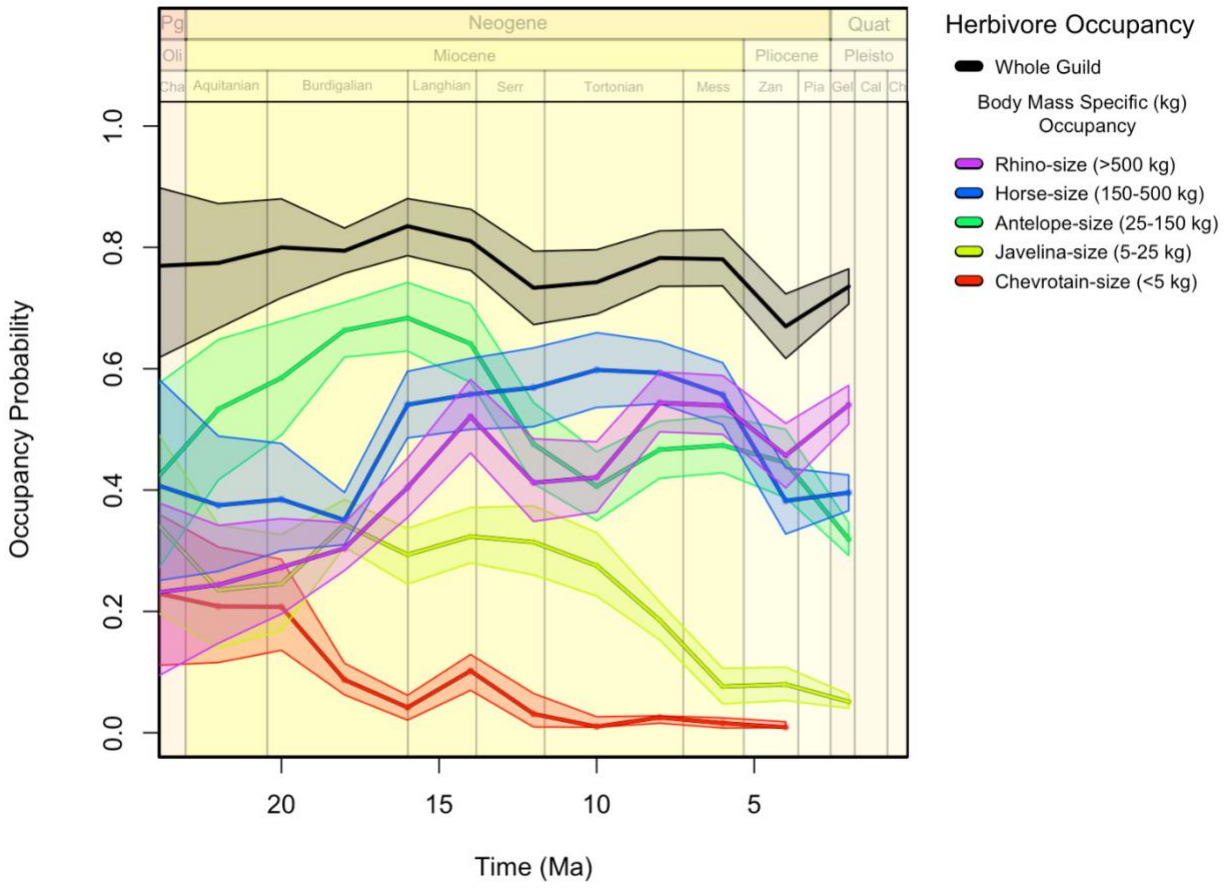

Figure 9. Occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

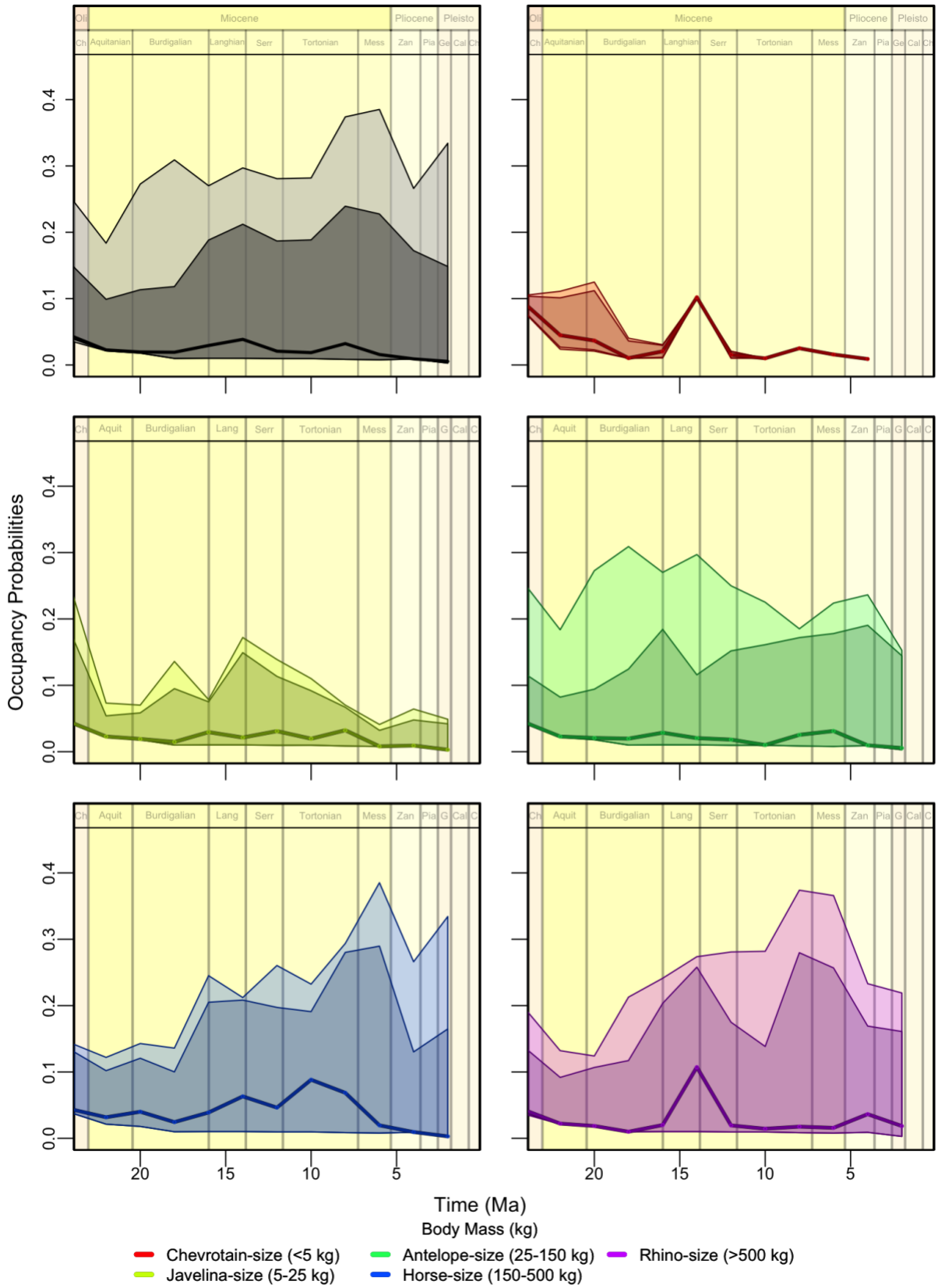
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Oli
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
G
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 10. Distribution of occupancy estimates for individual herbivore genera for the herbivore guild in its entirety (black) or individual size categories. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

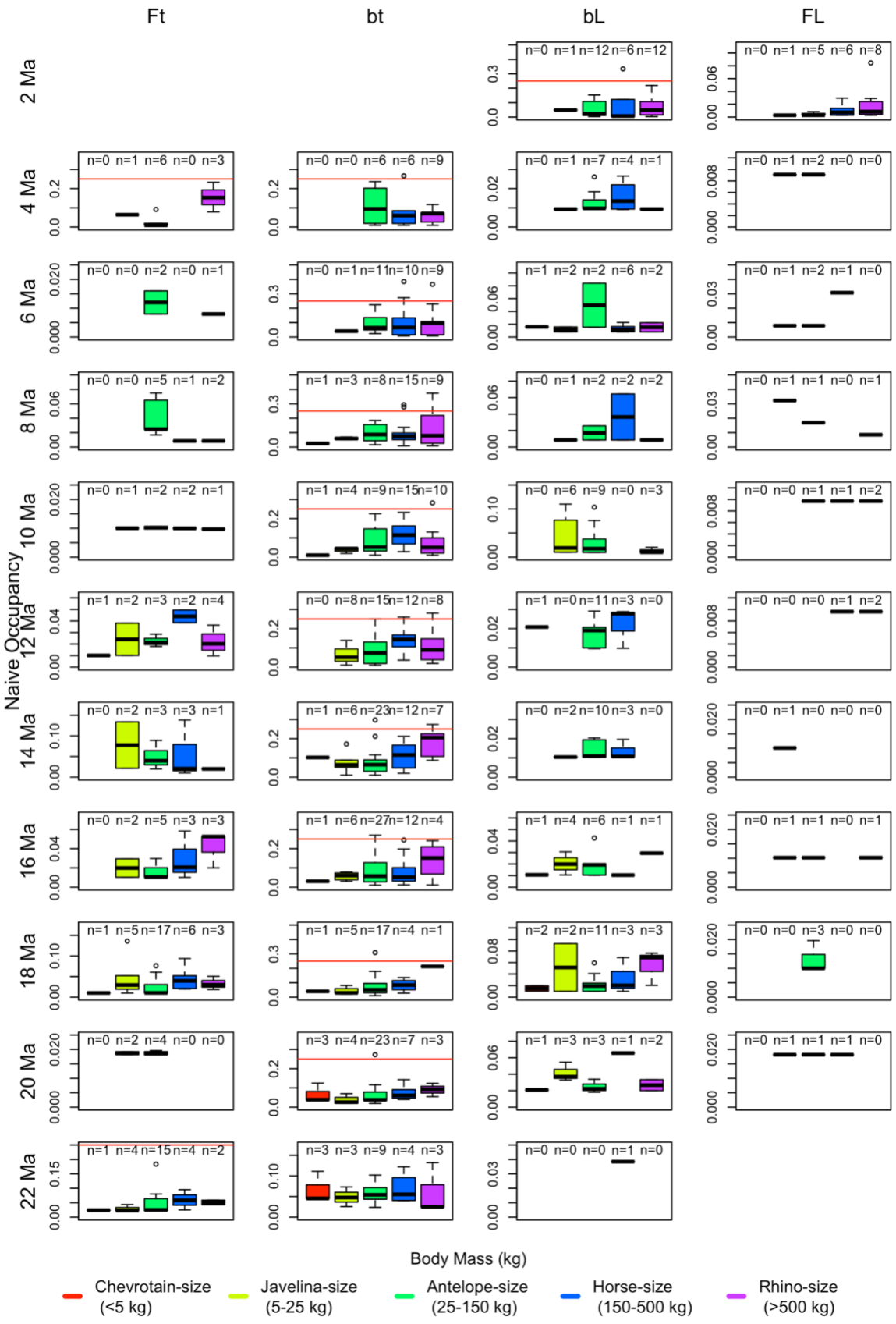
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 11. Distribution of generic occupancy of North American herbivores across the Neogene. Genera are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates. The horizontal red line marks the boundary between common (>0.25) and rare (<0.25) genera.

APPENDIX

Appendix A contains the data used to estimate herbivore body masses within this dissertation.

Appendix B contains figures and tables that are supplemental to the primary analyses of chapter 1.

Appendix C contains the methods, results, and discussion of sensitivity analyses related to chapter 1. These sensitivity analyses evaluate how our choice of the number of pseudoreplicate analyses, taxonomic scope, the body size categories used, our method of subsampling taxonomic occurrences, our assumption of taxa "range through" across their observed stratigraphic range, and temporal interval length influence our results.

Appendix D contains the methods, results, and discussion of sensitivity analyses related to chapter 2 and an evaluation of the observed differences between the result of chapter 2 and those of Juhn (Juhn, 2023). These sensitivity analyses evaluate how our choices of taxonomic level (species, genera), methods of subsampling, or the handling of range-through taxa influenced our results.

Appendix E contains the methods, results, and discussion of sensitivity analyses related to chapter 3. These sensitivity analyses evaluate how our choices of taxonomic level and our choice to aggregate Paleobiology Database collections into sites based on their geographical proximity.

APPENDIX A: DATASETS

All herbivore datasets are located on Proquest as supplementary files. The files are described as follows:

Supplementary Table 1 contains dental measurements of the cheek tooth row (upper and lower p2-m3) of Artiodactyla and Perissodactyla taken from scientific literature.

Supplementary Table 2 contains dental measurements of the cheek tooth row (p2-m3) for "archaic" ungulates and ungulate-like mammals (e.g., "Condylarthra", Dinocerata, Taeniodonta, Tillodontia, and Pantodonta) taken from the scientific literature.

Supplementary Table 3 contains dental measurements of the cheek tooth row (upper and lower p2-m3) of Artiodactyla and Perissodactyla taken from specimens housed at the American Museum of Natural History.

Supplementary Table 4 contains dental measurements of the cheek tooth row (upper and lower p2-m3) of Moschidae taken from specimens housed at the American Museum of Natural History.

Supplementary Table 5 contains information on how the regressions of Damuth (1990) were assigned to herbivore taxa. Regressions were typically assigned at the family-level, but individual genera were assigned their own regressions if they were not assigned to a family or when they exhibited different occlusal morphologies and/or hyposodonty compared to their confamiliars.

APPENDIX B: CHAPTER 1 SUPPLEMENTAL TABLES

Table 3. Spearman correlation matrix for the median species richness, with and without detrending (first-differences), within each size category for the large mammalian herbivore and combinations of the different dietary categories of the predator guild. Median species richness values were calculated across all 10,000 subsampled pseudoreplicates representative of actual median generic richness. Analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Median Richness Herbivores					First Differences Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg	<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (Hypercarnivore +Mesocarnivore)	<1 kg	0.331	-0.24	**-0.703****	-0.506	-0.301	0.577	-0.099	-0.376	-0.435	-0.302
	1 to 7gk	-0.329	**0.528***	**0.839*****	0.286	0.162	0.267	0.071	0.364	-0.119	0.023
	7 to 21 kg	0	**0.553***	0.402	-0.152	-0.18	0.176	0.453	0.134	-0.271	-0.038
	21 to 100 kg	-0.409	-0.302	0.047	**0.728*****	**0.762*****	-0.162	-0.042	0.081	0.462	0.213
	>100 kg	-0.88	0	0.385	0.471	0.536	-0.544	0.321	**0.674***	0.296	**0.627***
Predators (Hypercarnivore +Hypocarnivore)	<1 kg	**0.889***	**-0.889***	-0.289	-0.728	-0.437	0	0	**-0.894***	-0.447	0.344
	1to 7 kg	0.337	0.295	0.326	-0.449	**-0.543***	0.585	0.038	0.21	**-0.525***	-0.158
	7 to 21 kg	0.544	-0.201	0.045	-0.468	**-0.506***	**0.687***	-0.033	-0.168	-0.413	-0.308
	21 to 100 kg	**-0.7***	-0.163	0.206	**0.823*****	**0.87*****	0.065	0.094	0.194	0.45	0.296
	>100 kg	-0.492	0.479	**0.768****	0.54	0.405	-0.943	0.352	**0.695***	0.601	0.581
Predators (Mesocarnivore +Hypocarnivore)	<1 kg	-0.671	-0.107	0.024	0.221	0.345	--	0.106	0	0	-0.196
	1 to 7gk	**-0.639***	**0.768****	**0.963*****	**0.688****	**0.504***	-0.455	**0.606***	**0.782*****	**0.556***	0.475
	7 to 21 kg	-0.531	0.372	0.285	**0.538***	**0.531***	**-0.786***	0.327	0.098	0.187	0.084
	21 to 100 kg	--	--	--	--	--	--	--	--	--	--
	>100 kg	--	--	--	--	--	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 4. Intraguild Spearman correlation matrices for the detrended median species richness within each size category of the predator guild when all diets are considered together ("All Cenozoic"). Median species richness were calculated over 10,000 subsampled pseudoreplicates and a representative of actual median species richness. The correlations represent data covering the entire Cenozoic (~66 to 0 Ma).

		Predators				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Predators	<1 kg	--	0.281	0.27	0.276	-0.327
	1 to 7 kg	0.281	--	0.224	-0.093	0.272
	7 to 21 kg	0.27	0.224	--	-0.34	0.337
	21 to 100 kg	0.276	-0.093	-0.34	--	-0.003
	>100 kg	-0.327	0.272	0.337	-0.003	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Intraguild Spearman correlation matrices for the detrended median species richness within each size category and each of the predator dietary categories and their combinations. Median species richness were calculated over 10,000 subsampled pseudoreplicates and a representative of actual median species richness. These predator and herbivore correlations represent data covering the Oligocene to present (~34 Ma to 0 Ma).

		Hypercarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	--	--	-0.5	-0.5	--
	1 to 7 kg	--	--	0.748	0	-1
	7 to 21 kg	-0.5	0.748	--	0.434	**-0.843***
	21 to 100 kg	-0.5	0	0.434	--	-0.139
	>100 kg	--	-1	**-0.843***	-0.139	--
Mesocarnivores	<1 kg	**-1*****	--	0.612	0.056	-0.354
	1to 7 kg	--	0.5	-0.285	0.22	**0.719***
	7 to 21 kg	-0.5	0	-0.342	-0.311	-0.084
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	0	0.748	0.316	0.042	-0.483
	7 to 21 kg	--	--	--	-0.544	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	--	--	0.6	-0.345	-0.683
	1 to 7 kg	--	0.693	0.159	0.233	-0.335
	7 to 21 kg	0	**0.816***	0.447	-0.225	-0.196
	21 to 100 kg	--	0	0.374	**0.945*****	-0.165
	>100 kg	--	1	-0.272	0.025	0.468
Hypercarnivores +Hypocarnivores	<1 kg	**1*****	0	0.344	-0.75	-1
	1 to 7 kg	-0.5	**0.816***	0.418	-0.045	**-0.65***
	7 to 21 kg	0	**0.832***	**0.908*****	0.423	-0.59
	21 to 100 kg	-0.5	0	0.434	**1*****	-0.139
	>100 kg	--	-1	**-0.843***	-0.139	**1*****
Mesocarnivores +Hypocarnivores	<1 kg	**-1*****	--	0.612	0.056	-0.354
	1 to 7 kg	--	0.5	-0.285	0.22	**0.719***
	7 to 21 kg	-0.5	0	-0.342	-0.311	-0.084
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Continued.

		Mesocarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	**-1*** **	--	-0.5	--	--
	1 to 7 kg	--	0.5	0	--	--
	7 to 21 kg	0.612	-0.285	-0.342	--	--
	21 to 100 kg	0.056	0.22	-0.311	--	--
	>100 kg	-0.354	**0.719***	-0.084	--	--
Mesocarnivores	<1 kg	--	**-0.645***	0.6	--	--
	1to 7 kg	**-0.645***	--	0.008	--	--
	7 to 21 kg	0.6	0.008	--	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	-0.274	0.188	-0.23	--	--
	7 to 21 kg	**1*** **	-0.544	0.577	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	**0.787****	**-0.825****	**0.612***	--	--
	1 to 7 kg	**-0.69***	**0.571***	-0.173	--	--
	7 to 21 kg	0.396	0.074	0.505	--	--
	21 to 100 kg	0.142	0.152	-0.248	--	--
	>100 kg	-0.288	0.499	0.041	--	--
Hypercarnivores +Hypocarnivores	<1 kg	**-1*** **	-0.791	-0.645	--	--
	1 to 7 kg	-0.236	0.115	-0.179	--	--
	7 to 21 kg	0.312	-0.223	-0.468	--	--
	21 to 100 kg	0.056	0.22	-0.311	--	--
	>100 kg	-0.354	**0.719***	-0.084	--	--
Mesocarnivores +Hypocarnivores	<1 kg	**1*** **	**-0.645***	0.6	--	--
	1 to 7 kg	**-0.645***	**1*** **	0.008	--	--
	7 to 21 kg	0.6	0.008	**1*** **	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Continued.

		Hypocarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	--	0	--	--	--
	1 to 7 kg	--	0.748	--	--	--
	7 to 21 kg	--	0.316	--	--	--
	21 to 100 kg	--	0.042	-0.544	--	--
	>100 kg	--	-0.483	--	--	--
Mesocarnivores	<1 kg	--	-0.274	**1*** **	--	--
	1to 7 kg	--	0.188	-0.544	--	--
	7 to 21 kg	--	-0.23	0.577	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	--	--	-0.544	--	--
	7 to 21 kg	--	-0.544	--	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	--	-0.306	**1*** **	--	--
	1 to 7 kg	--	**0.711****	-0.544	--	--
	7 to 21 kg	--	0.241	0	--	--
	21 to 100 kg	--	-0.105	0	--	--
	>100 kg	--	0.031	0.5	--	--
Hypercarnivores +Hypocarnivores	<1 kg	--	-0.459	--	--	--
	1 to 7 kg	--	**0.918*****	-0.544	--	--
	7 to 21 kg	--	0.391	-0.333	--	--
	21 to 100 kg	--	0.042	-0.544	--	--
	>100 kg	--	-0.483	--	--	--
Mesocarnivores +Hypocarnivores	<1 kg	--	-0.274	**1*** **	--	--
	1 to 7 kg	--	0.188	-0.544	--	--
	7 to 21 kg	--	-0.23	0.577	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Continued.

		Hypercarnivores + Mesocarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	--	--	0	--	--
	1 to 7 kg	--	0.693	**0.816***	0	1
	7 to 21 kg	0.6	0.159	0.447	0.374	-0.272
	21 to 100 kg	-0.345	0.233	-0.225	**0.945*****	0.025
	>100 kg	-0.683	-0.335	-0.196	-0.165	0.468
Mesocarnivores	<1 kg	**0.787****	**-0.69***	0.396	0.142	-0.288
	1to 7 kg	**-0.825****	**0.571***	0.074	0.152	0.499
	7 to 21 kg	**0.612***	-0.173	0.505	-0.248	0.041
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	-0.306	**0.711****	0.241	-0.105	0.031
	7 to 21 kg	**1*****	-0.544	0	0	0.5
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	--	**-0.654***	**0.61***	-0.276	-0.34
	1 to 7 kg	**-0.654***	--	0.014	0.118	-0.095
	7 to 21 kg	**0.61***	0.014	--	-0.311	0.244
	21 to 100 kg	-0.276	0.118	-0.311	--	-0.003
	>100 kg	-0.34	-0.095	0.244	-0.003	--
Hypercarnivores +Hypocarnivores	<1 kg	0.816	-0.5	0.344	-0.791	1
	1 to 7 kg	-0.165	**0.707****	0.246	-0.185	-0.086
	7 to 21 kg	0.259	0.113	0.402	0.41	-0.058
	21 to 100 kg	-0.345	0.233	-0.225	**0.945*****	0.025
	>100 kg	-0.683	-0.335	-0.196	-0.165	0.468
Mesocarnivores +Hypocarnivores	<1 kg	**0.787****	**-0.69***	0.396	0.142	-0.288
	1 to 7 kg	**-0.825****	**0.571***	0.074	0.152	0.499
	7 to 21 kg	**0.612***	-0.173	0.505	-0.248	0.041
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Continued.

		Hypercarnivores + Hypocarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	**1*** **	-0.5	0	-0.5	--
	1 to 7 kg	0	**0.816***	**0.832***	0	**-1***
	7 to 21 kg	0.344	0.418	**0.908*****	0.434	-0.843
	21 to 100 kg	-0.75	-0.045	0.423	**1*****	-0.139
	>100 kg	-1	**-0.65***	-0.59	-0.139	**1*****
Mesocarnivores	<1 kg	**-1*****	-0.236	0.312	0.056	-0.354
	1to 7 kg	-0.791	0.115	-0.223	0.22	**0.719***
	7 to 21 kg	-0.645	-0.179	-0.468	-0.311	-0.084
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	-0.459	**0.918*****	0.391	0.042	-0.483
	7 to 21 kg	--	-0.544	-0.333	-0.544	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	0.816	-0.165	0.259	-0.345	-0.683
	1 to 7 kg	-0.5	**0.707****	0.113	0.233	-0.335
	7 to 21 kg	0.344	0.246	0.402	-0.225	-0.196
	21 to 100 kg	-0.791	-0.185	0.41	**0.945*****	-0.165
	>100 kg	1	-0.086	-0.058	0.025	0.468
Hypercarnivores +Hypocarnivores	<1 kg	--	-0.471	0.344	-0.75	-1
	1 to 7 kg	-0.471	--	0.401	-0.045	**-0.65***
	7 to 21 kg	0.344	0.401	--	0.423	-0.59
	21 to 100 kg	-0.75	-0.045	0.423	--	-0.139
	>100 kg	-1	**-0.65***	-0.59	-0.139	--
Mesocarnivores +Hypocarnivores	<1 kg	**-1*****	-0.236	0.312	0.056	-0.354
	1 to 7 kg	-0.791	0.115	-0.223	0.22	**0.719***
	7 to 21 kg	-0.645	-0.179	-0.468	-0.311	-0.084
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 5. Continued.

		Mesocarnivores + Hypocarnivores				
		<1 kg	1 to 7 kg	7 to 21 kg	21 to 100 kg	>100 kg
Hypercarnivores	<1 kg	**-1*** **	--	-0.5	--	--
	1 to 7 kg	--	0.5	0	--	--
	7 to 21 kg	0.612	-0.285	-0.342	--	--
	21 to 100 kg	0.056	0.22	-0.311	--	--
	>100 kg	-0.354	**0.719***	-0.084	--	--
Mesocarnivores	<1 kg	**1*** **	**-0.645***	0.6	--	--
	1to 7 kg	**-0.645***	**1*** **	0.008	--	--
	7 to 21 kg	0.6	0.008	**1*** **	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypocarnivores	<1 kg	--	--	--	--	--
	1 to 7kg	-0.274	0.188	-0.23	--	--
	7 to 21 kg	**1*** **	-0.544	0.577	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Hypercarnivores +Mesocarnivores	<1 kg	**0.787****	**-0.825****	**0.612***	--	--
	1 to 7 kg	**-0.69***	**0.571***	-0.173	--	--
	7 to 21 kg	0.396	0.074	0.505	--	--
	21 to 100 kg	0.142	0.152	-0.248	--	--
	>100 kg	-0.288	0.499	0.041	--	--
Hypercarnivores +Hypocarnivores	<1 kg	**-1*** **	-0.791	-0.645	--	--
	1 to 7 kg	-0.236	0.115	-0.179	--	--
	7 to 21 kg	0.312	-0.223	-0.468	--	--
	21 to 100 kg	0.056	0.22	-0.311	--	--
	>100 kg	-0.354	**0.719***	-0.084	--	--
Mesocarnivores +Hypocarnivores	<1 kg	--	**-0.645***	0.6	--	--
	1 to 7 kg	**-0.645***	--	0.008	--	--
	7 to 21 kg	0.6	0.008	--	--	--
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 6. Intraguild Spearman correlation matrix for the median species richness between each size category of the large mammalian herbivores. Median species richness were calculated over 10,000 subsampled pseudoreplicates and a representative of actual median species richness. These correlations represent data covering the entire Cenozoic (~66 to 0 Ma). Size categories are the same as Table 1.

	<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
<5 kg	--	0.375	-0.227	-0.309	-0.148
5-25 kg	0.375	--	**0.516****	0.255	0.267
25-150 kg	-0.227	**0.516****	--	**0.448***	**0.533****
150-500 kg	-0.309	0.255	**0.448***	--	**0.547****
>500 kg	-0.148	0.267	**0.533****	**0.547****	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

APPENDIX C: CHAPTER 1 SENSITIVITY ANALYSES

Sensitivity Analyses: Number of Pseudoreplicates

Methods. We determined the sensitivity of our results to the number of pseudoreplicates analyses by calculating the standard error of detrended correlation coefficient at successively greater numbers of pseudoreplicate analyses. Secondly, we repeatedly calculated the standard error of the correlation coefficients using the stats package (R Core Team, 2024) in R. From our complete sample of 10,000 pseudoreplicate analyses, we subsampled successively greater number of pseudoreplicates from 1 to 10,000. At each subsampling level (e.g., 1000 pseudoreplicates) we randomly sampled the correlation coefficients of individual pseudoreplicates to create a subsample with that particular number of pseudoreplicates, then calculated the standard error of the detrended correlation coefficients for the subset. A standard error that approaches the origin and lacks notable fluctuations indicates that the number of replicates used in our analyses was sufficient to accurately capture correlation coefficients. Alternatively, fluctuating or increasing standard error over cumulative replicates would indicate that more pseudoreplicates were required to reach stability in our parameter estimates.

Results and Discussion. The standard error of correlation coefficients for detrended species richness became rapidly constrained with increasing number of sampled pseudoreplicates for all size category pairings (Figure 12). This suggests that the 10,000 pseudoreplicates we used in our analyses were more than sufficient to ensure stable correlation coefficients.

Sensitivity Analyses: Taxonomic Level of Analysis

Methods. Our choice to analyze occurrences at the species level might also influence

our results. Previous studies have questioned the validity of species-level analyses due to the dubious nature of some species identifications (Prothero, 2015), and genus-level identifications might be more reliable. Furthermore, analysis at the species-level excludes numerous occurrences identified at the generic level., but indeterminate at the species level (e.g., Equus sp.). For example, the terrestrial North American fossil record within the PBDB has ~34,963 total occurrences of Mammalia assigned at the species level with an additional ~11,932 occurrences accepted at the generic level (as of 9/27/2023). We repeated our analyses at generic levels to determine whether this influenced our results.

Results and Discussion. Analyses at the species-and genus-level showed largely similar total and body-size-specific richness trends (Figure 13), but some notable differences were observed. For example, the peak species richness of predators occurs within the Late Oligocene (between 25 and 23 Ma), but peak generic richness occurs later, during to the early and late Miocene (between 21 Ma and 19 Ma and 11 Ma and 9 Ma, respectively). Overall, generic richness showed reduced amplitude of fluctuations in total and size-specific richness over the Cenozoic for both guilds, in comparison with the same analyses at the species level.

Correlation strength and significance of multiple body size category pairings was also found to differ between the generic and species level (All Cenozoic) analyses (Table 7). Based on genera, increased correlation strength and/or significance were identified for the wild-cat- to wolf-size predators with the javelina-, antelope- and horse-size herbivores. However, the correlation between the lion-size predators and the rhino-size herbivores lost significance and became weaker in the generic analyses.

Sensitivity Analyses: Body Size Categories

Methods. As described above, we binned herbivore taxa into previously published body size categories, which have been justified theoretically as ecologically meaningful based on observations of extant taxa (Janis, 2000; Juhn, 2023). Nevertheless, these subjective categories have not been established empirically, so we also estimated the impact of both the number of body mass categories and the placement of their boundaries using unsupervised clustering methods. For these analyses, we used the logarithm of body masses ($\log_{10}$(kg)) of extant ungulates and carnivorans from the MOM dataset (v. 10.2; Smith et al., 2003). We excluded two entries, *Moschus fuscus* (Index 1924) and *Potamochoerus larvatus* (Index 3081), as their listed weights in grams appeared to be typos when compared to other members of their species within the dataset. We performed a one-dimensional *K*-means test using the cluster package in R (Maechler et al., 2022). We estimated the optimal number of categories using an elbow test with the optimal number of breaks being calculated using the pathviewr package in R (Baliga, Armstrong & Press, 2021). The "break" point between two categories was calculated by taking the average of the species that represented the extremes of adjacent clusters (e.g., the minimum of the wildcat-size category and the maximum of the weasel-sized category). We then repeated our analyses using fossil taxa assigned to these statistically determined categories.

Results and Discussion. Unsupervised clustering identified five distinct body size categories within both extant predators and herbivores (Figure 14a and d; Table 8). These body size categories for the herbivores were largely similar to those of Janis (2000), but we note that differences in the placement of category boundaries (Figure 14b and c). For example, the placement of the upper boundary of the smallest herbivore size category differed slightly

between Janis (2000) and our unsupervised kmeans clustering (i.e., 5 kg versus approximately 11.4 kg, respectively) whereas the absolute difference between the lower bound of largest herbivore size category differed more substantially (i.e., 500 kg versus approximately 451.86 kg, respectively). Predator body mass categories varied more substantially between those of Juhn (2023) and the unsupervised kmeans clustering (Figure 14e and f). The wolf- (21-100kg) and lion-size (>100kg) categories of Juhn (2023) were largely combined into a single category (>27.1 kg) whereas the wild-cat-size (1-7 kg) category was divided into two separate categories (0.6-1.96 kg and 1.96-5.76 kg).

Correlation strength and significance between the unsupervised size categories were mostly different from the primary analysis (Table 9). Nonetheless, significant correlations were observed between the largest predator category (>27.1 kg) and herbivores between 115.28 and 451.66 kg, a result that is roughly equivalent to wolf- and lion-size predator correlating with antelope- and horse-size herbivores within the "All Cenozoic" analysis when predator diets are considered in aggregate.

Sensitivity Analyses: Preservation Rate

Methods. The rate at which taxa, mammals included, have been preserved and subsequently sampled within the fossil record has not remained consistent through time (Alroy, 1999; Foote, 2001). The uneven distribution of fossil occurrences through time can hamper and bias inferences made of evolutionary patterns if not corrected for using analytical methods (e.g., subsampling) (Foote & Raup, 1996; Miller & Foote, 1996b). We evaluated how well sampled the Cenozoic mammal fossil record is using the sampling probability parameter within the three timer models of Alroy (2008, 2014). We calculated the sampling probability over all

pseudoreplicates within our analysis. We used these results to inform our decision on whether to apply subsampling to the PBDB occurrences.

Results and Discussion. We observed that sampling probabilities for Mammalia varied over the North American Cenozoic (Figure 15). We corrected for the unequal distribution of occurrences over the Cenozoic by applying subsampling in our primary analyses.

Sensitivity Analyses: Subsampling and Range Through

Methods. We evaluated the influence of subsampling and making taxa "range through" intervening intervals by performing our analyses without those procedures and comparing the results to our primary analysis.

Results and Discussion. We observed that subsampling and including range-through taxa did little to affect the overall pattern of species richness (Figures 16 to 18). Adding range-through taxa into intervening intervals largely reduced interval-to-interval variation of the total and size-specific richness. We observed that subsampling substantially reduced richness within most intervals, but the overall pattern of median species richness was largely retained.

We observed a greater number of significant correlations between predator and prey richness without subsampling and/or using only sampled taxa (i.e., not assuming range throughs) (Table 10 to Table 12). Novel positive correlations were generally weak to moderate in strength whereas the negative correlations were generally moderate to strong in strength. Existing correlations between lion-size predators and antelope-size herbivores strengthened in the absence of subsampling when diets were analyses in aggregate or restricted to hypercarnivorous taxa.

Alternatively, existing correlations for wild-cat-size mesocarnivores were observed to vary only slightly with the removal of subsampling.

Sensitivity Analyses: Subsampling and Temporal Interval Length

Methods. The effect of subsampling was further evaluated alongside temporal bin length because the bins with the fewest occurrences determined the subsampling quota for a given pseudoreplicate. Shorter temporal intervals usually resulted in smaller numbers of occurrences within each interval, exacerbating the influence of the smallest bin on the overall subsampling quota, increasing the risk of the random subsample lacking sufficient occurrences to properly capture the richness of predators and/or herbivores present by the loss of statistical power (McMurdie & Holmes, 2014; Weiss et al., 2017; Cameron et al., 2021), muting of richness trends (Alroy, 2010), and/or changing rank order of community richness (Gotelli & Colwell, 2001). To evaluate this issue, we compared the within-interval number of raw and subsampled total species richness over temporal intervals of 0.5 Mya to 3 Mya lengths. Moreover, we also calculated the correlation coefficient of detrended median species richness to determine how temporal interval length was affecting our results.

Results and Discussion. We observed a greater number of significant, albeit weak, positive correlations within the analyses conducted using shorter time intervals (0.5 and 1 Ma) (Table 13). Lion-size predators and antelope-size herbivores were observed to have significant moderate to strong correlation for the 1 Mya to 3 Mya interval analyses. Despite having an increase in the number of positive correlations the smallest bin sizes (0.5 Mya) failed to capture changes in species richness over the Oligocene and Neogene (Figure 19). We observed that subsampling reduced the total richness of the 0.5 Mya length intervals to the point where the

increased richness of Oligocene and Neogene was obscured in both guilds. Our use of 2 Ma intervals adequately preserves median species richness trends while simultaneously allowing for ecologically significant positive correlations to be identified.

P-Value Correction for Multiple Tests

Methods. We evaluated the incidence of false-positives within our correlation p-values by performing a Bonferroni correction and comparing the results to our primary analysis.

Results and Discussion. Our application of the Bonferroni correction on our primary analysis resulted in the loss of significance for most correlations within our primary analyses (Table 14). Only the correlation between the wild-cat size mesocarnviores and antelope-size herbivores remained significant.

Herbivores
Chevrotain-size
(<5 kg)
Javelina-size
(5-25 kg)
Antelope-size
(25-150 kg)
Horse-size
(150-500 kg)
Rhino-size
(>500 kg)
Predators
Weasel-size
(<1 kg)
Wild-cat-size
(1-7 kg)
Coyote-size
(7-21 kg)
Wolf-size
(21-100 kg)
Lion-size
(>100 kg)
0
5000
10000
Number of Cumulative Pseudoreplicates

Figure 12. Standard Error of Spearman Correlation coefficients for detrended median species richness of large mammalian herbivore and prey guilds over an increasing number of sampled observations. Increasing the number of randomly sampled pseudoreplicates (with replacement) leads to a rapid decrease in standard error within correlation coefficients between the herbivore and predator guilds.

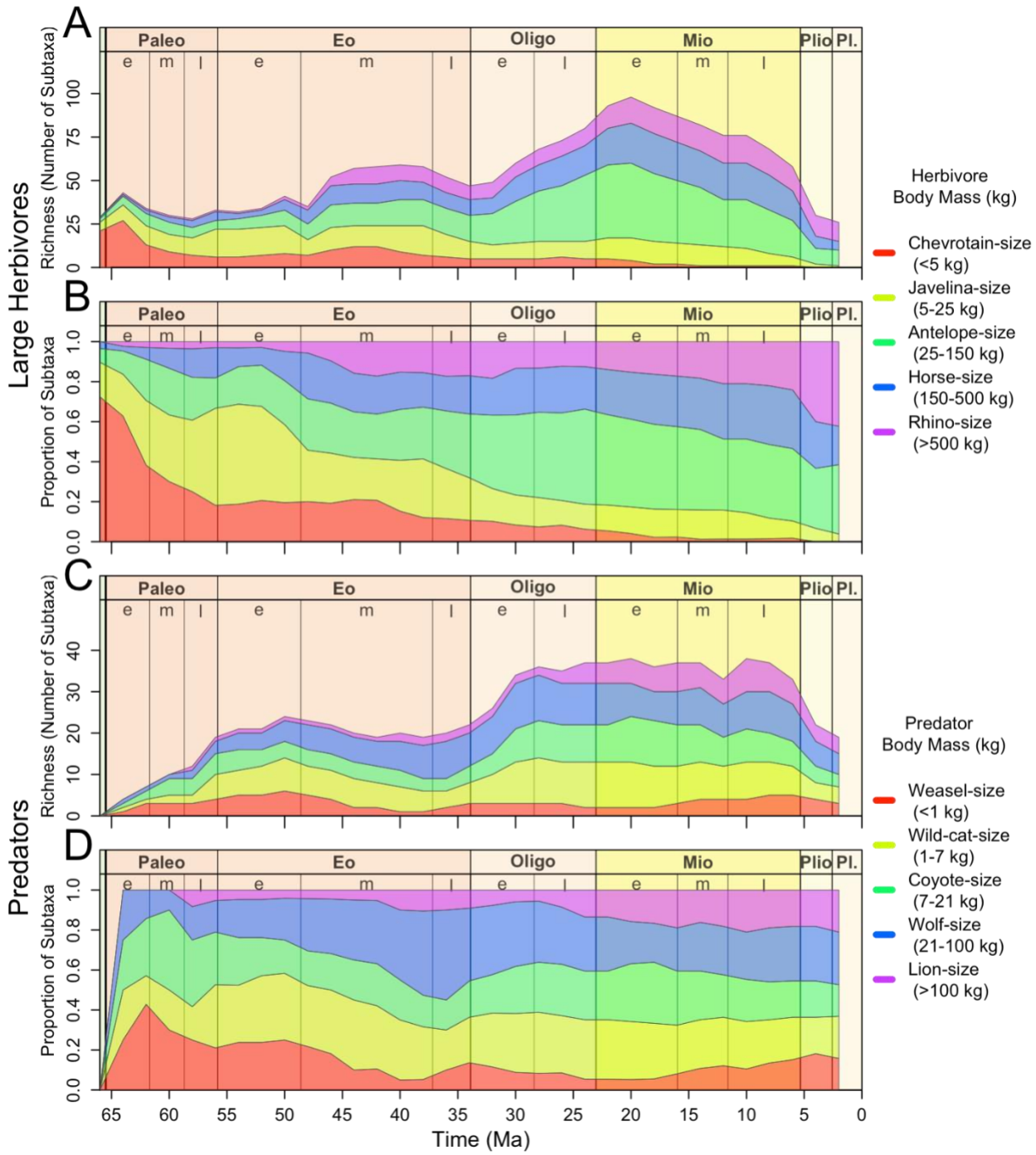
A
B
C
D
Large Herbivores
Predators
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Proportion of Subtaxa
Herbivore Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)
Predator Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)
Time (Ma)

Figure 13. Total (A and C) and proportional (B and D) median generic richness of both the large mammalian herbivore and predator guilds through the Cenozoic. Median generic richness values were calculated across all 10,000 subsampled pseudoreplicates representative of actual median generic richness. Each guild is subset into distinct size categories following Janis (2000) for the large herbivores and by the author for the predator guild (Table 1).

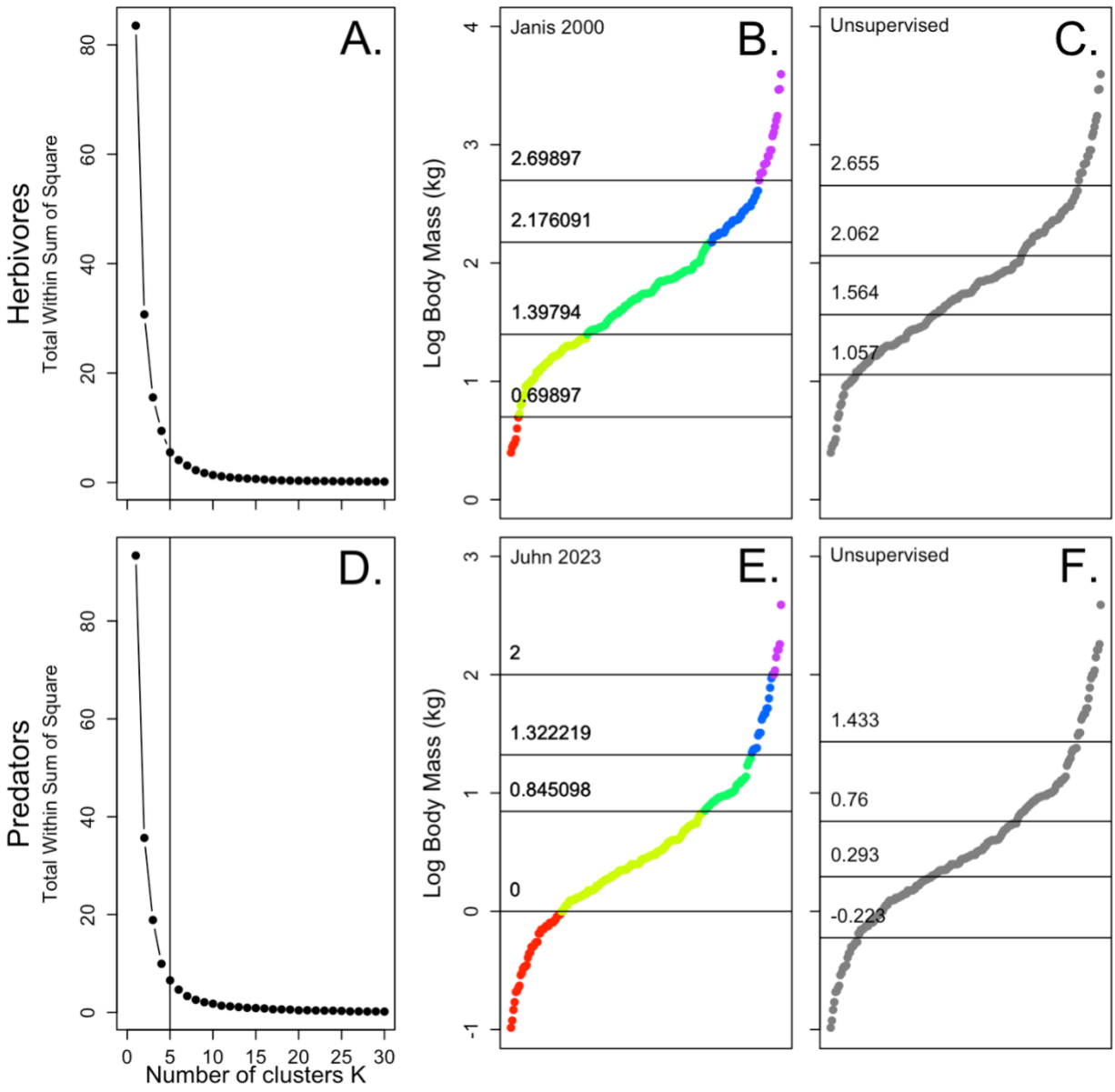

Figure 14. Comparison of body size categories taken from published sources (B and E) and those estimated using unsupervised kmeans (C and F) clustering for extant large herbivores (top) and predator (bottom). Elbow tests (A and D) indicate that optimal clustering occurs with five clusters for both guilds.

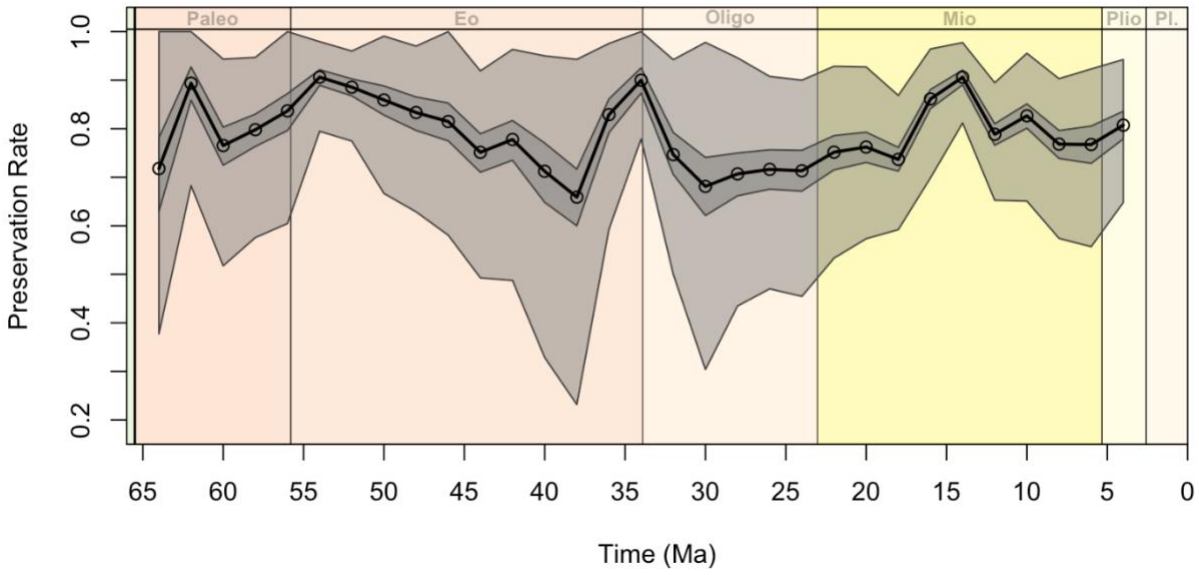

Figure 15. Sampling probability of Mammalia over the North American Cenozoic. Sampling probability was calculated across 10,000 pseudoreplicates using the three timer models of Alroy (2008, 2014) and occurrences drawn from the Paleobiology Database. The solid black line is the median sampling rate across all pseudoreplicates. The surrounding dark grey region represents the 25% and 75% confidence intervals whereas the light grey region represents the minimum and maximum bounds of observed sampling probabilities.

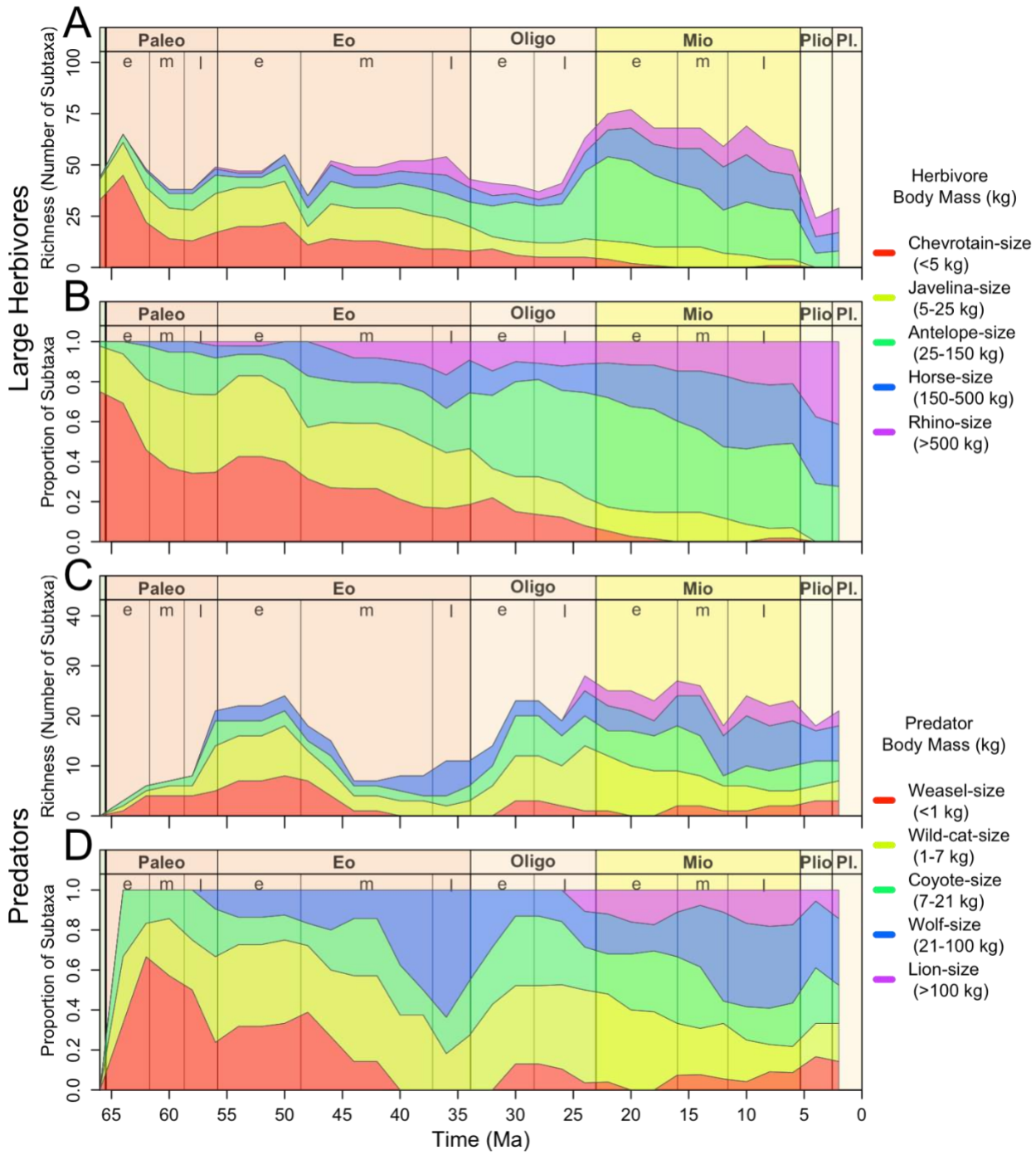
A
B
C
D
Large Herbivores
Predators
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Proportion of Subtaxa
Time (Ma)
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Herbivore Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)
Predator Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)

Figure 16. Total (A and C) and proportional (B and D) median species richness of both the large mammalian herbivore and predator guilds through the Cenozoic. Median species richness values were compiled across all 10,000 pseudoreplicates with subsampling being performed but no taxa being "ranged through" intervening intervals. Median species richness values are representative and are not exact due to subsampling. Each guild is subset into distinct size categories following Janis (2000) for the large herbivores and by the author for the predator guild (Table 1).

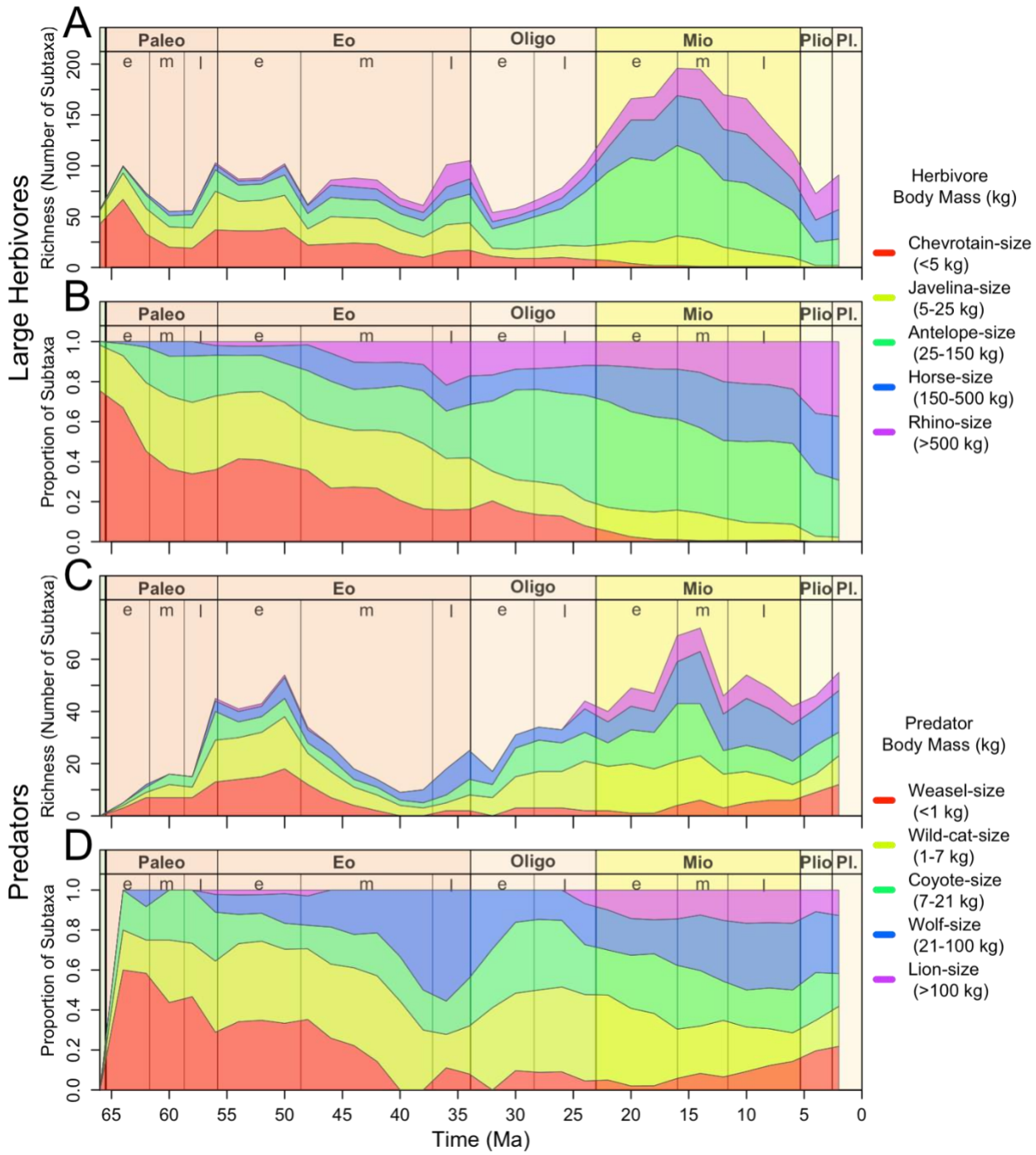
A
B
C
D
Large Herbivores
Predators
Richness (Number of Subtaxa)
Proportion of Subtaxa
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Time (Ma)
Herbivore Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)
Predator Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)

Figure 17. Total (A and C) and proportional (B and D) median species richness of both the large mammalian herbivore and predator guilds through the Cenozoic. Median species richness values were compiled across all 10,000 pseudoreplicates with no subsampling being performed but taxa were "ranged through" intervening intervals. Median species richness values are representative and not exact due to subsampling. Each guild is subset into distinct size categories following Janis (2000) for the large herbivores and by the author for the predator guild (Table 1).

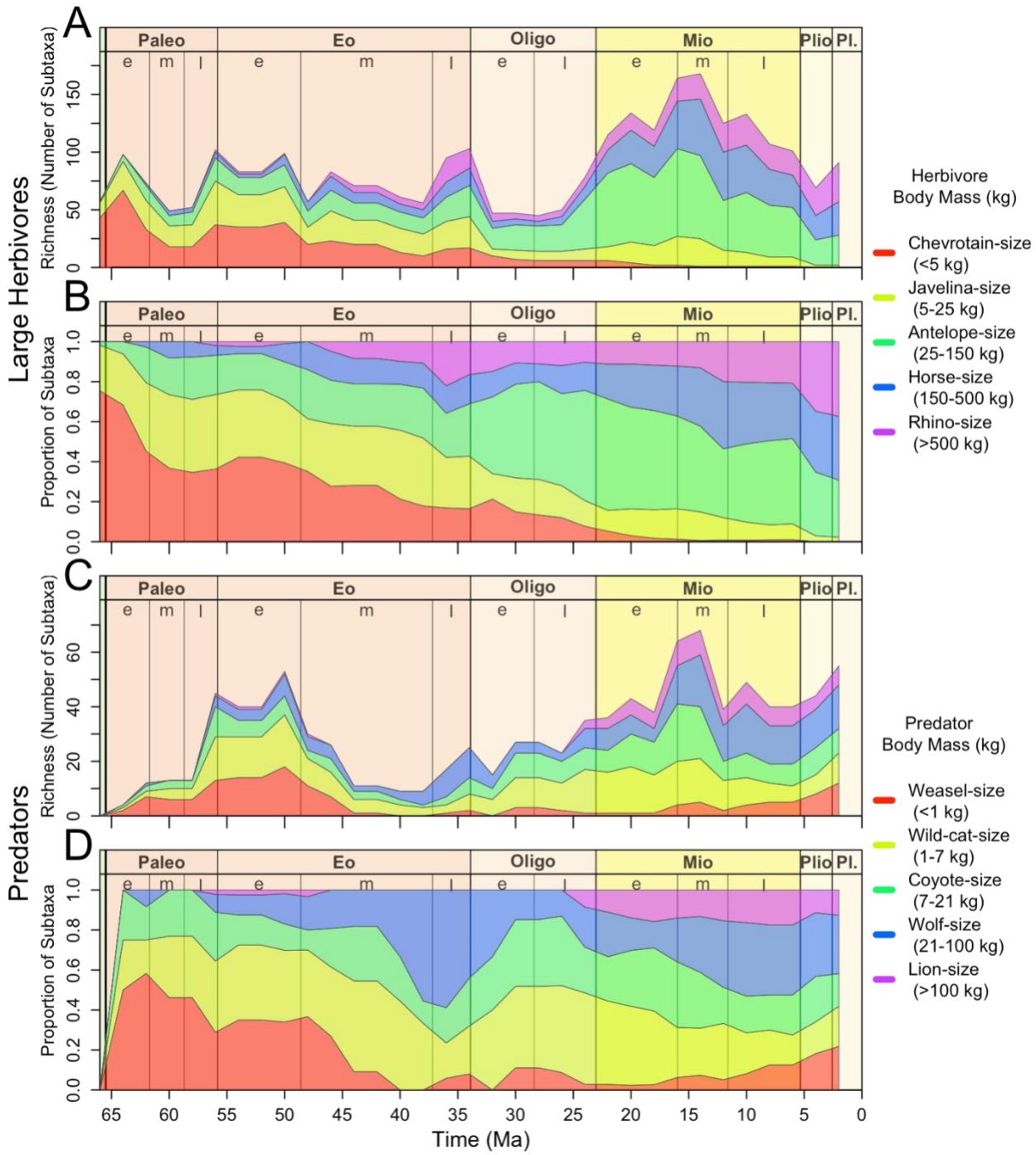
A
B
C
D
Large Herbivores
Predators
Richness (Number of Subtaxa)
Proportion of Subtaxa
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Time (Ma)
Herbivore Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)
Predator Body Mass (kg)
Weasel-size (<1 kg)
Wild-cat-size (1-7 kg)
Coyote-size (7-21 kg)
Wolf-size (21-100 kg)
Lion-size (>100 kg)

Figure 18. Total (A and C) and proportional (B and D) median species richness of both the large mammalian herbivore and predator guilds through the Cenozoic. Median species richness values were compiled across all 10,000 pseudoreplicates. No subsampling or "ranging through" taxa were performed. Each guild is subset into distinct size categories following Janis (2000) for the large herbivores and by the author for the predator guild (Table 1).

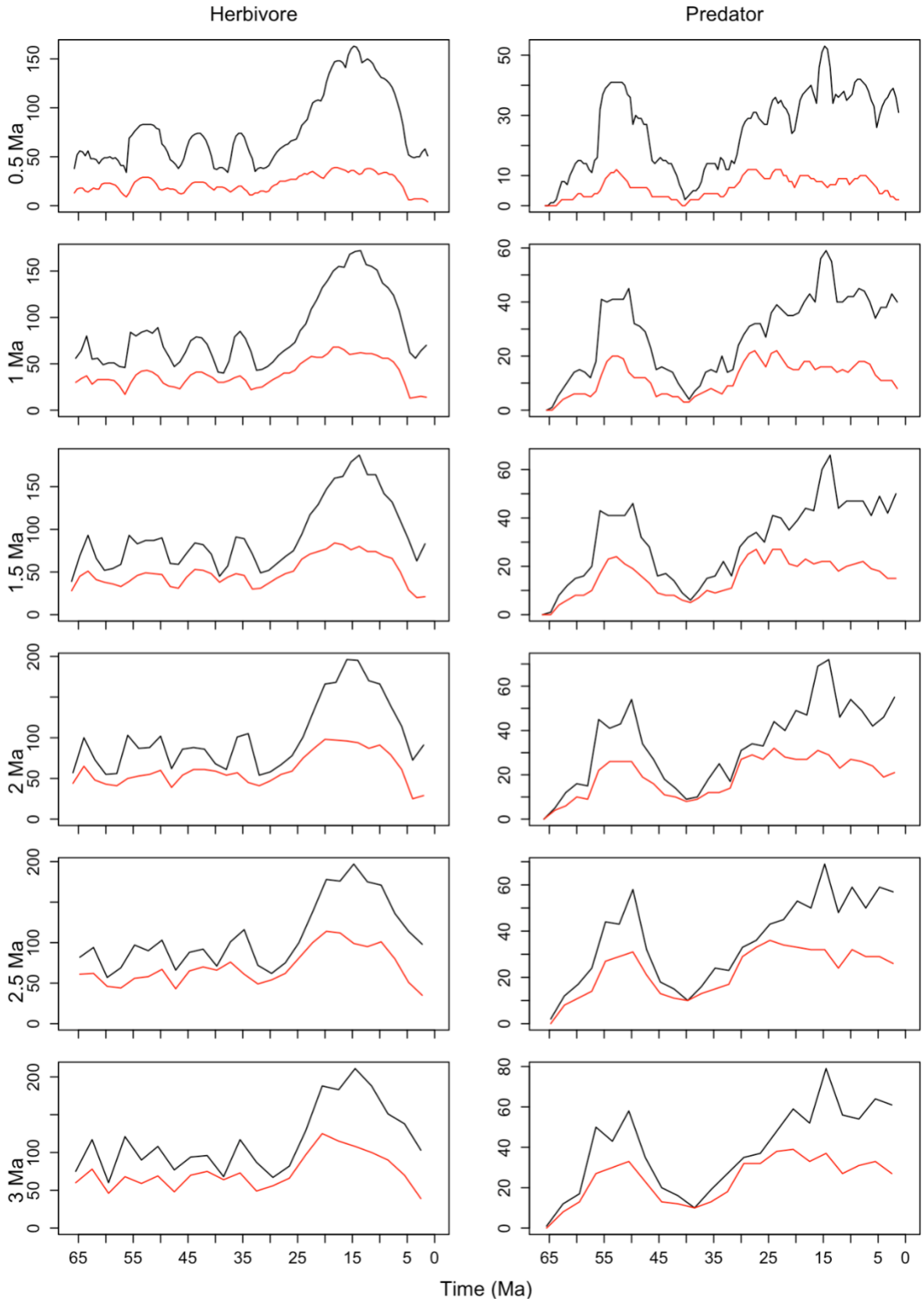
Herbivore
Predator
0.5 Ma
1 Ma
1.5 Ma
2 Ma
2.5 Ma
3 Ma
Time (Ma)
65
55
45
35
25
15
5
0

Figure 19. Subsampled (red) and unsubsampled (black) median species richness of large mammal herbivore and predator guilds from North American Cenozoic given temporal interval of different length (0.5 Ma to 3 Ma). Median species richness were calculated over 10,000 pseudoreplicates.

Table 7. Spearman correlation matrix for the median generic richness between herbivore and predator guilds. Median generic richness were calculated over 10,000 subsampled pseudoreplicates and are representative of actual median species richness. These correlations represent data covering the entire Cenozoic (~66 to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators	<1 kg	-0.15	-0.015	-0.157	-0.072	-0.139
	1 to 7gk	0.041	**0.368***	**0.57*****	**0.431***	0.174
	7 to 21 kg	-0.23	0.268	**0.56****	**0.626*****	0.214
	21 to 100 kg	-0.075	0.132	0.181	0.085	-0.07
	>100 kg	-0.096	0.299	**0.505****	0.37	0.296

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 8. Published and Unsupervised Size Categories for fossil large herbivore and predator guilds. Body masses for extant species were taken from the MOM database (version 10.2) (Smith et al., 2003) whereas the body mass of fossil taxa were from this study. Unsupervised categories were calculated using kmeans clustering.

	Published Categories Juhn (2023)			Unsupervised Categories		
Guild	Size Range	# Extant Species	# Fossil Species	Size Range	# Extant Species	# Fossil Species
Predator						
	<1 kg	42	64	<0.6 g	23	40
	1-7 kg	119	119	0.6-1.96 kg	61	63
	7-21 kg	39	93	1.96-5.76 kg	71	67
	21-100 kg	18	89	5.76-27.1 kg	50	121
	>100 kg	7	35	>27.1	20	109
	Total	225	400		225	400
Large Herbivore	Janis (2000)					
	<5 kg	7	220	<11.4 kg	21	330
	5-25 kg	56	220	11.41-36.65 kg	65	167
	25-150 kg	103	338	36.65-115.28 kg	72	233
	150-500 kg	39	197	115.28-451.66 kg	47	231
	>500 kg	19	154	>451.66 kg	19	168
	Total	224	1129		224	1129

Table 9. Spearman correlation matrix for the median species richness between the unsupervised herbivore and predator size categories. Median species richness were calculated over 10,000 subsampled pseudoreplicates and a representative of actual median species richness. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<11.4 kg	11.41-36.65 kg	36.65-115.28 kg	115.28-451.66 kg	>451.66 kg
Predators (All Cenozoic)	<0.6 g	-0.089	-0.196	-0.247	-0.485	-0.382
	0.6-1.96 kg	0.199	0.013	0.133	-0.215	-0.188
	1.96-5.76 kg	0.161	0.267	0.005	-0.144	0.008
	5.76-27.1 kg	0.199	0.353	0.038	0.056	0.255
	>27.1	0.106	0.066	0.037	**0.383***	0.391
Predators (Hypercarnivores)	<0.6 g	--	--	--	--	--
	0.6-1.96 kg	--	--	--	--	--
	1.96-5.76 kg	--	--	--	--	--
	5.76-27.1 kg	**0.624***	0.209	-0.11	-0.057	-0.174
	>27.1	0.445	0.259	0.302	0.475	0.426
Predators (Mesocarnivores)	<0.6 g	--	0	-0.316	-0.316	-0.333
	0.6-1.96 kg	-0.247	**0.646***	0.408	0.509	0.211
	1.96-5.76 kg	0.482	0.033	0.05	0.183	0.034
	5.76-27.1 kg	-0.266	0.149	0.176	0.351	0.28
	>27.1	--	-0.52	-0.612	-0.635	-0.52
Predators (Hypocarnivores)	<0.6 g	--	--	--	--	--
	0.6-1.96 kg	0.535	0.108	0.158	-0.291	-0.022
	1.96-5.76 kg	-0.174	0	0.26	-0.441	-0.11
	5.76-27.1 kg	0.655	0.553	0.509	0.587	**0.636***
	>27.1	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 10. Spearman correlation matrix for the detrended herbivore and predator median species richness calculated over 10,000 subsampled pseudoreplicates without ranging through. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (All Cenozoic)	<1 kg	0.103	0.193	-0.116	-0.303	**-0.55***
	1 to 7gk	0.221	0.256	**0.383***	-0.139	-0.08
	7 to 21 kg	0.111	0.31	0.196	-0.042	-0.005
	21 to 100 kg	0.217	0.302	0.159	**0.613*****	**0.581****
	>100 kg	-0.816	-0.213	**0.677***	0.218	0.595
Predators (Hypercarnivores)	<1 kg	--	--	0.5	0	0.866
	1 to 7gk	0	0	-0.674	-0.544	-0.204
	7 to 21 kg	**-0.731***	0.437	-0.231	-0.141	-0.318
	21 to 100 kg	0.199	0.396	0.305	**0.595***	0.488
	>100 kg	-0.816	-0.118	0.582	0.286	0.421
Predators (Mesocarnivores)	<1 kg	--	0.144	-0.099	0	-0.363
	1to 7 kg	-0.229	0.532	0.469	0.264	0.256
	7 to 21 kg	-0.029	0.279	-0.024	0.129	0.328
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Predators (Hypocarnivores)	<1 kg	--	--	--	--	--
	1 to 7gk	0.168	0.049	0.226	-0.363	-0.155
	7 to 21 kg	--	**-1*****	0.5	-0.866	-0.5
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 11. Spearman correlation matrix for the detrended herbivore and predator median species richness calculated over 10,000 pseudoreplicates without subsampling but ranging through was performed. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (All Cenozoic)	<1 kg	0.174	0.09	0.095	0.065	-0.123
	1 to 7gk	0.037	**0.36***	**0.483****	**0.37***	0.022
	7 to 21 kg	0.158	**0.531****	**0.466****	0.238	-0.022
	21 to 100 kg	0.259	**0.481***	**0.561****	**0.604*****	**0.395***
	>100 kg	-0.221	**0.591***	**0.907*****	**0.763*****	**0.575***
Predators (Hypercarnivores)	<1 kg	--	-0.405	-0.405	0.135	0.27
	1 to 7gk	0.465	-0.047	-0.115	-0.37	-0.308
	7 to 21 kg	0.282	0.219	0.083	-0.165	-0.34
	21 to 100 kg	0.057	**0.508***	**0.572***	**0.628****	0.41
	>100 kg	-0.273	**0.713***	**0.784****	**0.737****	0.562
Predators (Mesocarnivores)	<1 kg	-0.086	0.149	0.213	0.056	-0.196
	1to 7 kg	-0.523	**0.549***	**0.665****	**0.583***	0.478
	7 to 21 kg	-0.451	0.415	0.341	0.388	0.258
	21 to 100 kg	0.696	0.109	-0.218	-0.165	0.274
	>100 kg	--	-0.415	-0.577	-0.577	-0.249
Predators (Hypocarnivores)	<1 kg	--	--	--	--	--
	1 to 7gk	-0.301	-0.071	0.213	0.017	-0.184
	7 to 21 kg	0.172	0.198	0.341	0.07	-0.353
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 12. Spearman correlation matrix for the detrended herbivore and predator median species richness calculated over 10,000 pseudoreplicates without subsampling or ranging through. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (All Cenozoic)	<1 kg	0.268	0.271	0.311	0.176	0.044
	1 to 7gk	0.223	**0.557****	**0.532****	**0.509****	0.055
	7 to 21 kg	**0.393***	**0.723*****	**0.626*****	**0.422***	0.083
	21 to 100 kg	**0.428***	**0.503****	**0.667*****	**0.657*****	**0.435***
	>100 kg	-0.046	**0.657****	**0.873*****	**0.826*****	0.423
Predators (Hypercarnivores)	<1 kg	--	0.333	0.775	0.544	0.775
	1 to 7gk	0.282	0.154	0.228	-0.087	0.061
	7 to 21 kg	0.178	0.398	0.365	0.2	0.103
	21 to 100 kg	0.26	**0.584***	**0.735****	**0.765*****	0.442
	>100 kg	-0.329	**0.804****	**0.739****	**0.837****	0.301
Predators (Mesocarnivores)	<1 kg	0.295	0.064	0.335	0.048	-0.024
	1to 7 kg	-0.167	**0.667****	**0.775*****	**0.65****	0.327
	7 to 21 kg	-0.18	0.35	0.266	0.391	0.381
	21 to 100 kg	0.866	0.229	-0.224	0.229	0.671
	>100 kg	--	-0.444	-0.289	0	0.577
Predators (Hypocarnivores)	<1 kg	--	--	--	--	--
	1 to 7gk	-0.332	0.247	0.34	0.192	-0.048
	7 to 21 kg	0	0.292	0.579	0.137	-0.746
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 13. Spearman correlation matrix for herbivore and predator median species richness as subset by different temporal interval lengths. Median species richness were calculated over 10,000 subsampled pseudoreplicates and is representative of species richness trends of the Cenozoic. These correlations represent data covering the entire Cenozoic (~66 to 0 Ma). Size categories are the same as Table 1.

		0.5 Ma		Herbivores			1.0 Ma		Herbivores		
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg	<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators	<1 kg	**0.333***	0.276	0.084	0.161	0	0.354	**0.363***	0.086	0.075	-0.155
	1 to 7gk	**0.255***	**0.327***	**0.256****	0.173	0.005	**0.396****	**0.398****	0.189	0.007	-0.02
	7 to 21 kg	0.208	0.092	0.164	0.008	**0.286***	**0.359***	**0.271***	0.244	0.011	0.249
	21 to 100 kg	0.115	0.065	**0.222***	**0.496*****	**0.232***	0.123	0.148	0.156	**0.437*****	0.146
	>100 kg	--	-0.295	0.086	0.2	0.25	--	0.446	**0.714*****	0.353	**0.502***

		1.5 Ma					2.0 Ma				
Predators	<1 kg	0.16	0.089	-0.309	**-0.408***	**-0.659****	0.07	-0.009	-0.27	-0.197	-0.333
	1 to 7gk	0.319	0.23	0.189	-0.112	-0.037	0.24	0.192	0.235	-0.265	-0.091
	7 to 21 kg	0.081	0.136	0.063	-0.167	-0.049	0.247	0.222	0.053	-0.125	0.07
	21 to 100 kg	0.175	0.128	0.212	**0.41***	0.189	-0.225	-0.161	-0.084	0.377	0.21
	>100 kg	-0.5	0.214	**0.811*****	0.478	**0.549***	-0.544	0.321	**0.674***	0.296	**0.627***

		2.5 Ma					3.0 Ma				
Predators	<1 kg	0.353	0.034	-0.442	-0.452	**-0.501***	0.228	0.028	-0.195	-0.282	-0.439
	1 to 7gk	0.136	0.047	0.182	-0.211	-0.198	0.23	0.082	0.355	-0.11	-0.062
	7 to 21 kg	-0.007	-0.058	0.094	-0.201	-0.059	0.098	0.102	0.146	-0.081	-0.006
	21 to 100 kg	0.008	0.14	0.058	0.381	0.271	0.153	-0.076	-0.005	0.268	0.259
	>100 kg	-0.738	0.561	**0.922*****	**0.668***	**0.735***	-0.5	0.118	**0.963*****	0.51	0.524

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

Table 14. Spearman correlation p-values for herbivore and predator median species richness of our primary analyses after Bonferroni correction. Median species richness were calculated over 10,000 subsampled pseudoreplicates and are representative of actual median species richness. The "All Cenozoic" predator and herbivore correlations represent data covering the entire Cenozoic (~66 to 1 Ma) while the analyses utilizing the dietary subdivisions of the predator guild cover the Oligocene to present (~34 Ma to 0 Ma). Size categories are the same as Table 1.

		Herbivores				
		<5 kg	5-25 kg	25-150 kg	150-500 kg	>500 kg
Predators (All Cenozoic)	<1 kg	19.889	24.217	5.32	9.515	4.782
	1 to 7gk	6.468	7.978	5.063	3.919	16.65
	7 to 21 kg	6.106	6.19	19.4	12.781	18.512
	21 to 100 kg	8.483	11.031	16.9	1.318	7.867
	>100 kg	11.392	9.99	0.573	9.43	0.974
Predators (Hypercarnivores)	<1 kg	--	--	8.333	25	8.333
	1 to 7gk	11.916	12.109	25	3.714	1.238
	7 to 21 kg	8.228	12.367	14.653	4.773	1.595
	21 to 100 kg	21.679	18.763	11.806	2.01	6.66
	>100 kg	1.43	8.818	0.44	1.258	1.523
Predators (Mesocarnivores)	<1 kg	--	20.054	25	25	14.7
	1to 7 kg	6.427	0.7	**0.014***	0.783	1.842
	7 to 21 kg	0.517	6.902	18.212	12.627	19.173
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--
Predators (Hypocarnivores)	<1 kg	--	--	--	--	--
	1 to 7gk	3.113	24.515	5.884	1.437	23.959
	7 to 21 kg	--	4.588	25	18.545	18.545
	21 to 100 kg	--	--	--	--	--
	>100 kg	--	--	--	--	--

* = p <= 0.05; ** = p <= 0.01; *** = p <= 0.001

APPENDIX D: CHAPTER 2 SENSITIVITY ANALYSES

Taxonomic Level of Analysis

Methods. We performed sensitivity analyses regarding taxonomic scope to test whether our results could be influenced by: 1) the dubious nature of some species-level identifications (Prothero, 2015) and 2) the incorporation of PBDB occurrences that have only been identified to the generic level (n = 11,932). We repeated our analyses at the generic level to evaluate this influence on our results.

Results and Discussion. We observed four and two regime shifts in the distribution of body mass for the herbivores and predators, respectively (Figure 20). Two of these shifts (47 Ma and 28 Ma) were coincident between the guilds. These correspondent shifts were characterized by an expansion of antelope-size and larger herbivores and wild-cat- to wolf-size predators. Lion-size predators were absent during the 47 Ma shift but expanded following the 27 Ma shift.

Two regime shifts were identified within the taxonomic composition of both guilds (Figures 21 and 22). Both regime shifts within the herbivore guild were roughly coeval with the body mass regime shifts. On the other hand, the taxonomic regime shifts of the predator guild failed to align with the body mass regime shifts.

Subsampling and Range Through

Methods. We evaluated the influence of subsampling and making taxa "range through" intervening intervals by conducting our analyses without performing those methods and then comparing the results to our primary analysis.

Results and Discussion. The withholding of subsampling and ranging taxa through intervening intervals had a limited effect on our observed results (Figures 23 to 32). The lack of ranging taxa through did not alter the number, timing, and character of the regime shifts within

the subsampled analysis except for the 47 Ma herbivore shift now being recovered at 49 Ma. However, we identified nine herbivore (63, 49, 43, 39, 33, 27, 17, 13, and 5 Ma) and five predator regime shifts when subsampling was not applied. Within the unsubsampled analyses, we observed a slight difference in the timing of the predator regime shifts depending on whether we had ranged taxa through (45, 31, 27, 17, and 9 Ma) or avoided the procedure (45, 31, 23, 17, and 9 Ma). Correspondence between the guilds was mostly maintained between the guilds despite changes in the timing of regime shifts. The underlying changes in the distribution of body mass underlying correspondent shifts were similar to those observed and discussed in the primary analysis.

We observed similar regime shifts related to changes in the taxonomic structure of the predator and herbivore guilds. The ranging through of taxa did not affect the timing of taxonomic regime shifts in the predator guild compared to the primary analyses (39, 31, and 9 Ma). The regime shifts of the herbivore guild (57, 47, 35, and 17 Ma) exhibited a slight change with the shift near 19 Ma now occurred at 17 Ma. The removal of subsampling resulted in a greater difference in the timing of regime shifts. Herbivores were identified to have shifts at 57, 49, 39, 29, and 17 Ma with and without taxon range through. Predators were identified to have shifts at 57, 39, 31, and 17 Ma or 57, 39, 27, and 13 Ma depending on whether taxonomic range through was applied or not, respectively.

Differences with Juhn (2023)

Methods. We identified notable differences in the results of our analyses and those of Juhn (2023) despite our use of the same body mass estimate data. We identified a regime shift at 31Ma that was lacking in Juhn (2023) and Juhn (2023) identified regime shifts unique to their study at 12.57Ma, and 5.91Ma. Moreover, Juhn (2023) failed to recover a shift at the He1-He2

boundary (17.34 Ma), which would have been close to our 17Ma shift, but instead identified two shifts at the preceding A4-He1 boundary (18.5Ma) and following He2-Ba1 boundary (15.97Ma). The dissimilarity in the timing of regime shifts between these studies resulted from differences in the underlying distribution of species richness for the Oligocene and Neogene. For example, Juhn (2023, Figure 3) observed elevated richness over their Arikareean (29.75Ma to 18.5Ma) intervals, including peak richness during A2 (28Ma to 22.2Ma), compared to our equivalent sensitivity analysis (no subsampling but taxa were ranged through intervening intervals) (Figure 26). This suggests that one or more other methodological differences between our studies (e.g., our use of the PBDB and 2 Myr intervals) may be driving these discrepancies.

We evaluated whether observed differences in our patterns of species richness were caused by 1) our use of 2 Myr intervals and 2) our use of the Paleobiology Database (PBDB) occurrences, rather than those combined from the New and Old World (NOW) database (The NOW Community, 2023) and the MioMap database (Carrasco et al., 2005), to determine the stratigraphic extent of taxa by applying the temporal binning methods of Juhn (2023) to the PBDB data. We evaluated temporal interval length by conducting this sensitivity analysis using both 2 Myr intervals and the same sub-North American Land Mammals Age (NALMA) intervals as Juhn (2023) and comparing the results. Differences in the PBDB and the combined NOW-MioMap databases (henceforth referred to as NOW-MioMap) were also evaluated by comparing species richness of the Carnivoramorph and Creodonta within our subNALMA analysis with the results of Juhn (2023) in order to pinpoint temporal intervals of interest. We then compared the occurrence data within each database to determine how differences in the data structure (e.g., number of species and/or occurrences) was contributing to, or outright driving, observed differences in species richness over those intervals.

We also investigated whether the data standards of each database, specifically those concerned with how the minimum and maximum date estimates are handled, influenced the disparity between our studies. Currently, North American localities within the NOW and MioMap databases are predominantly assigned to subNALMA (e.g., Wasatchian-1, Arikareean-1 to Arikareean-2, etc.) or NALMA (e.g., Wasatchian, Arikareean) intervals whereas collections within the PBDB are binned into a wide array of different time intervals of different geological and biochronologic ranks (e.g., epoch, sub-epochs, stages, NALMA's, etc.) (Uhen et al., 2023). Variance in the fidelity of assigned time intervals has resulted in some PBDB collections having minimum and maximum date estimates that are temporal expansive (e.g., collection 18025 is assigned as Miocene, 23.03 Ma to 5.3Ma) whereas others are constrained (e.g., collection 17447 is assigned as Arikareean, 29.5 Ma to 18.5 Ma). We used NOW locality minimum and maximum date estimates to determine the stratigraphic extent of many PBDB collections throughout our study to mitigate this problem, but approximately a third of the PBDB collections could not be corresponded to a NOW locality (n=3300). We evaluated the effect of these non-correspondent collections by 1) comparing the minimum and maximum date estimates of species shared between the PBDB and the combined NOW and MioMap occurrence datasets.

Results and Discussion: Interval Length. We observed notable differences in species richness patterns between the 2 Myr and sub-Nalma interval analyses when applying the temporal binning method of Juhn (2023) (Figure 33). The 2 Myr interval analysis resulted in a roughly similar pattern of overall and size-specific species richness as our equivalent pseudoreplicate analysis (no subsampling but taxa were ranged through) (Figure 26). but was differentiated through elevated overall and size-specific richness values over the Oligocene to Middle Miocene and a sustained net decline in richness following peak Cenozoic richness. Our

sub-NALMA analysis also exhibited elevated species richness values over much of the Cenozoic but showed a markedly different pattern of richness over portions of the Oligocene and Neogene. Specifically, species richness values remained relatively stable over the Late Oligocene to Early Miocene in contrast to our 2Myr analysis.

Differences between the 2 Myr and sub-NALMA analyses was largely driven by the variable length of the sub-NALMA intervals. This variation in interval length led to species occurrences, and by extension species richness, being aggregated (e.g., the species from multiple 2My intervals being combined into a single interval) or split relative to our study. For example, the Arikareean-2 was ~6 My long and aggregated species richness across approximately four 2Myr intervals. Overall, differences in the underlying patterns of species richness between our 2Myr and sub-NALMA analyses suggest that temporal interval length contributed to the differences between our results and those of Juhn (2023).

Results and Discussion: Differences between the PBDB, NO, and MioMap Databases. Comparisons of the results from our PBDB sub-NALMA analysis (Figure 32) and that of Juhn (2023; Figure 3) showed broad similarities but also notable disparities over the Oligocene and Neogene. First, both studies observed increasing species richness over the early Oligocene (Orellan and Whitneyan) and through part of the late Oligocene (Arikareean-2) but we failed to recover a decline in richness over the Arikareean-3 (Ar-3) to Hemingfordian-2 (He-2). Instead, we observed a relatively stable overall and size-specific richness over the Ar-3 to He-2 interval. Second, both studies observed a spike (> 20 species increase) in overall richness within the Barstovian-1 interval but this increase led to a notably higher overall species richness (>80 species) in the PBDB analysis compared to Juhn (2023) (~65 species).

We observed minor differences in the taxonomic composition of both the PBDB and NOW-MioMap occurrence datasets. In total, 469 predator species were shared between the PBDB and NOW-MioMap datasets, while 142 and 29 species were unique to each, respectively. However, many of these taxa lacked a body mass estimate and would not have been incorporated into the results of Juhn (2023) or our pseudoreplicate and subNalma analyses. When body mass estimates were accounted for, we observed 367 predator species that were shared between the PBDB and NOW-MioMap datasets, 18 species unique to the PBDB (Table 15), and no species unique to the combined NOW-MioMap dataset. Overall, the species unique to the PBDB had limited to no effect on the difference observed between our analyses and those of Juhn (2023) because these species were restricted to the Plio-Pleistocene and later (4.91 Ma to present).

Our comparisons of the minimum and maximum date estimates of species shared between the PBDB and NOW-MioMap datasets identified that a notable proportion of species (*n*=278 out of 367 species) had different min and/or max date estimates. Interestingly, only 84 of these species can be associated with PBDB collections that were not linked to a NOW locality and thus were not assigned NOW date estimates. The remaining species were exclusively from PBDB collections that were assigned NOW date estimates. Different temporal standards (e.g., subtle differences in how the upper and lower bounds subNalma and Nalma intervals were defined) between the NOW and MioMap drove the majority of differences in the remaining species. Nonetheless, differences in the minimum and/or maximum date estimates among the 216 species were mostly minimal (< 1 Myr) but some outliers (upwards of 13.33 Myr) were evident due to the PBDB date estimates (Figure 33). Removal of the collections dated using PBDB date estimates resulted in species richness patterns that were more reminiscent of Juhn (2023) (Figure 34). Namely, we observed a decline in overall species richness over the early

Miocene (Ar-3 to He-2)., albeit not to the same extent as Juhn (2023). Overall, differences in temporal standards across the three databases contributes to the observed discrepancies between the results of our pseudoreplicate analyses and those of Juhn (2023).

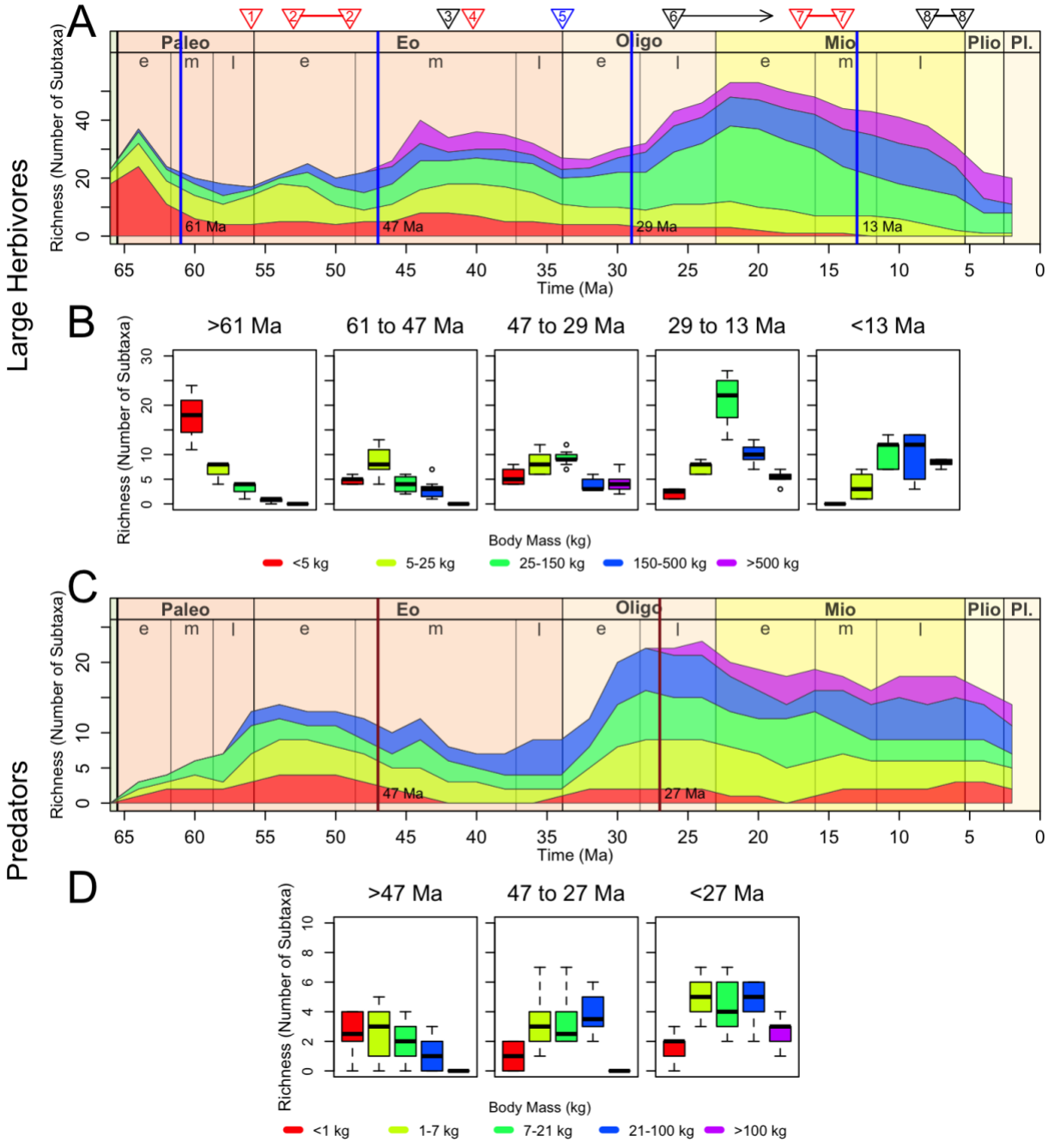
Large Herbivores
A
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
61 Ma
47 Ma
29 Ma
13 Ma
Time (Ma)
B
>61 Ma
61 to 47 Ma
47 to 29 Ma
29 to 13 Ma
<13 Ma
Body Mass (kg)
<5 kg
5-25 kg
25-150 kg
150-500 kg
>500 kg
Predators
C
47 Ma
27 Ma
D
>47 Ma
47 to 27 Ma
<27 Ma
<1 kg
1-7 kg
7-21 kg
21-100 kg
>100 kg

Figure 20. Distribution of North American herbivore (A and B) and predator (C and D) generic richness and body mass throughout the Cenozoic. Solid, vertical blue and red lines represent locations temporal boundaries between regimes – distinct assemblages of body mass for herbivores and predators, respectively. Inverted triangles at the top mark the occurrence of major climatic warming (red) and cooling (blue) events and vegetation transitions (black). Inverted triangles correspond to the Paleocene-Eocene Thermal Maximum (1), Early Eocene Climatic Optimum (2), earliest inferred open habitats within North America (3), Middle Eocene Climatic Optimum (4), Eocene-Oligocene Boundary (5), onset and spread of grass dominated habitats within North America (6), Middle Miocene Climatic Optimum (7), and C3/C4 transition (8) (Zachos, Dickens & Zeebe, 2008; Townsend et al., 2010; Strömberg, 2011; Strömberg & McInerney, 2011; Westerhold et al., 2020). Boxplots (B and D) display the distribution of generic richness within size categories within each regime.

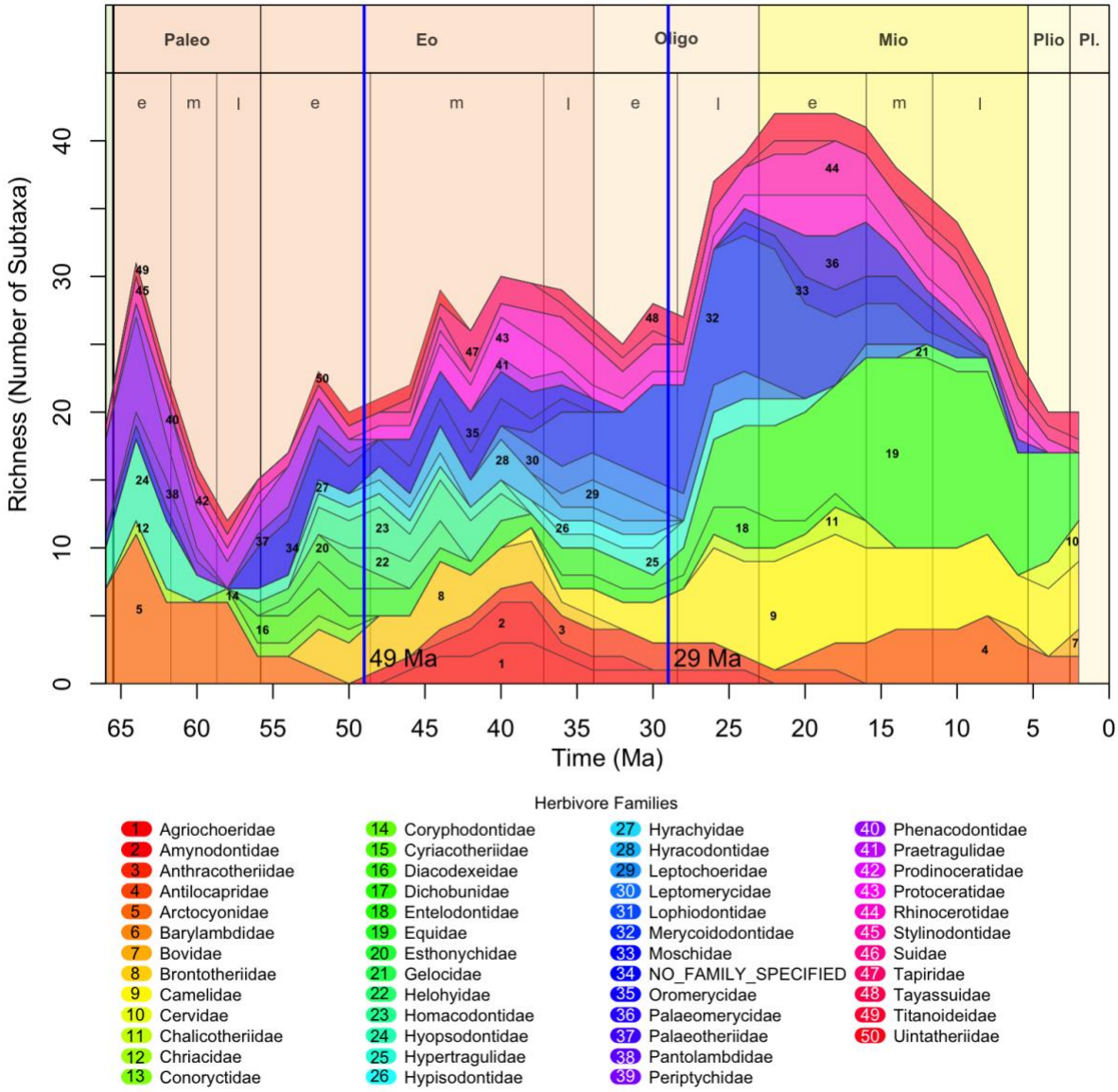

Figure 21. Generic richness of the herbivore guild throughout the Cenozoic as partitioned by taxonomic family. Solid, vertical blue lines represent locations temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

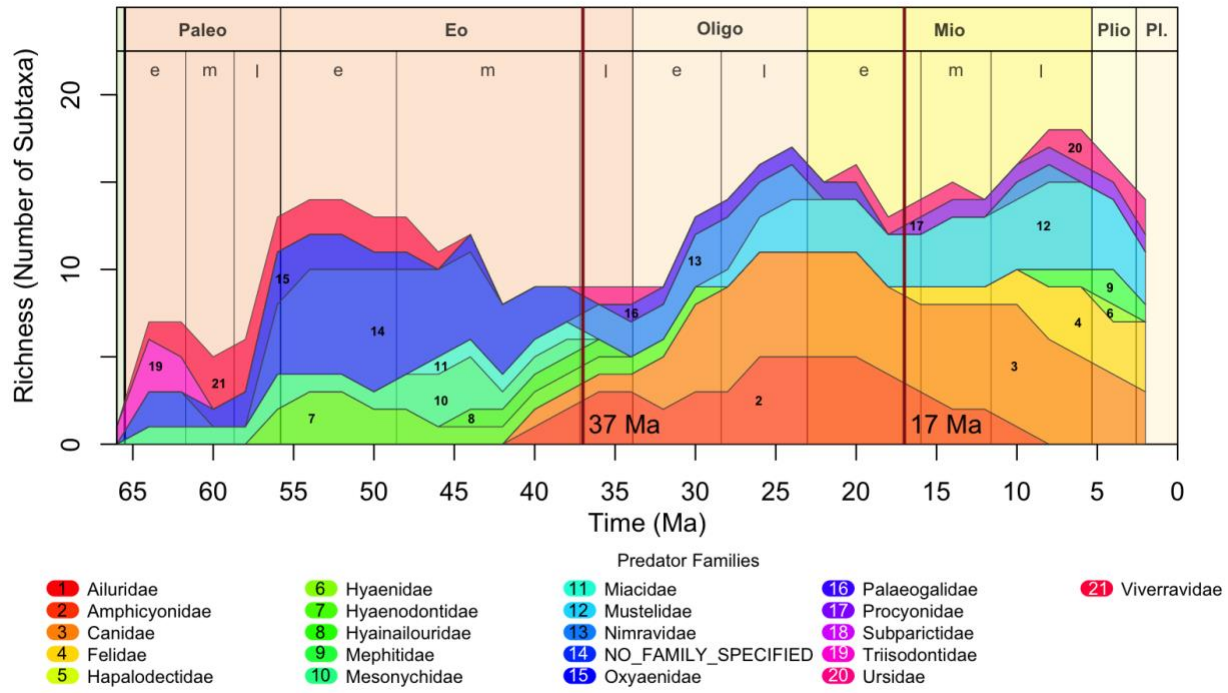

Figure 22. Generic richness of the predator guild across the Cenozoic as partitioned by taxonomic family. Solid, vertical red lines represent temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

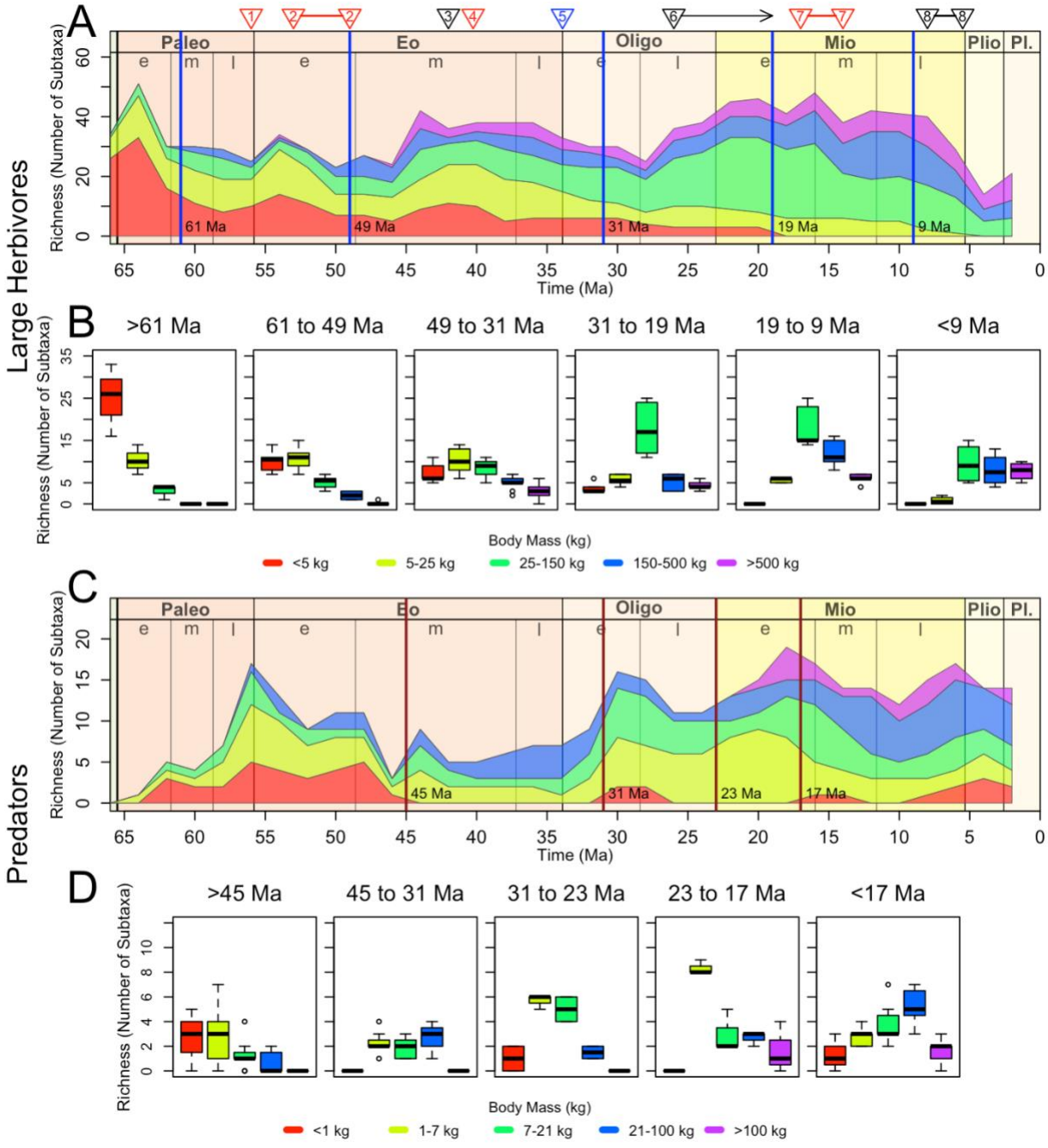
Large Herbivores
A
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
61 Ma
49 Ma
31 Ma
19 Ma
9 Ma
Time (Ma)
B
>61 Ma
61 to 49 Ma
49 to 31 Ma
31 to 19 Ma
19 to 9 Ma
<9 Ma
Body Mass (kg)
<5 kg
5-25 kg
25-150 kg
150-500 kg
>500 kg
Predators
C
45 Ma
31 Ma
23 Ma
17 Ma
D
>45 Ma
45 to 31 Ma
31 to 23 Ma
23 to 17 Ma
<17 Ma
<1 kg
1-7 kg
7-21 kg
21-100 kg
>100 kg

Figure 23. Distribution of North American herbivore (A and B) and predator (C and D) species richness and body mass throughout the Cenozoic. Median species richness values were compiled across all 10,000 pseudoreplicates with subsampling being performed but no taxa being "ranged through" intervening intervals. Solid, vertical blue and red lines represent temporal boundaries between body mass regimes – distinct assemblages of body mass for herbivores and predators, respectively. Inverted triangles at the top mark the occurrence of major climatic warming (red) and cooling (blue) events and vegetation transitions (black). Inverted triangles correspond to the Paleocene-Eocene Thermal Maximum (1), Early Eocene Climatic Optimum (2), earliest inferred open habitats within North America (3), Middle Eocene Climatic Optimum (4), Eocene-Oligocene Boundary (5), onset and spread of grass dominated habitats within North America (6), Middle Miocene Climatic Optimum (7), and C3/C4 transition (8) (Zachos, Dickens & Zeebe, 2008; Townsend et al., 2010; Strömberg, 2011; Strömberg & McInerney, 2011; Westerhold et al., 2020). Boxplots (B and D) display the distribution of species richness within size categories within each regime.

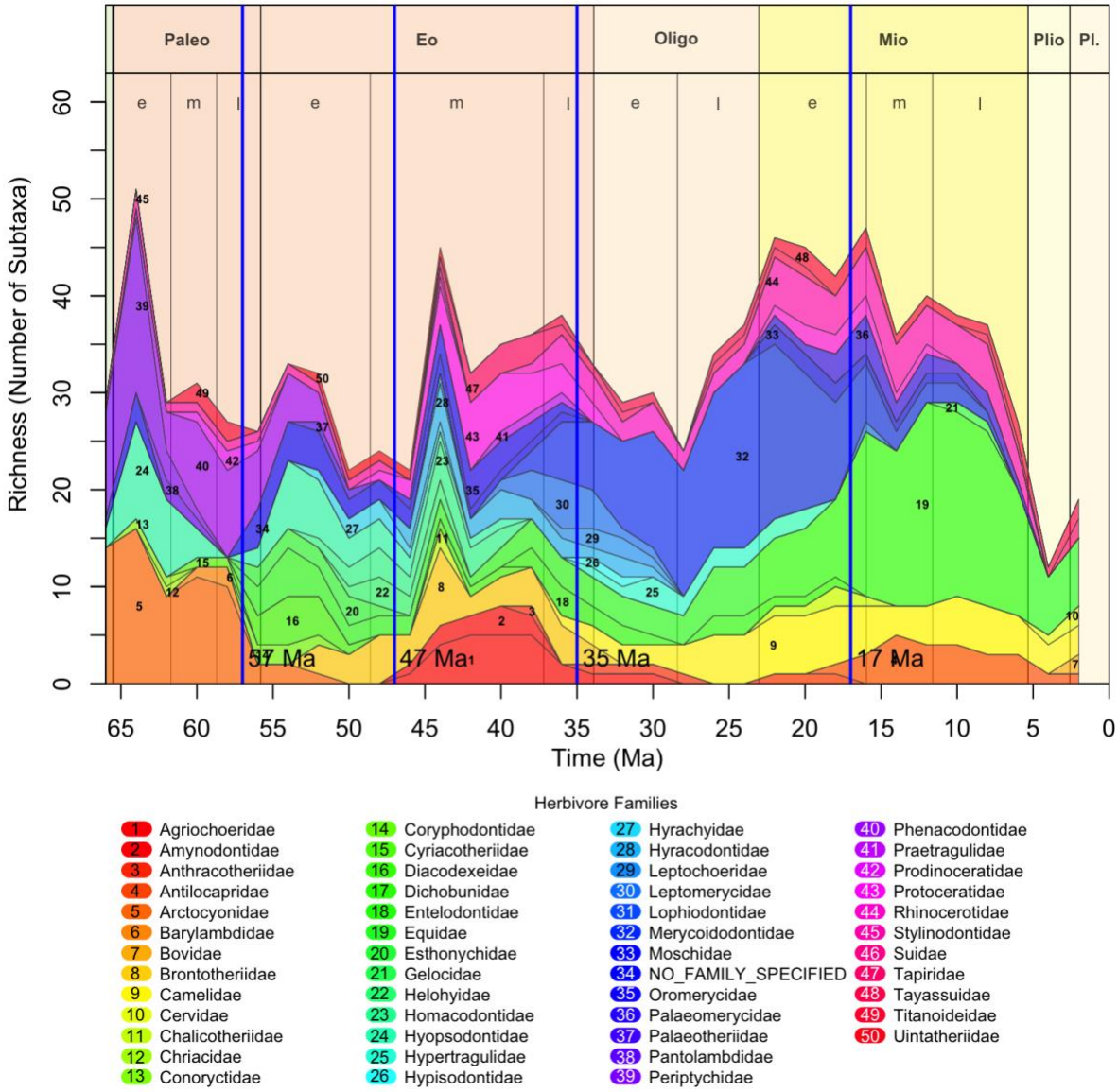

Figure 24. Species richness of the herbivore guild throughout the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates with subsampling being performed but no taxa being "ranged through" intervening intervals. Solid, vertical blue lines represent locations temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

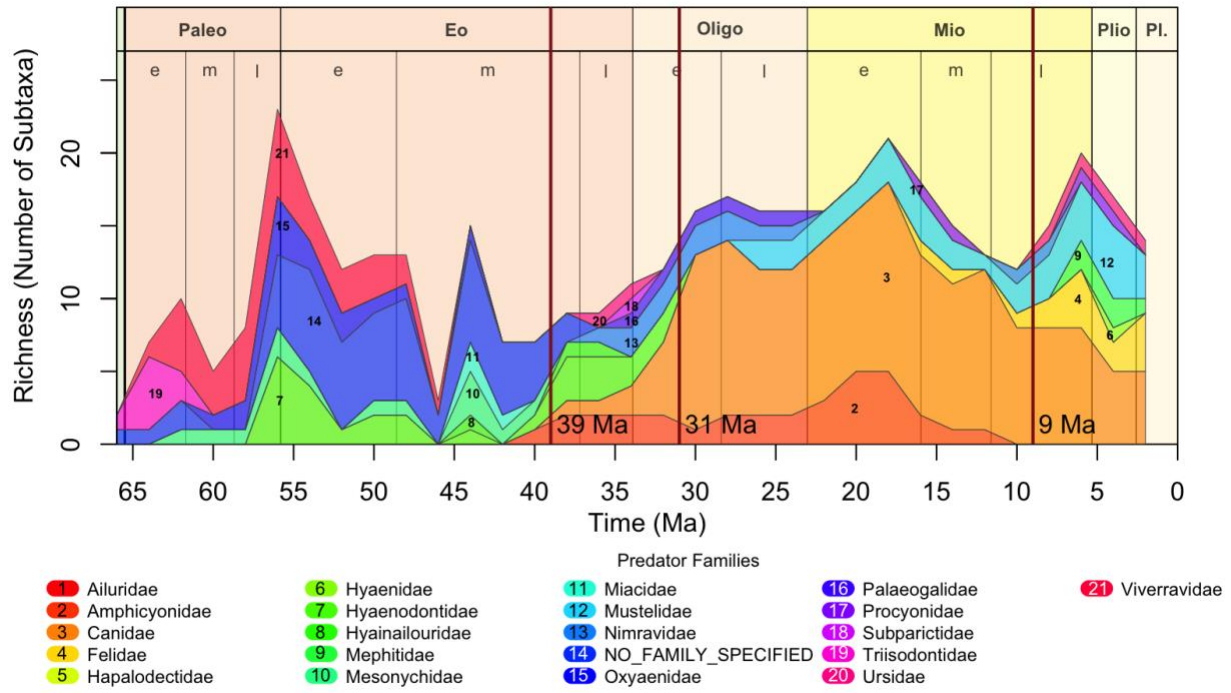

Figure 25. Species richness of the predator guild across the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates with subsampling being performed but no taxa being "ranged through" intervening intervals. Solid, vertical red lines represent temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

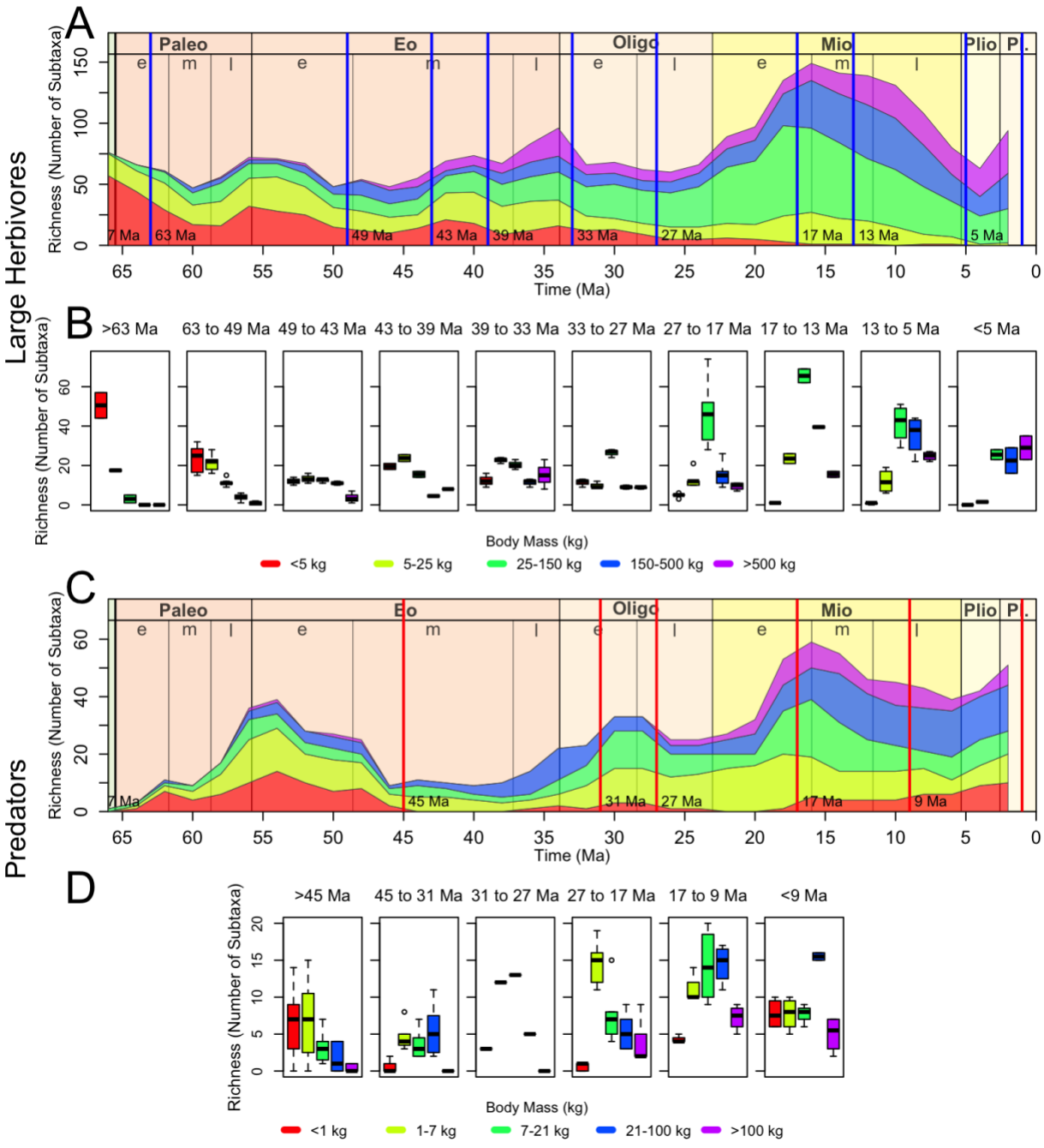
Large Herbivores
A
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Time (Ma)
7 Ma
63 Ma
49 Ma
43 Ma
39 Ma
33 Ma
27 Ma
17 Ma
13 Ma
5 Ma
B
>63 Ma
63 to 49 Ma
49 to 43 Ma
43 to 39 Ma
39 to 33 Ma
33 to 27 Ma
27 to 17 Ma
17 to 13 Ma
13 to 5 Ma
<5 Ma
Body Mass (kg)
<5 kg
5-25 kg
25-150 kg
150-500 kg
>500 kg
Predators
C
45 Ma
31 Ma
9 Ma
D
>45 Ma
45 to 31 Ma
31 to 27 Ma
27 to 17 Ma
17 to 9 Ma
<9 Ma
<1 kg
1-7 kg
7-21 kg
21-100 kg
>100 kg

Figure 26. Distribution of North American herbivore (A and B) and predator (C and D) species richness and body mass throughout the Cenozoic. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling but allowing taxa to "range through" their entire stratigraphic range. Solid, vertical blue and red lines represent locations where shifts between regimes–distinct assemblages of body mass–occur. Boxplots (B and D) display the distribution of richness across the different size categories for each regime.

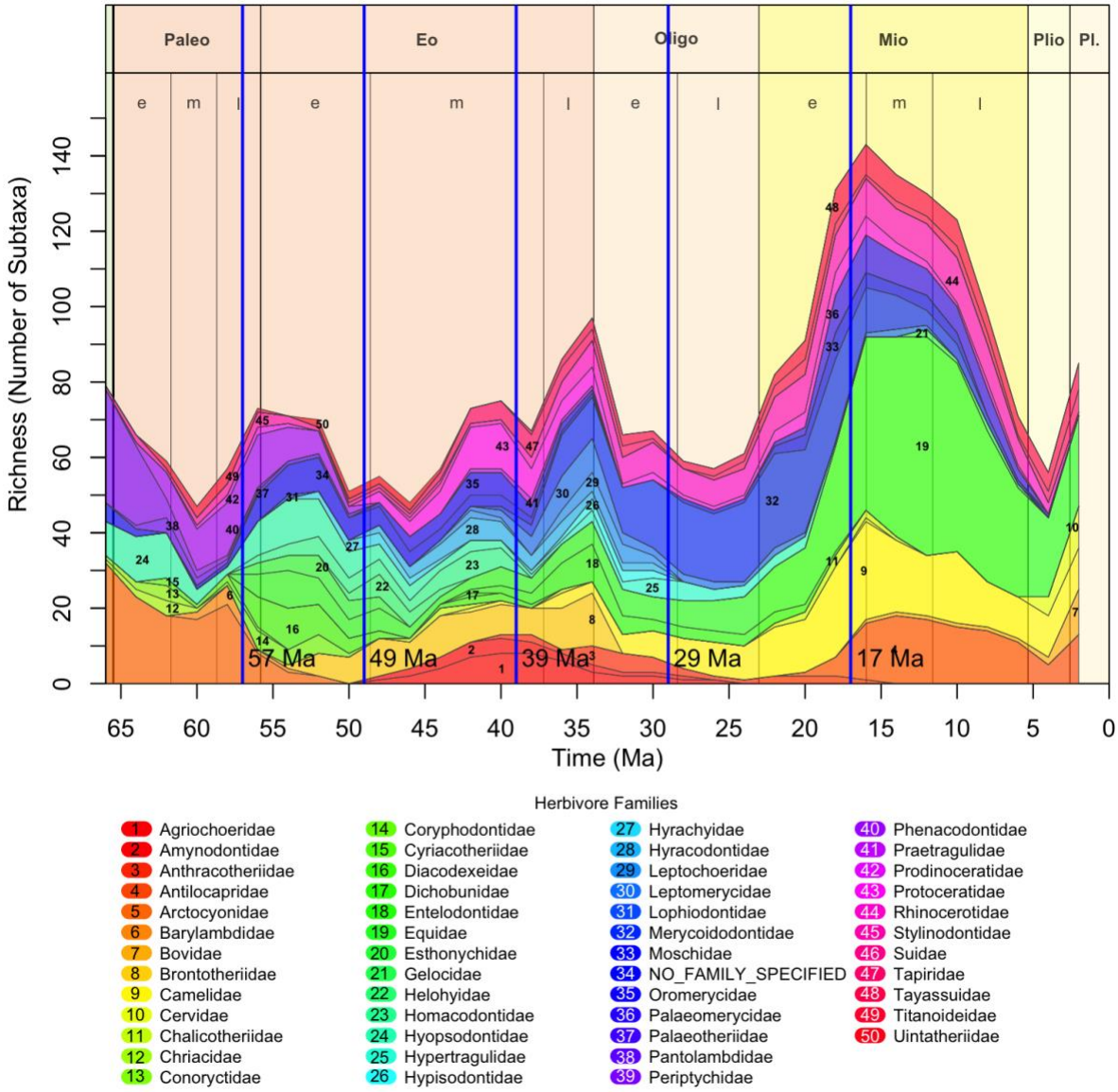

Figure 27. Species richness of the herbivore guild across the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling being performed but taxa were "ranged through" intervening intervals. Solid, vertical blue lines represent locations where shifts between regimes–distinct assemblages of taxonomic composition–occur.

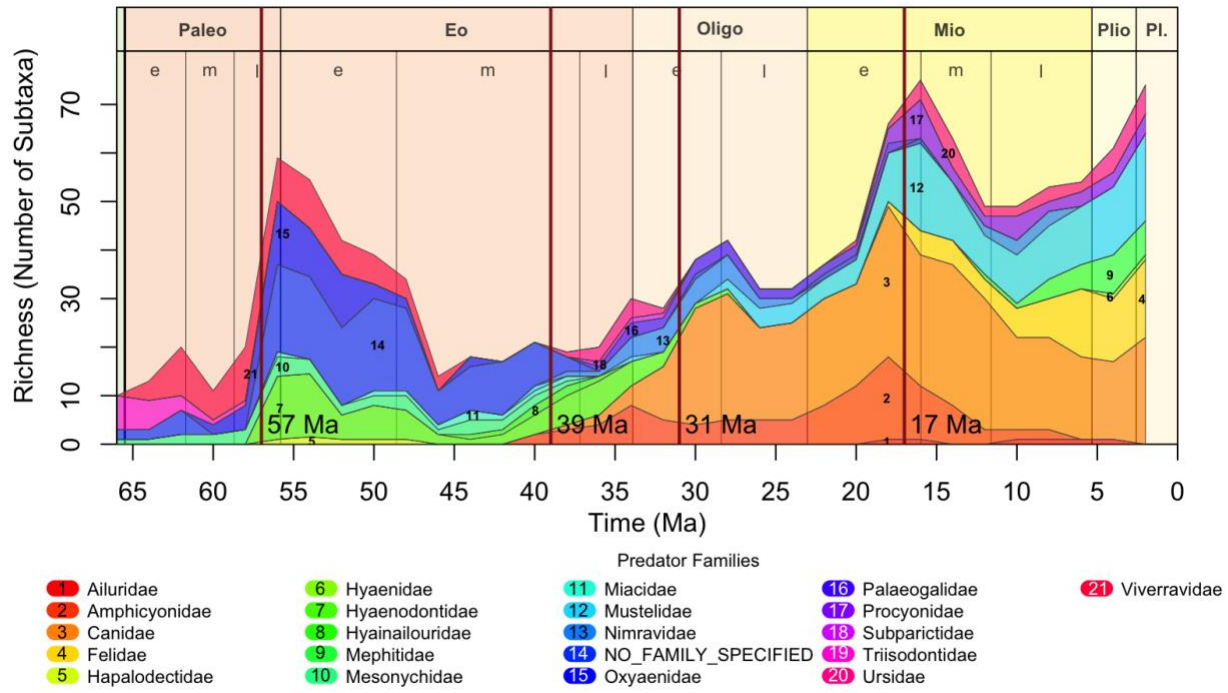

Figure 28. Species richness of the predator guild across the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling being performed but taxa were "ranged through" intervening intervals. Solid, vertical red lines represent locations where shifts between regimes–distinct assemblages of taxonomic composition–occur.

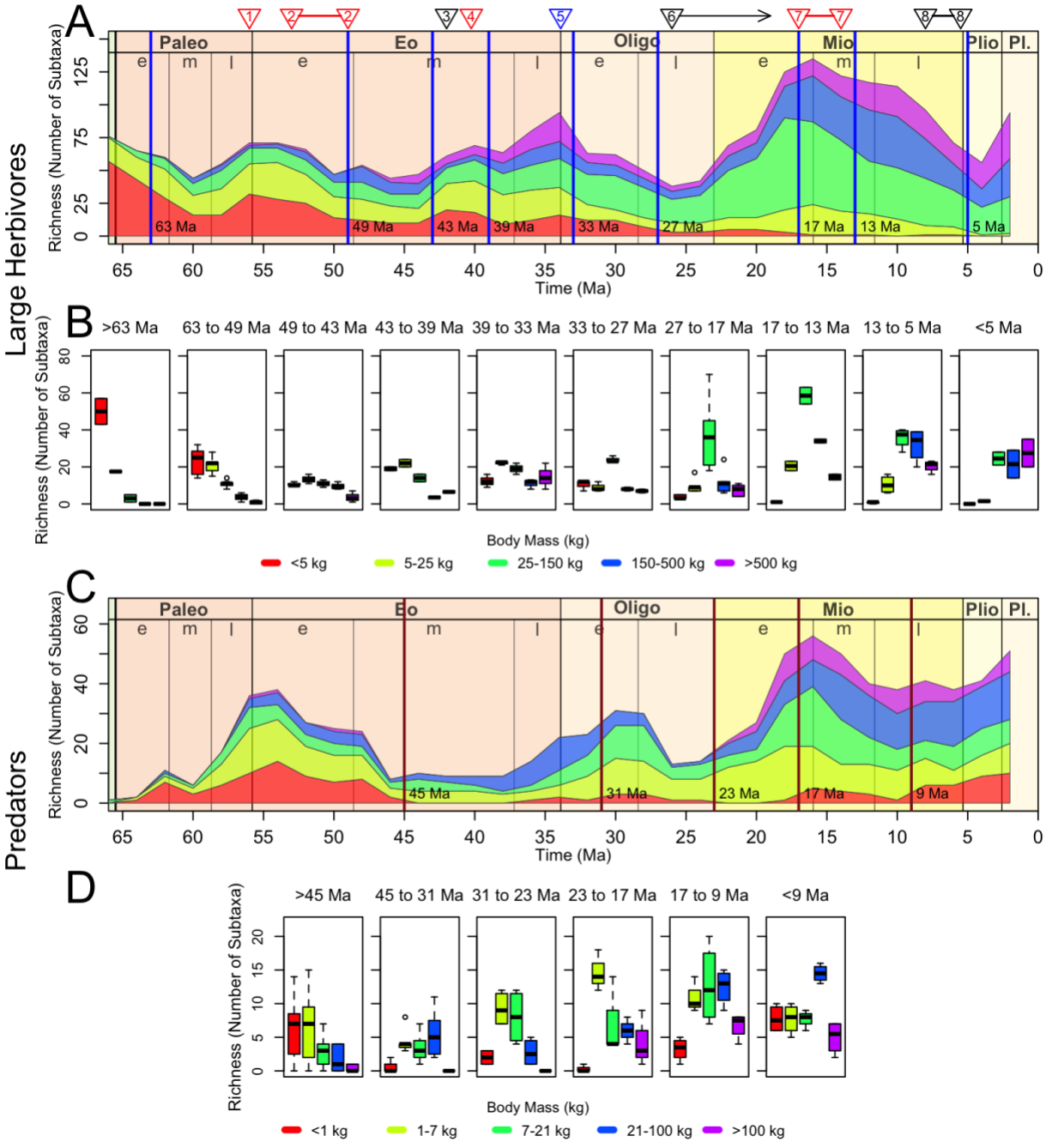
Large Herbivores
A
Paleo
Eo
Oligo
Mio
Plio
Pl.
e
m
l
Richness (Number of Subtaxa)
Time (Ma)
63 Ma
49 Ma
43 Ma
39 Ma
33 Ma
27 Ma
17 Ma
13 Ma
5 Ma
B
>63 Ma
63 to 49 Ma
49 to 43 Ma
43 to 39 Ma
39 to 33 Ma
33 to 27 Ma
27 to 17 Ma
17 to 13 Ma
13 to 5 Ma
<5 Ma
Body Mass (kg)
<5 kg
5-25 kg
25-150 kg
150-500 kg
>500 kg
Predators
C
45 Ma
31 Ma
23 Ma
17 Ma
9 Ma
D
>45 Ma
45 to 31 Ma
31 to 23 Ma
23 to 17 Ma
17 to 9 Ma
<9 Ma
<1 kg
1-7 kg
7-21 kg
21-100 kg
>100 kg

Figure 29. Distribution of herbivore (A and B) and predator (C and D) species richness across the Cenozoic partitioned into distinct body mass regimes. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling being performed and taxa being "ranged through" intervening intervals. Solid, vertical blue and red lines represent temporal boundaries between body mass regimes – distinct assemblages of body mass for herbivores and predators, respectively. Inverted triangles at the top mark the occurrence of major climatic warming (red) and cooling (blue) events and vegetation transitions (black). Inverted triangles correspond to the Paleocene-Eocene Thermal Maximum (1), Early Eocene Climatic Optimum (2), earliest inferred open habitats within North America (3), Middle Eocene Climatic Optimum (4), Eocene-Oligocene Boundary (5), onset and spread of grass dominated habitats within North America (6), Middle Miocene Climatic Optimum (7), and C_3/C_4 transition (8) (Zachos, Dickens & Zeebe, 2008; Townsend et al., 2010; Strömberg, 2011; Strömberg & McInerney, 2011; Westerhold et al., 2020). Boxplots (B and D) display the distribution of species richness within size categories within each regime.

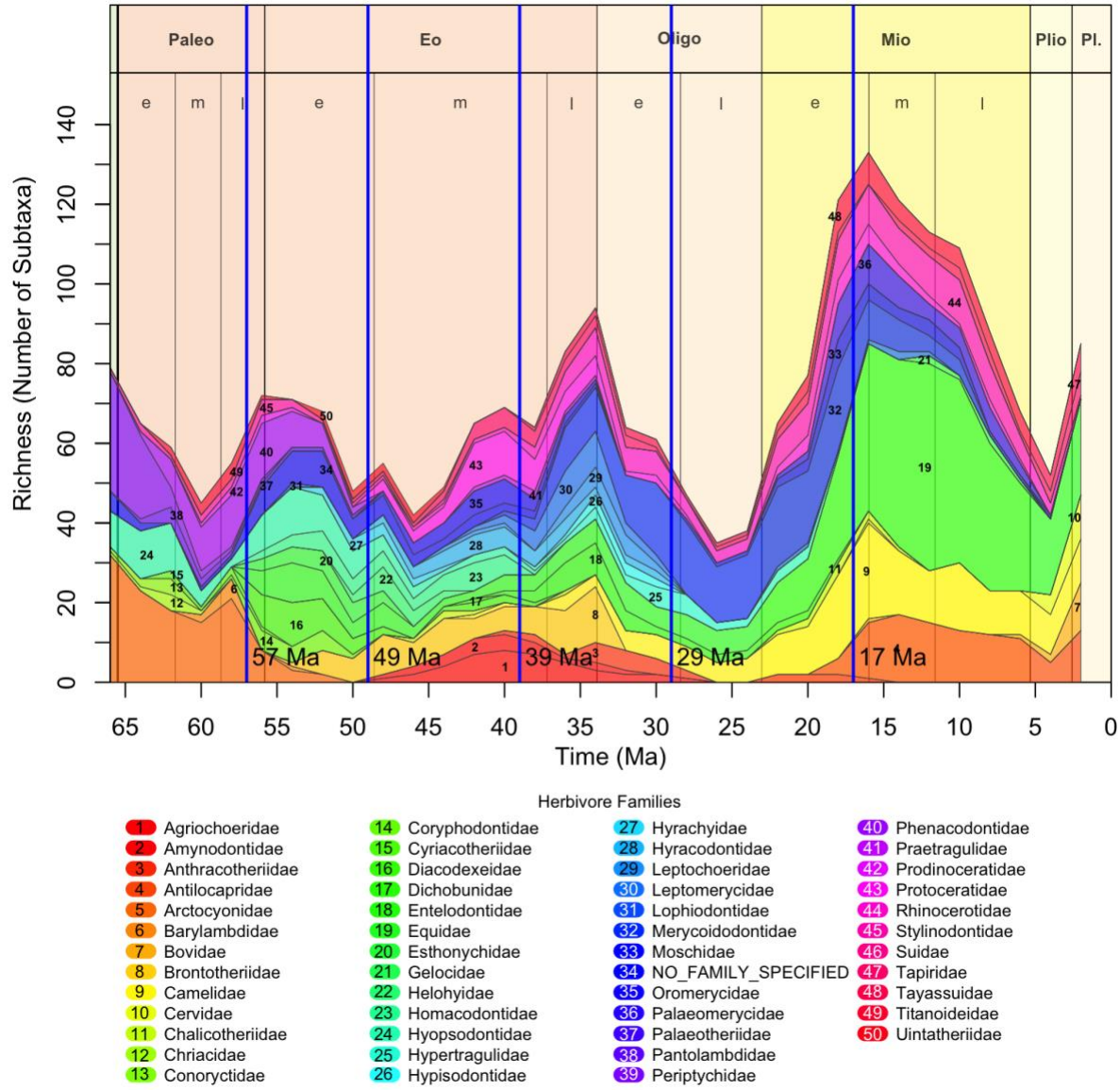

Figure 30. Species richness of the herbivore guild throughout the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling or ranging taxa through intervening intervals. Solid, vertical blue lines represent locations temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

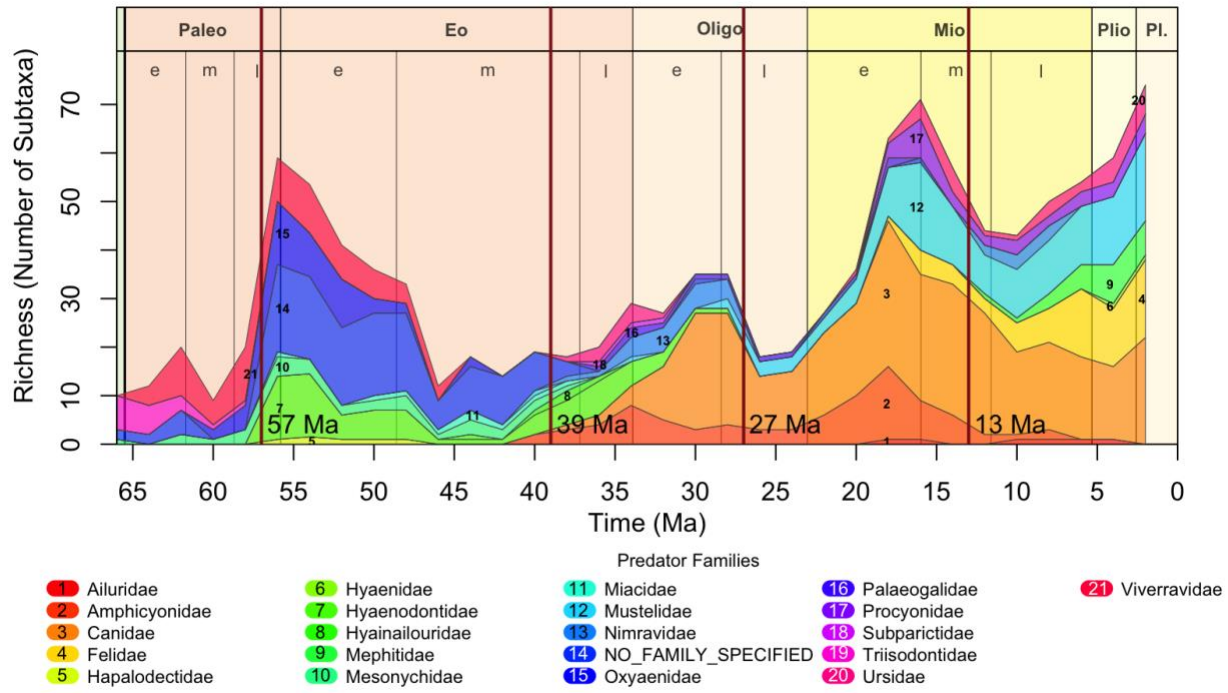

Figure 31. Species richness of the predator guild across the Cenozoic as partitioned by taxonomic family. Median species richness values were compiled across all 10,000 pseudoreplicates without subsampling or ranging taxa through intervening intervals. Solid, vertical red lines represent temporal boundaries between taxonomic regimes – distinct assemblages of taxonomic composition.

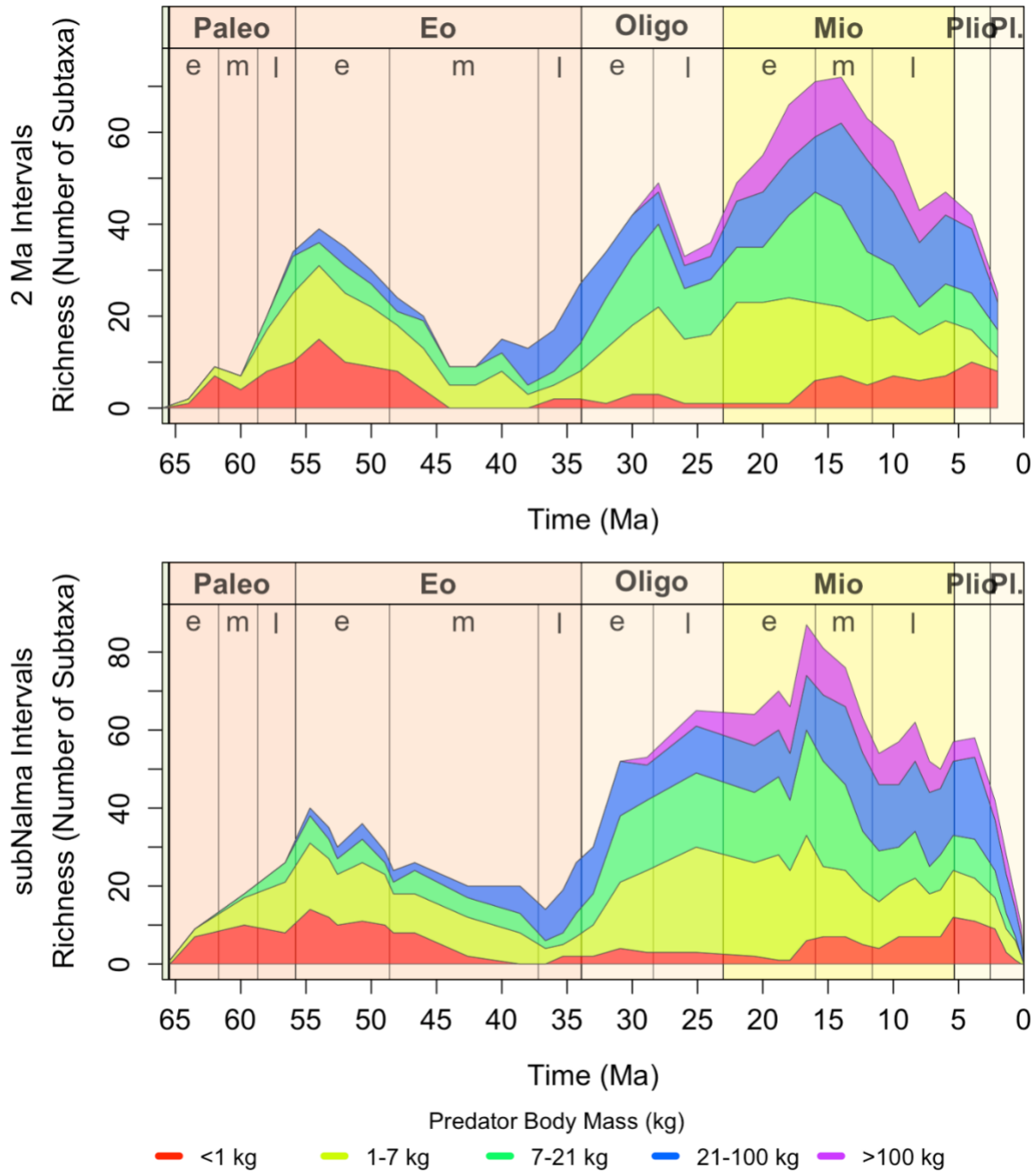

Figure 32. Species richness of the predator guild across the Cenozoic. Taxa were binned temporally into 2Myr (top) and sub-NALMA (bottom) intervals using the methods of Juhn (2023).

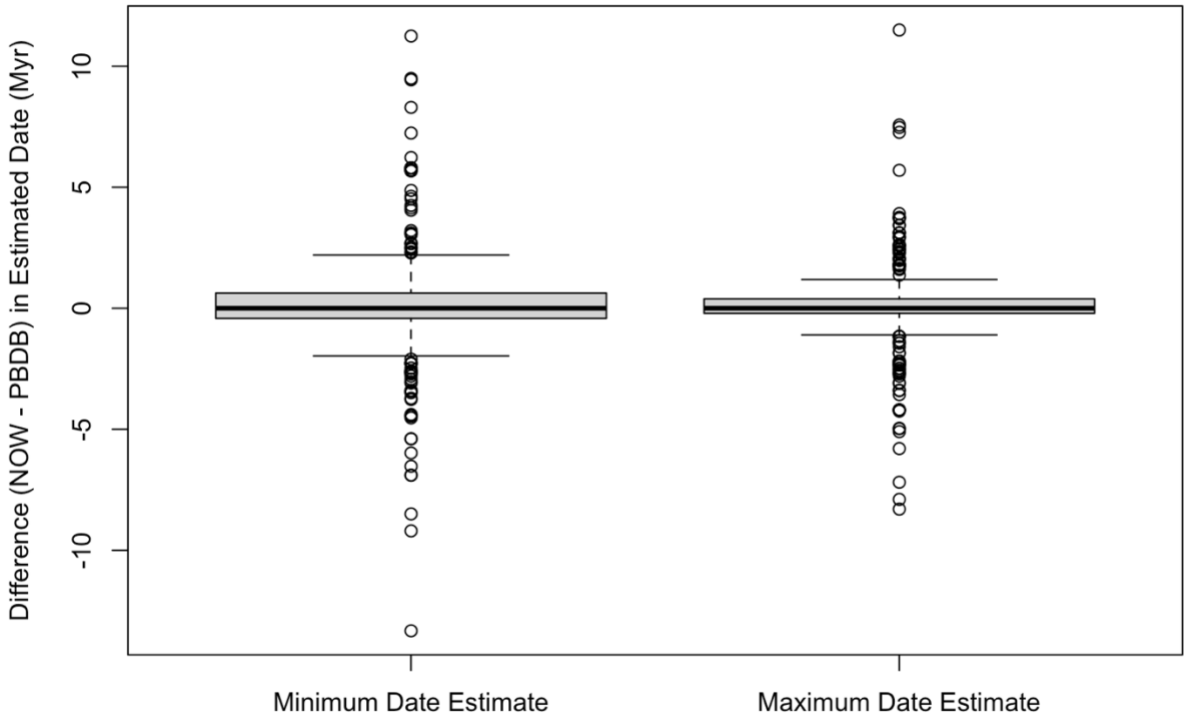

Figure 33. Difference in the minimum and maximum date estimates (Ma) for predator (Carnivoramorpha and Creodonta) species (*n*=117) shared between the Paleobiology Database (PBDB) and a combination of the New and Old World Database (NOW) and Miocene Mammal Mapping Project (MioMap) Databases. Note that negative values indicates that the PBDB had an older date estimate than the NOW date while a positive value indicates that the PBDB date was younger that the NOW date.

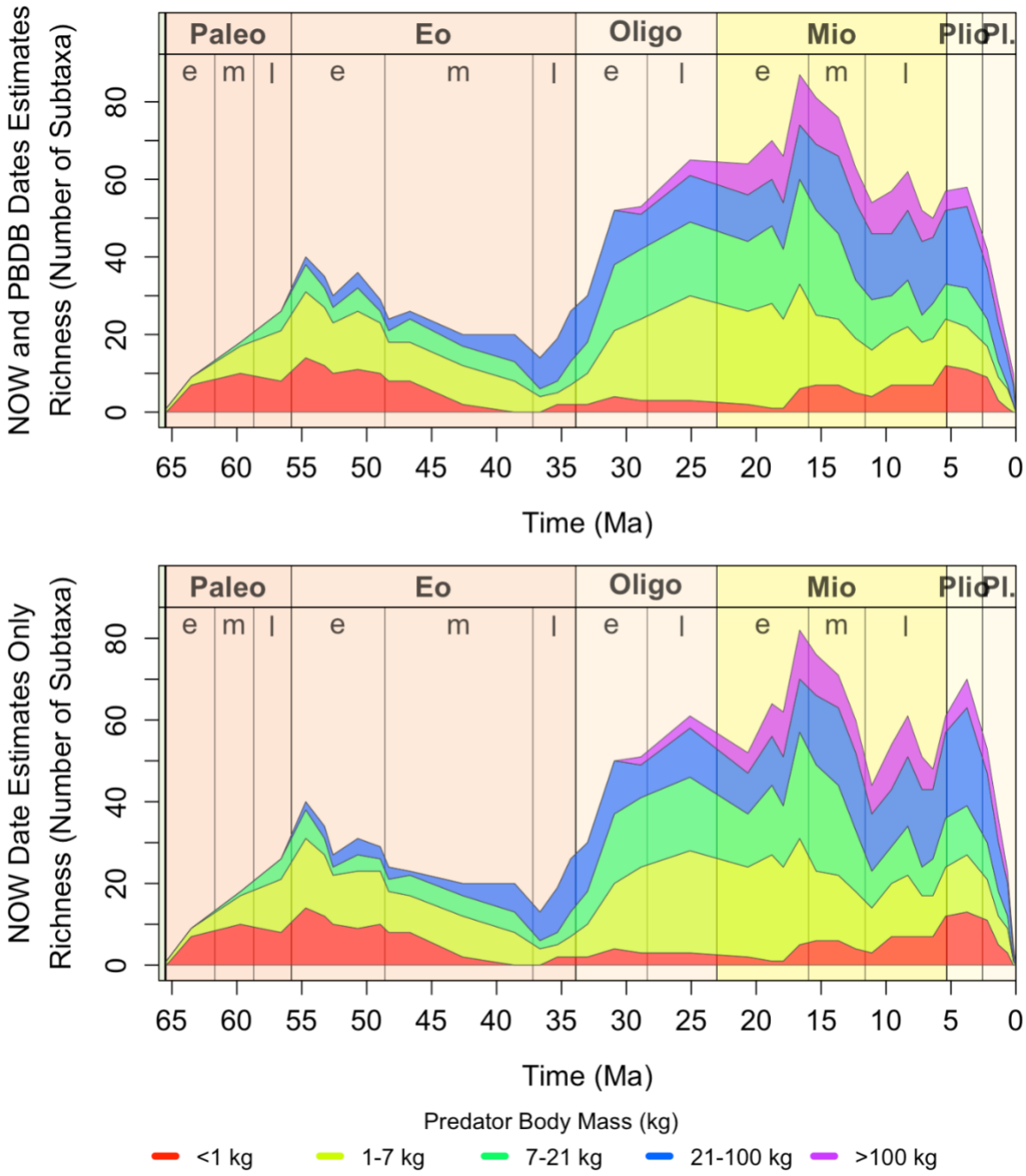

Figure 34. Species richness of the predator guild across the Cenozoic. Stratigraphic duration of these species was drawn from PBDB collections dated using minimum and maximum date estimates from both the PBDB collections and NOW localities (top) or just the NOW localities. Taxa were binned temporally into sub-NALMA intervals using the methods of Juhn (2023)

Table 15. Minimum and maximum first- and last-appearance date estimates for predator species found within the Paleobiology Database but not the New and World Database or MioMap Database.

Species	Maximum First-Appearance Date	Minimum Last-Appearance Date
Aenocyon dirus	2.63	0.0117
Arctodus simus	2.63	0
Bassariscus astutus	1.8	Extant
Canis latrans	4.91	Extant
Canis lupus	2.588	Extant
Gulo gulo	1.8	Extant
Homotherium latidens	2.588	0.0117
Mustela erminea	1.8	Extant
Mustela nigripes	1.8	Extant
Mustela nivalis	2.588	Extant
Neogale vison	1.8	Extant
Pekania pennanti	0.126	Extant
Puma concolor	4.91	Extant
Smilodon fatalis	2.63	0
Urocyon cinereoargenteus	2.63	Extant
Ursus americanus	2.63	Extant
Ursus arctos	2.588	Extant
Vulpes vulpes	2.588	Extant

APPENDIX E: CHAPTER 3 SENSITIVITY ANALYSES

Sensitivity Analyses: Taxonomic Scope

Methods. We performed sensitivity analyses regarding taxonomic scope to evaluate whether our aggregation of taxa at the generic-level was inflating the commonness of certain genera. We repeated our analyses at the species-level and then compared the results to our primary analysis.

Results and Discussion.

Overall Occupancy of the Herbivore Guild and Size-categories. We observed lower occupancies for all groupings (e.g., entire guild or size categories) for the species-level analysis (Figure 35), compared to our primary analysis. Nonetheless, the trends of the species-level results for the occupancy of the entire herbivore guild and each size-category were broadly similar to that of the primary analysis.

Occupancy as Informed by Generic Identity. We observed a notable reduction in the occupancy of individual genera (Figure 36) compared to the primary analysis. Unlike the primary analysis, no common (occupancy greater than 0.25) genera were present in an interval. Nonetheless, we observed that surviving genera tended to exhibit a greater occupancy than those genera that went extinct within an interval (Figure 37).

Sensitivity Analyses: Aggregation of Collections by Spatial Proximity

Methods. We evaluated whether our aggregation of PBDB collections by geospatial proximity influenced our results. We conducted our analyses by treating collections as our sites for occupancy estimation (no aggregation) or by aggregating collections that were contained within the same 0.25-, 0.5-, or 1-degree grid square and then compared the results of these sensitivity analyses to our primary analysis.

Results and Discussion.

Comparisons of Occupancy across Grid Use and Size. We observed broad similarity between the analyses that utilized aggregated sites (e.g., 0.25-, 0.5-, and 1-degree squares; Figures 38 to 46) and the primary analysis (0.125-degree squares; Figures 9 to 11). Occupancy estimates for the entire guild, individual size-categories, and individual genera appeared to marginally increase alongside grid-square size, but the overall character of these occupancy patterns remained relatively similar between analyses.

Alternatively, we observed more notable differences between the analysis using collections as sites (Figures 47 to 49) and the analyses that used aggregated sites, the primary analysis included. Occupancy estimates for the entire guild and size-categories were reduced (upwards of an ~0.3 difference) within the collections analysis, relative to the primary analysis, for multiple intervals. Likewise, the occupancy estimates for individual genera were greatly reduced which resulted in notably fewer "common" (occupancy > 0.25) genera being recovered (e.g., *Equus, Dinohippus*, and *Teleoceras*) when using unaggregated collections for sites.

The subtle and major differences we observed are likely a result of variation in the within-interval number of sites between the different aggregated and unaggregated analyses. Foote (2016) observed that mean occupancy probabilities decrease alongside cell or grid size, or, in other words, resolution increases. They indicated that increases in resolution would lead to increases in both occupied and unoccupied sites, but the latter would grow more rapidly than the former. We likely observed this phenomenon since the number of sites increased as we reduce the size of our grid squares (1-degree, 0.5-degree, 0.25-degree, and 0.125-degree) until we reached our maximum resolution with the collection-based analysis (Figure 50).

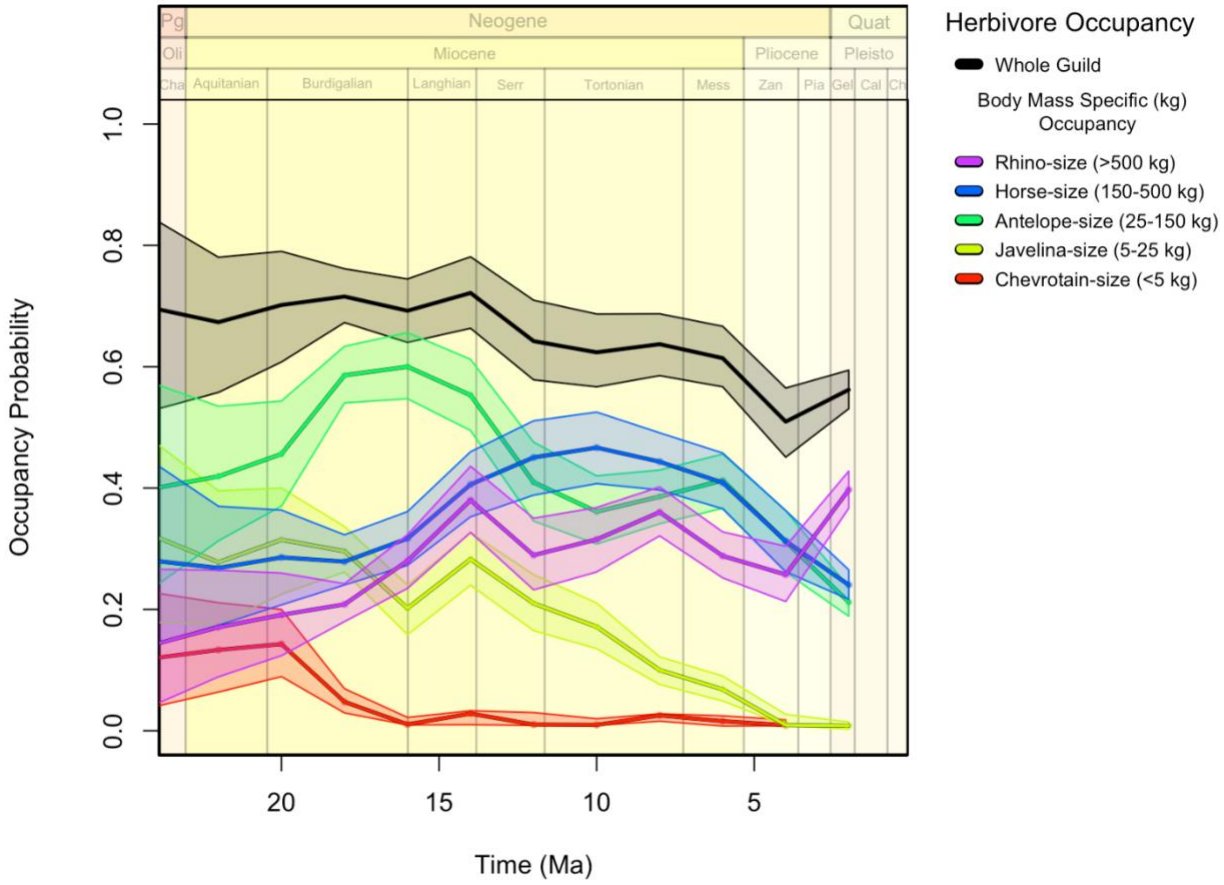

Figure 35. Species-level occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.125-degree squares. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

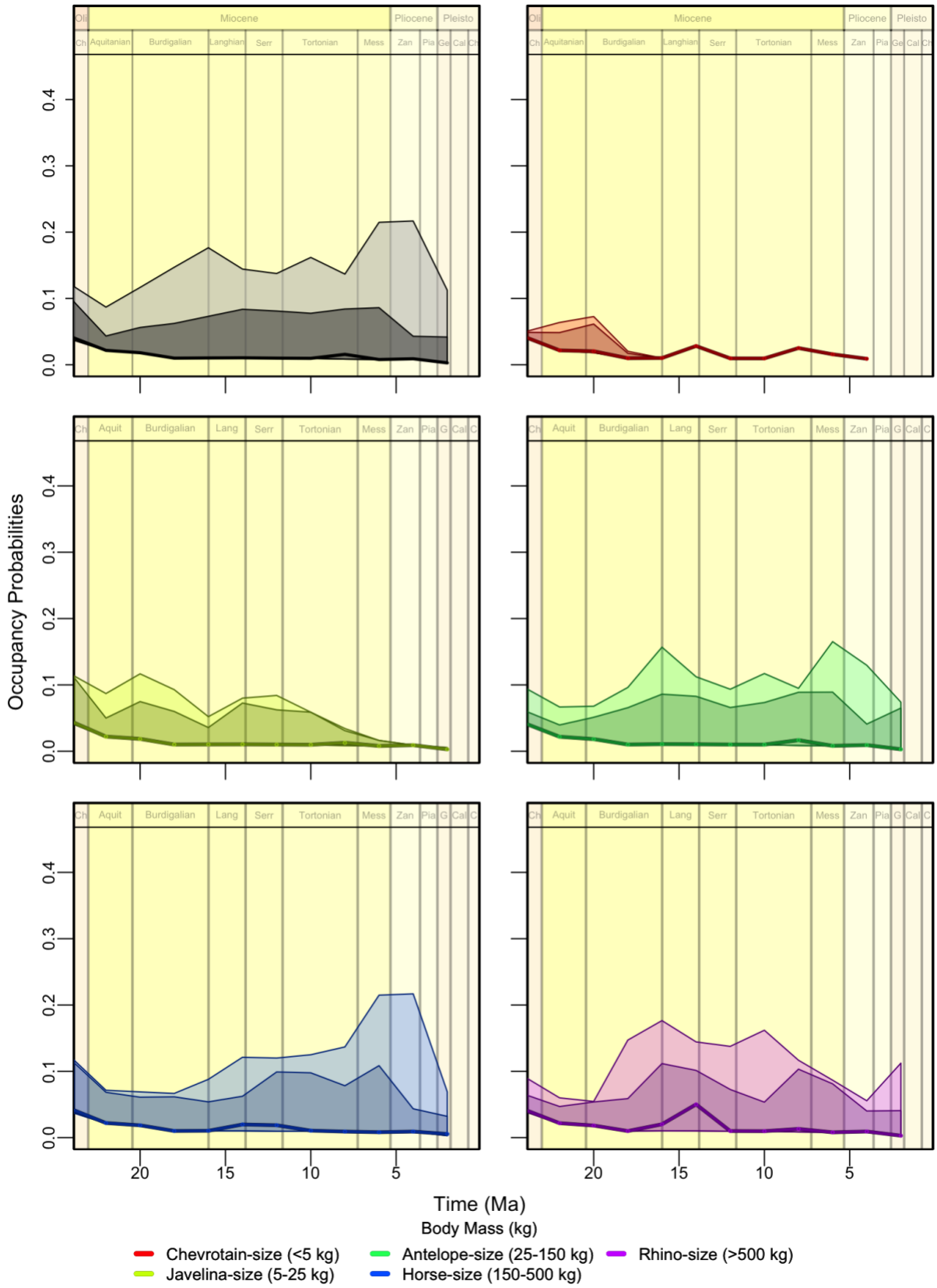
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Oli
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
G
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 36. Distribution of occupancy estimates for individual herbivore species for the herbivore guild in its entirety (black) or individual size categories. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.25-degree squares. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

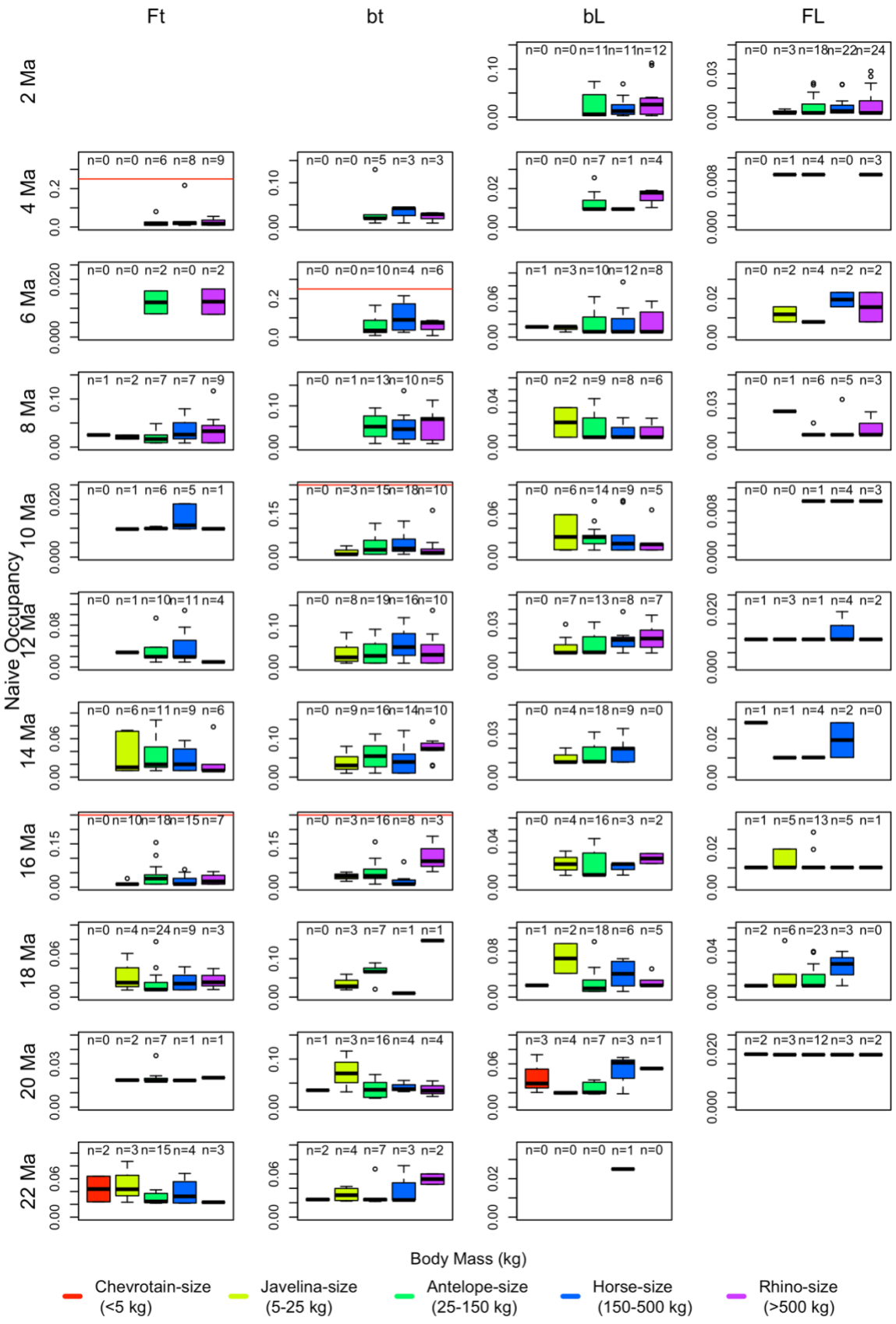
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 37. Distribution of species occupancy of North American herbivores across the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.125-degree squares. Species are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates.

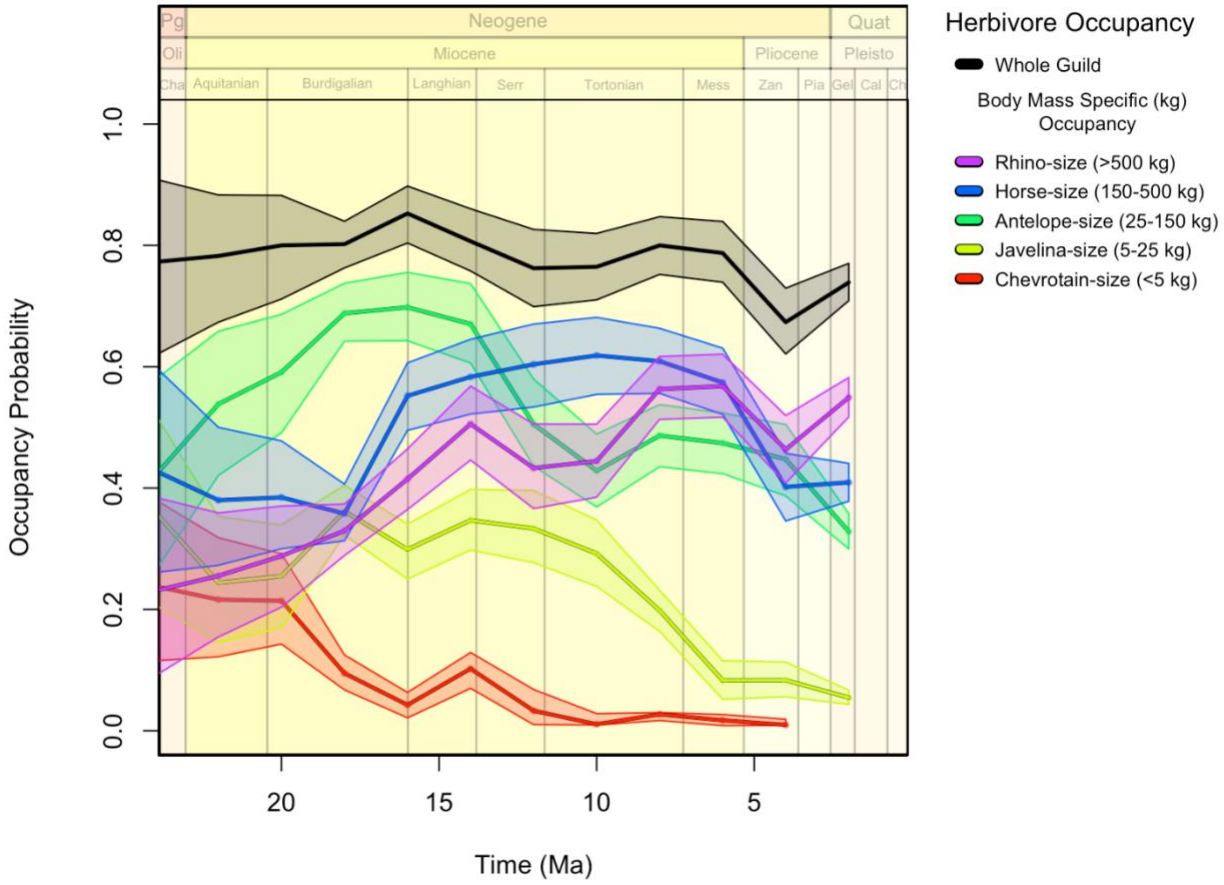

Figure 38. Occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.25-degree squares. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

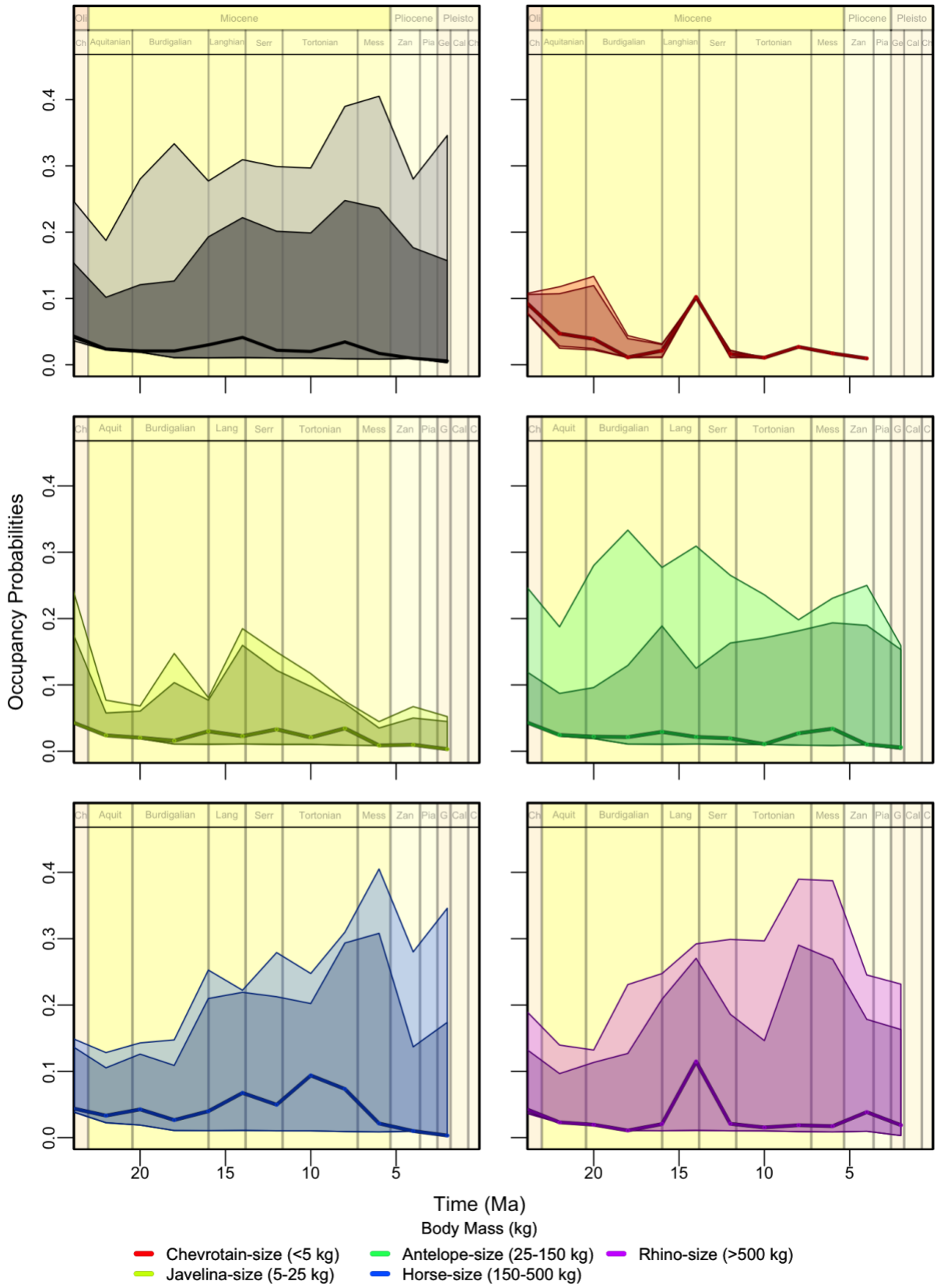
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Olig
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
G
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 39. Distribution of occupancy estimates for individual herbivore genera for the herbivore guild in its entirety (black) or individual size categories. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.25-degree squares. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

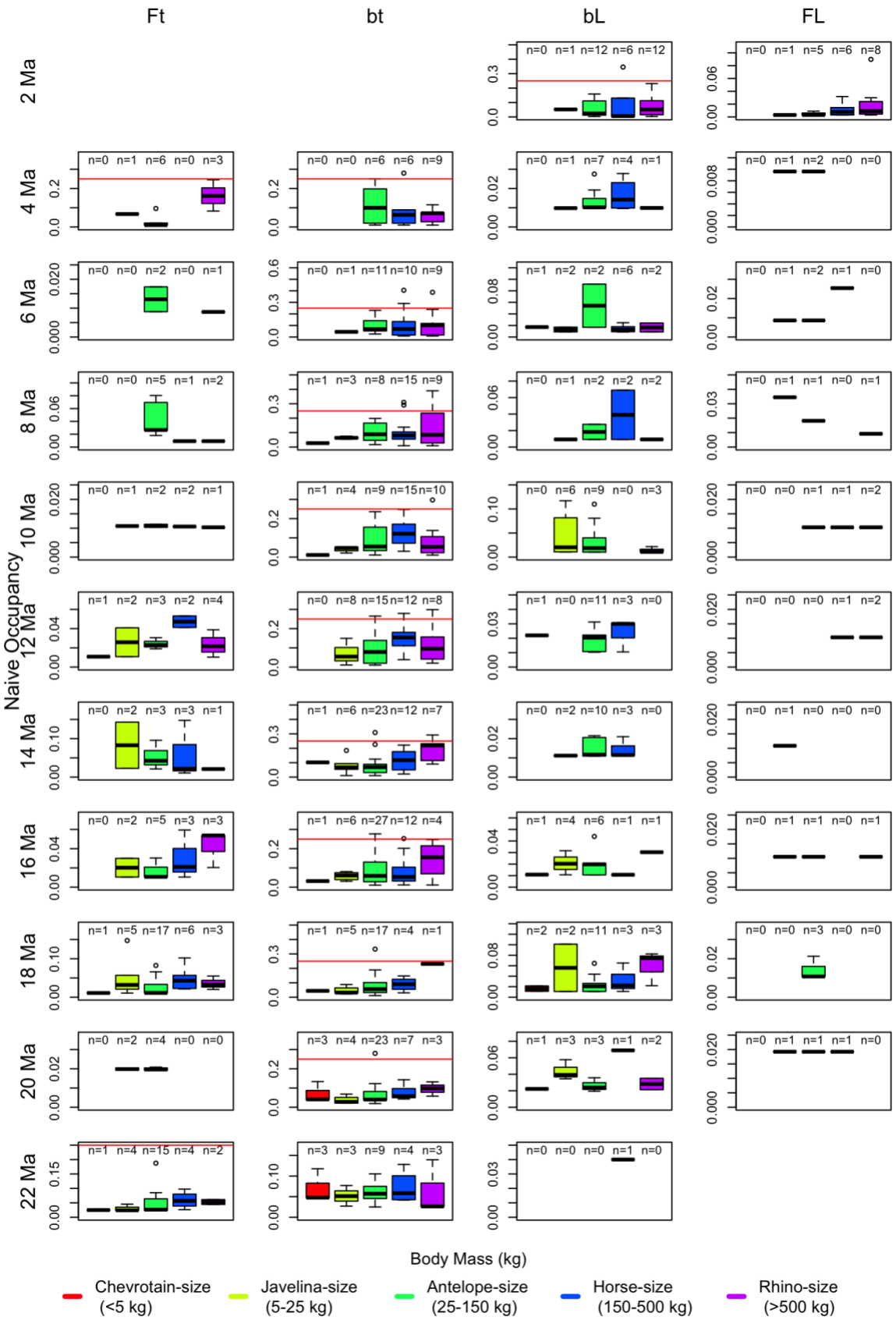
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 40. Distribution of generic occupancy of North American herbivores across the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.25-degree squares. Genera are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates.

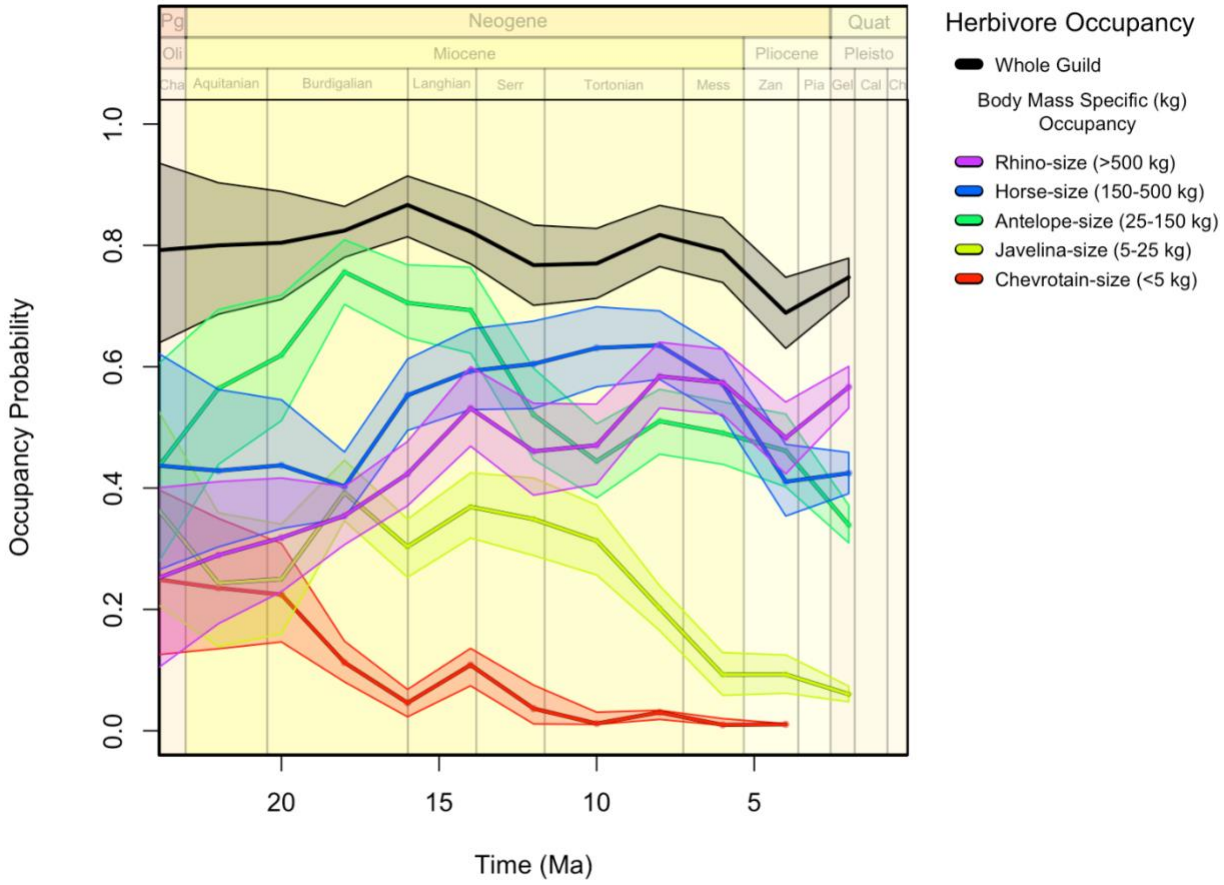

Figure 41. Occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.5-degree squares. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

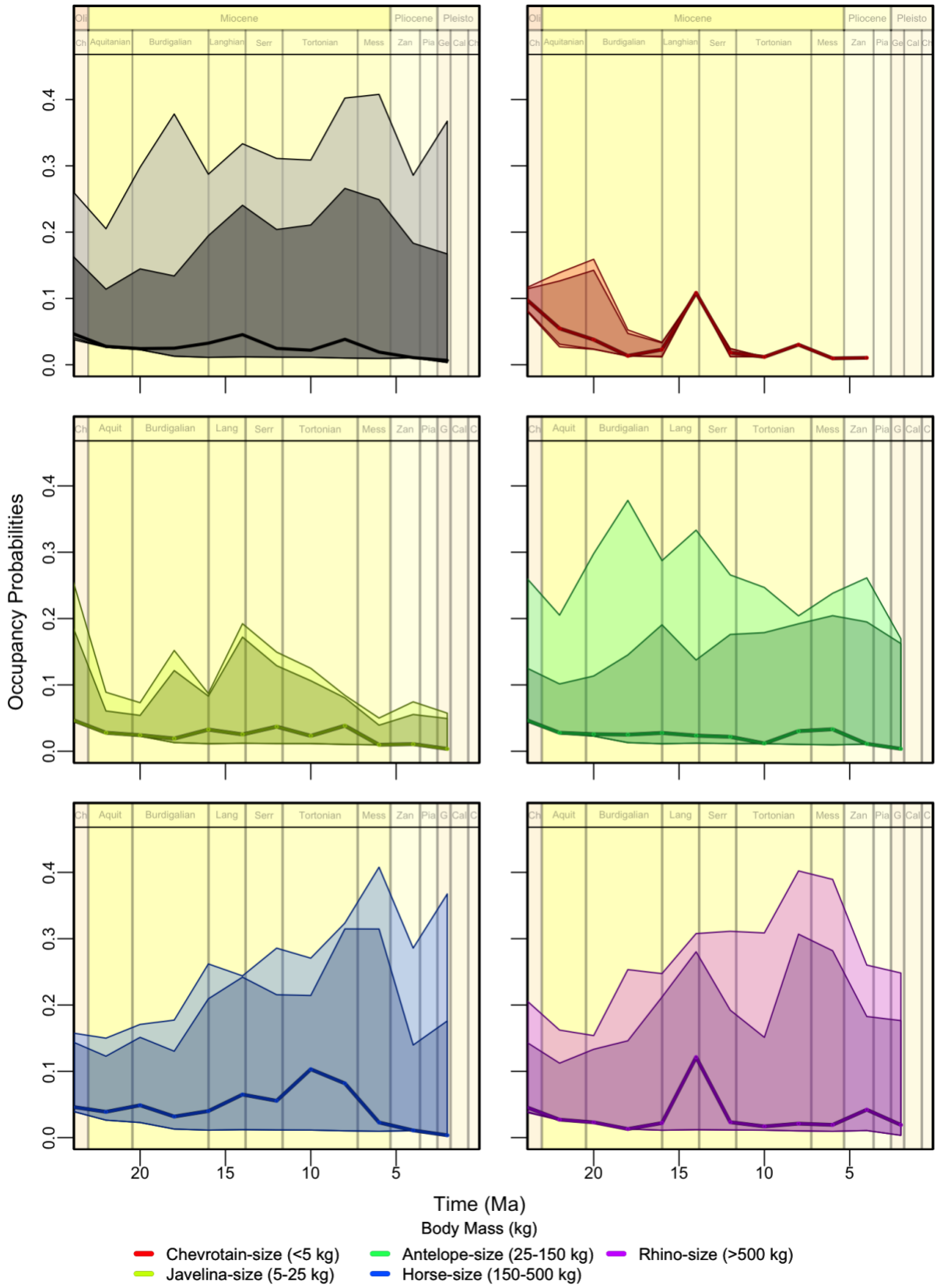
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Olig
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
G
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 42. Distribution of occupancy estimates for individual herbivore genera for the herbivore guild in its entirety (black) or individual size categories. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.5-degree squares. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

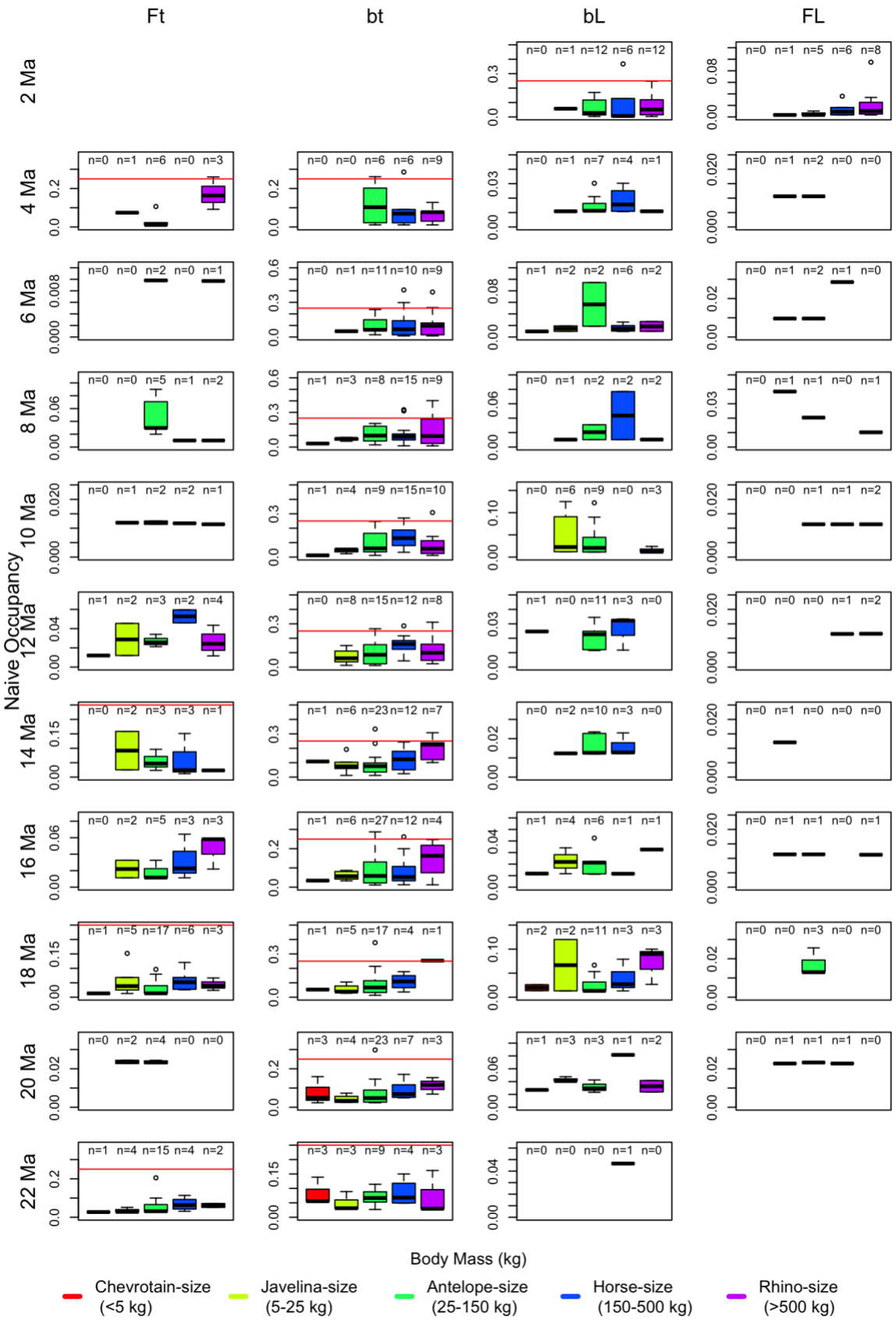
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 43. Distribution of generic occupancy of North American herbivores across the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 0.5-degree squares. Genera are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates.

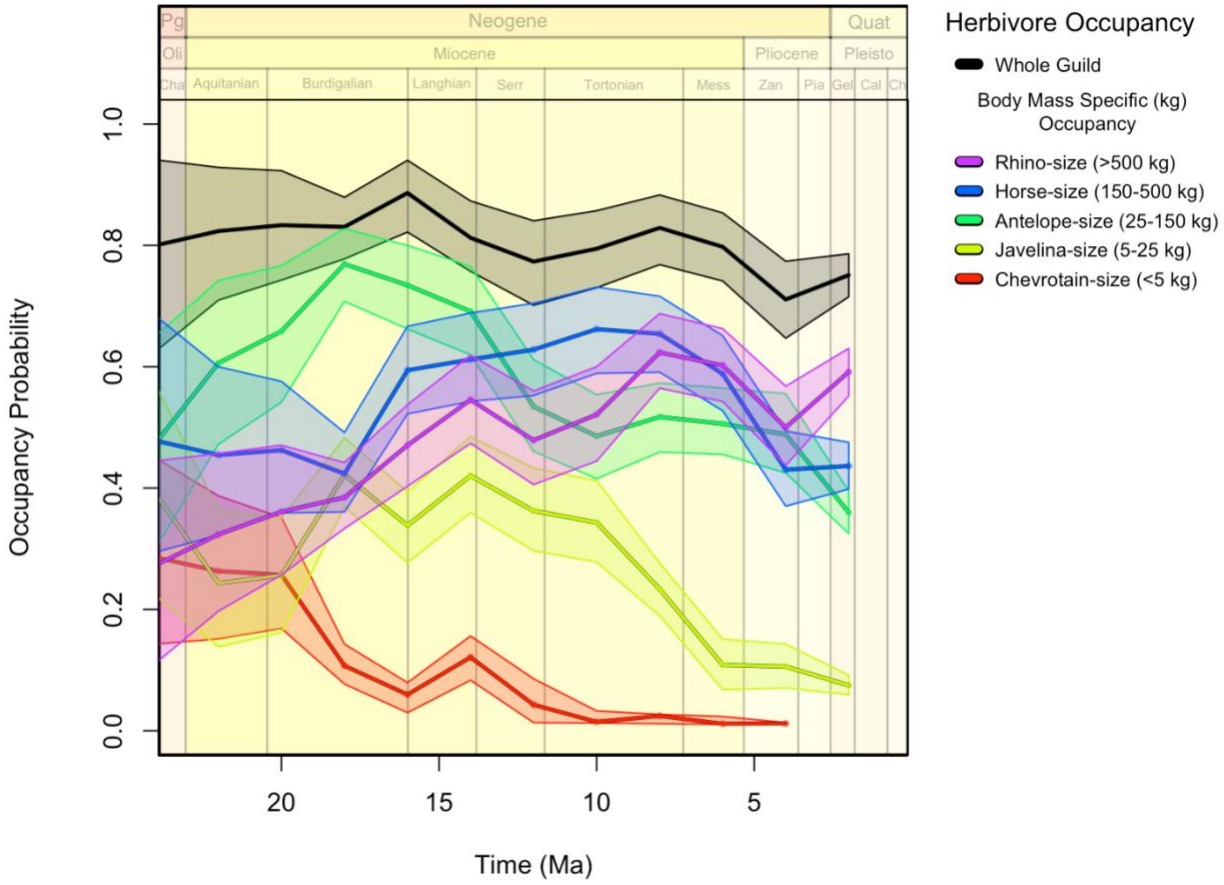

Figure 44. Occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 1-degree squares. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

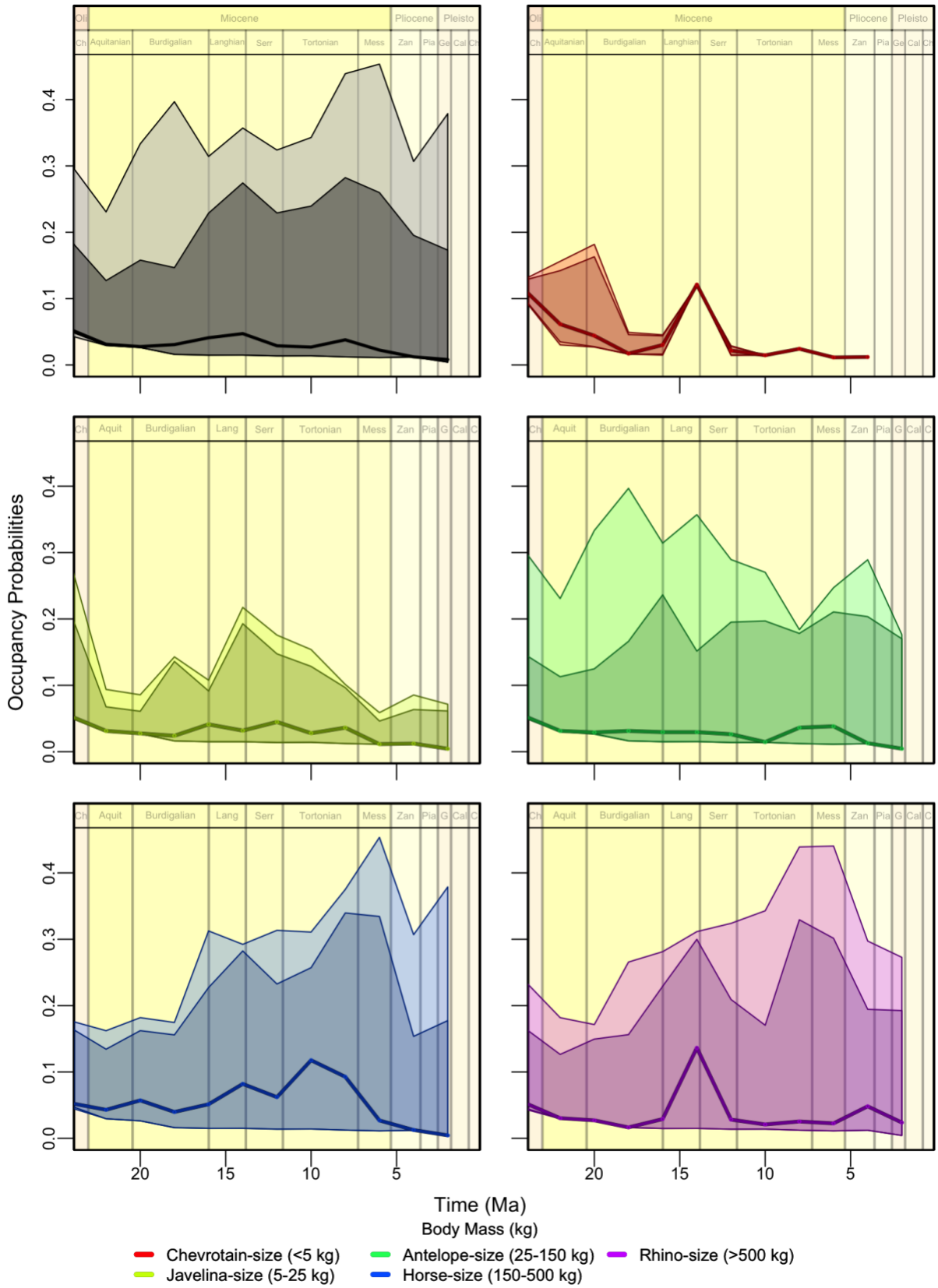
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Olig
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 45. Distribution of occupancy estimates for individual herbivore genera for the herbivore guild in its entirety (black) or individual size categories. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 1-degree squares. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

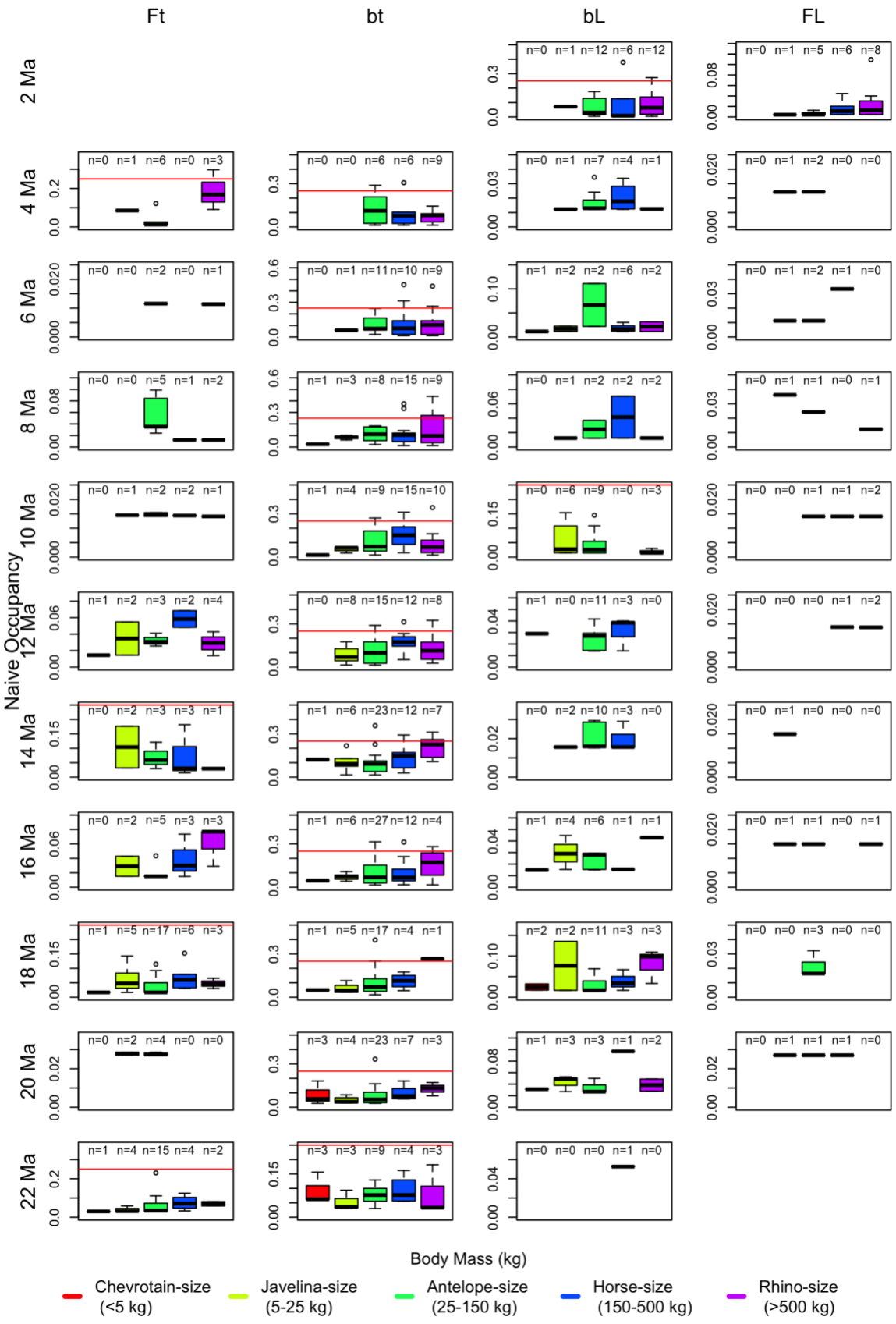
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 46. Distribution of generic occupancy of North American herbivores across the Neogene. Occupancy was estimated using sites that were an aggregation of Paleobiology Database collections that were contained within 1-degree squares. Genera are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates.

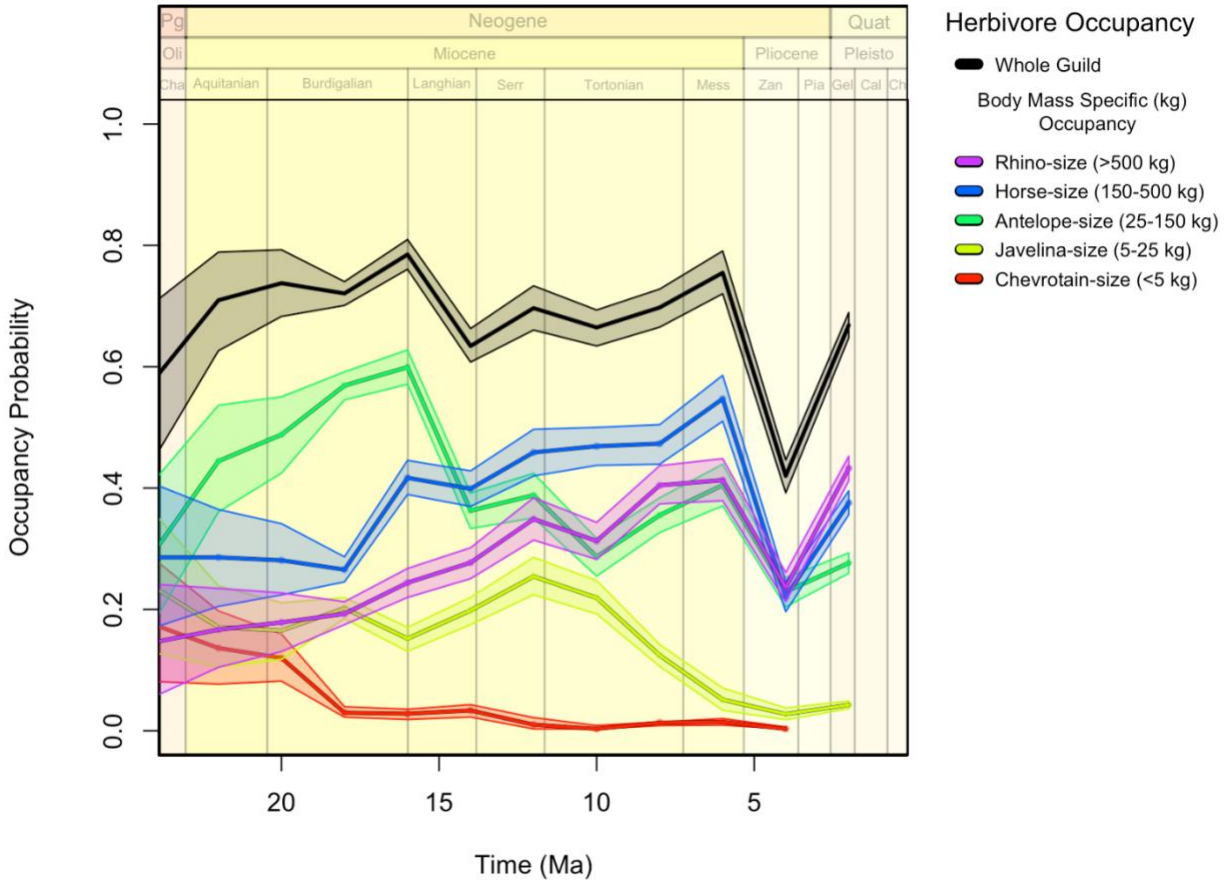

Figure 47. Occupancy estimates for the North American herbivore guild, both as a whole (black) or body mass specific (see legend), throughout the Neogene. Occupancy was estimated using Paleobiology Database without geographical aggregation. Thicker lines represent the median occupancy of each category as calculated from 2500 pseudoreplicates. The colored region around the median is the 95% confidence interval of occupancy estimates from those pseudoreplicates.

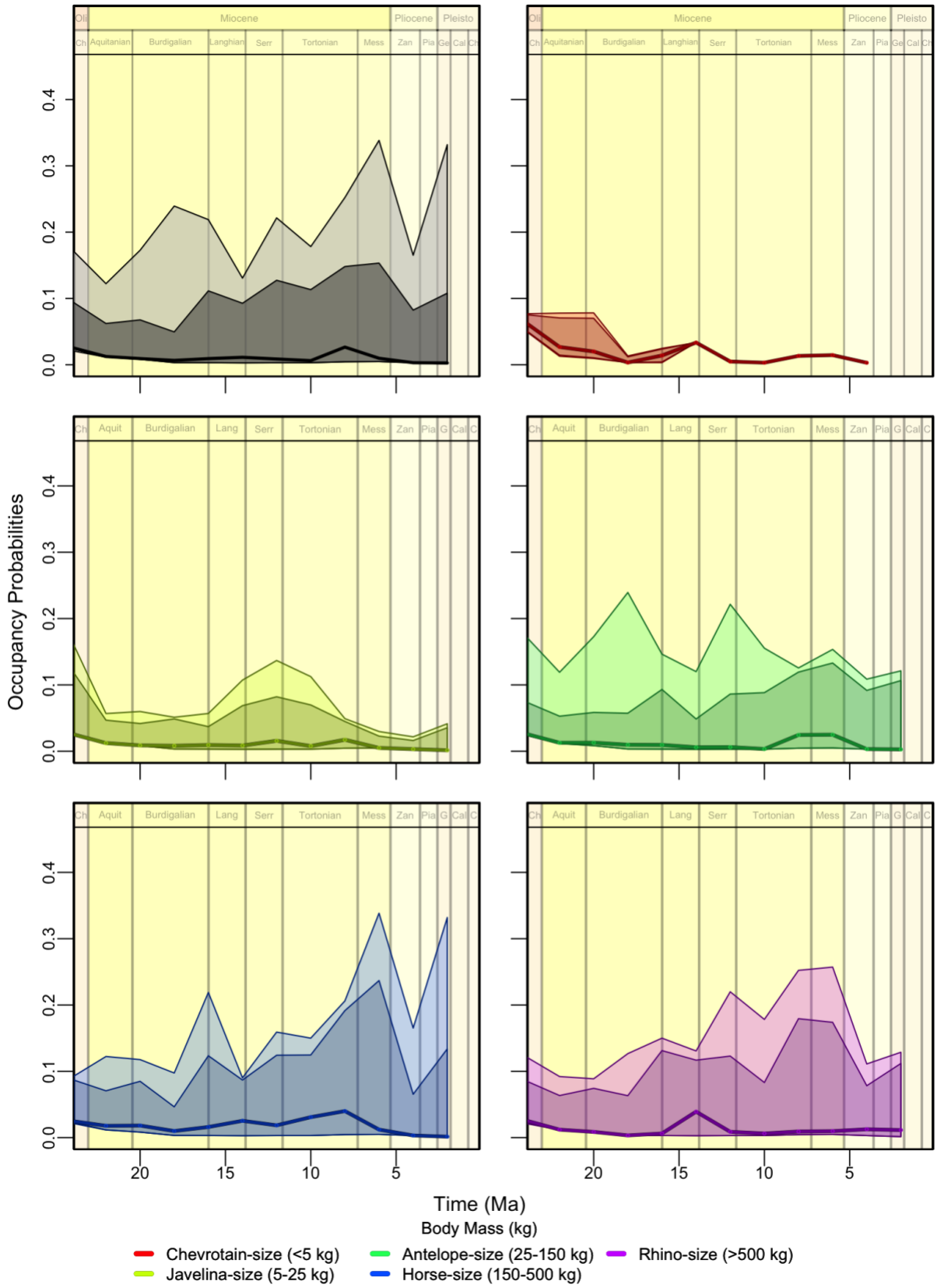
Occupancy Probabilities
0.0
0.1
0.2
0.3
0.4
Oli
Miocene
Pliocene
Pleisto
Ch
Aquitanian
Burdigalian
Langhian
Serr
Tortonian
Mess
Zan
Pia
Ge
Cal
Aquit
Lang
G
20
15
10
5
Time (Ma)
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 48. Distribution of occupancy estimates for individual herbivore genera for the herbivore guild in its entirety (black) or individual size categories. Occupancy was estimated using Paleobiology Database without geographical aggregation. The thick line represents the median occupancy of individual genera in each category. Colored regions surrounding the median are representative of the 90% confidence interval (darker color) and the minimum and maximum bounds for each category.

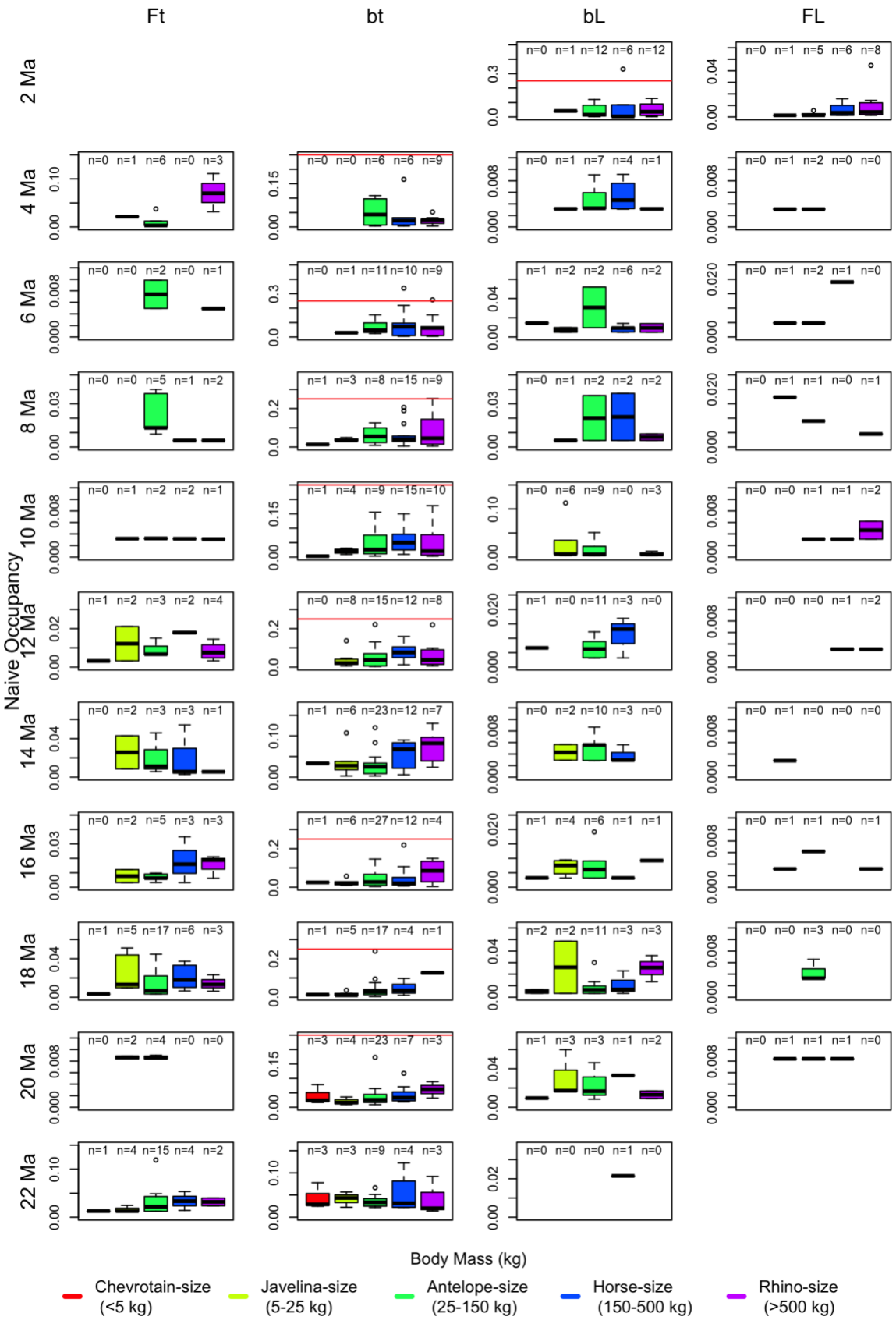
Ft
bt
bL
FL
2 Ma
4 Ma
6 Ma
8 Ma
10 Ma
12 Ma
14 Ma
16 Ma
18 Ma
20 Ma
22 Ma
Naive Occupancy
Body Mass (kg)
Chevrotain-size (<5 kg)
Javelina-size (5-25 kg)
Antelope-size (25-150 kg)
Horse-size (150-500 kg)
Rhino-size (>500 kg)

Figure 49. Distribution of generic occupancy of North American herbivores across the Neogene. Occupancy was estimated using Paleobiology Database without geographical aggregation. Genera are binned into the four fundamental classes of taxa (Foote, 2000) dependent on whether genera originated in an interval and persisted into the next (Ft), fully ranged through an interval (bt), entered the interval but went extinct (bL), originated and went extinct in the same interval (FL). Boxplots represent the distribution of median occupancy for each genus taken across 2500 pseudoreplicates.

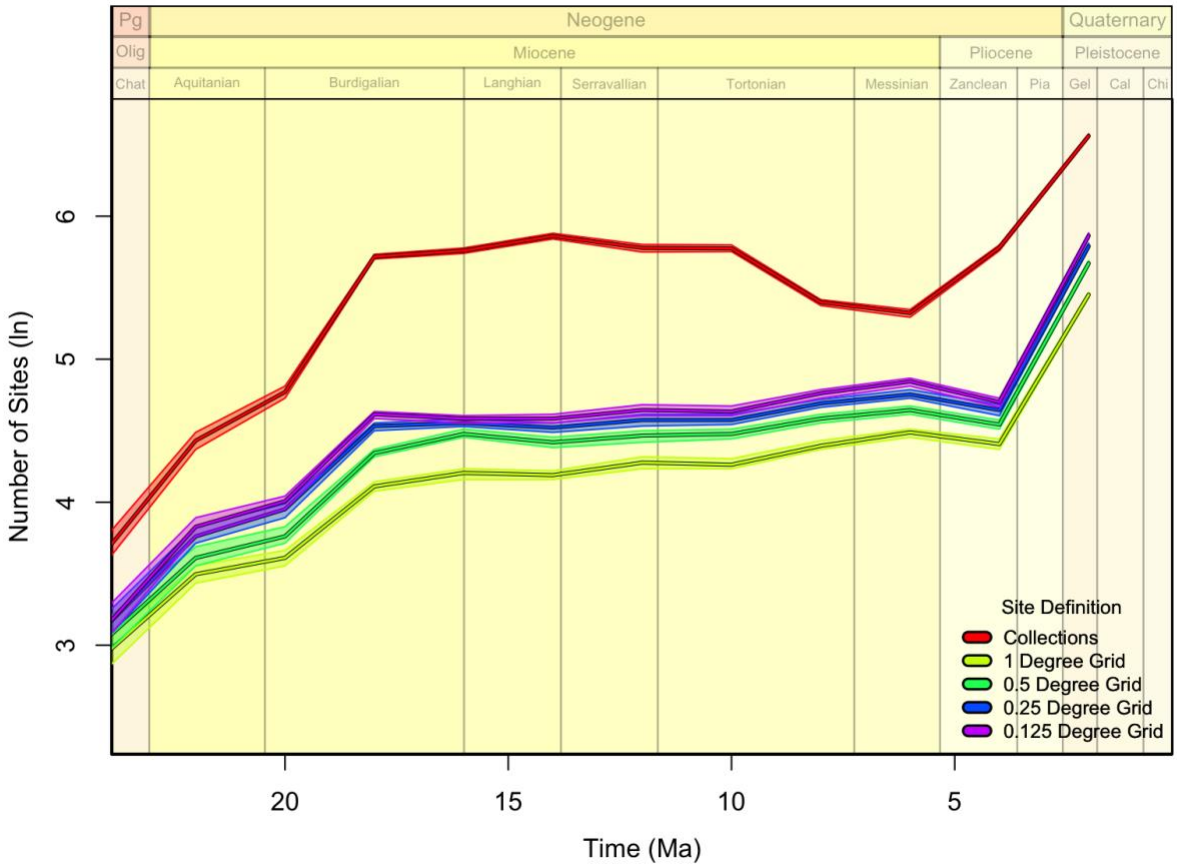

Figure 50. Number of sites present within North America over the Neogene. Sites are either equivalent to PBDB collections (red) or aggregations of PBDB collections that occur within the same 0.125- (purple), 0.25- (blue), 0.5- (green), or 1-degree (yellow) of latitude and longitude squares. The thicker solid line is the median number of sites present within and interval with the lighter shaded region being the 95% confidence interval. Both the median and confidence interval were calculated across 2500 pseudoreplicates.

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