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S. Kathleen Lyons

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Mammal community structure through the Paleocene-Eocene Thermal Maximum

Danielle Fraser^{1,2,3} and S. Kathleen Lyons⁴

Affiliations: ¹ Palaeobiology, Canadian Museum of Nature, PO Box 3443 Stn “D”, Ottawa ON K1P 6P4

² Biology & Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

³ Department of Paleobiology, Smithsonian Institution, National Museum of Natural History, 10th and Constitution NW, Washington, DC 20560-0121

⁴ School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE, 68502 USA

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ABSTRACT

Human-mediated species invasion and climate change are leading to global extinctions and are predicted to result in the loss of important axes of phylogenetic and functional diversity. However, the long-term robustness of modern communities to invasion is unknown, given the limited timescales over which they can be studied. Using the fossil record of the Paleocene-Eocene Thermal Maximum (PETM; ~ 56 Ma) in North America, we evaluate mammalian community-level response to a rapid global warming event (5° to 8°C) and invasion by three Eurasian mammalian orders and by species undergoing northward range shifts. We assembled a database of 144 species body sizes and created a time scaled composite phylogeny. We calculated the phylogenetic and functional diversity of all communities before, during, and after the PETM. Despite increases in the phylogenetic diversity of the regional species pool, phylogenetic diversity of mammalian communities remained relatively unchanged, a pattern that is invariant to the tree dating method, uncertainty in tree topology, and resolution. Similarly, body size dispersion and the degree of spatial taxonomic turnover of communities remained similar across the PETM. We suggest that invasion by new taxa had little impact on Paleocene-Eocene mammal communities because niches were not saturated. Our findings are consistent with the numerous studies of modern communities that record little change in community-scale richness despite turnover in taxonomic composition during invasion. What remains unknown is whether long-term robustness to biotic and abiotic perturbation are retained by modern communities given global anthropogenic landscape modification.

INTRODUCTION

Human activities are leading to the worldwide translocation of species (Vitousek et al. 1997, McKinney and Lockwood 1999, Myers and Knoll 2001, Early et al. 2016) and widespread range shifts under anthropogenic climate and land use change (Parmesan 2006, Chen et al. 2011, Kerr et al. 2015). Anthropogenic drivers are further implicated in significant changes in the formation of species assemblages, including biotic homogenization and loss of fundamental species associations (Vitousek et al. 1996, Vitousek et al. 1997, McKinney and Lockwood 1999, Parmesan and Yohe 2003, Vermeij 2005, Qian and Ricklefs 2006, Ricciardi 2007, Chen et al. 2011, Dornelas et al. 2014, Toth et al. 2014, Magurran et al. 2015, Early et al. 2016, Lyons et al. 2016a, Lyons et al. 2016b, McCreless et al. 2016, Seebens et al. 2017, Longman et al. 2018, Tóth et al. 2019). Significant losses of phylogenetic and functional diversity are also forecast under the current anthropogenic regime (Olden et al. 2004, Fritz and Purvis 2010, Huang et al. 2011). However, the timescales over which the responses of modern species assemblages can be studied are typically too short to address their long-term eco-evolutionary responses to abiotic and biotic perturbation (Dietl et al. 2015, Barnosky et al. 2017). Climate change (Zachos et al. 2001, Zachos et al. 2008) and species invasion via various mechanisms including migration over temporary land bridges, range expansions, and other long-distance dispersal modes (Simpson 1947, Vermeij 1991, Kerfoot and Weider 2004, Vermeij 2005, Ricciardi 2007, Woodburne 2010) have occurred numerous times throughout the past 66 Ma. The fossil record of these perturbations therefore provides an unparalleled opportunity for understanding and comparing their effects on timescales over which they are fully realized (Dietl et al. 2015, Barnosky et al. 2017).

The transition from Paleocene into the Eocene was marked by a rapid global warming event of 5° to 8°C known as the Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma) that followed an abrupt carbon isotope excursion (CIE) lasting 21 ky or less, signifying a significant shift in the global carbon cycle (Wing 2000, Gingerich 2003, Wing et al. 2005, Gingerich 2006, Woodburne et al. 2009, McInerney and Wing 2011). The PETM was accompanied by invasion of North American faunas by Eurasian species (the first appearances of Perissodactyla, Artiodactyla, and Primates on the continent) and northward range shifts of endemic mammals (Table S1) (Bowen et al. 2002, Gingerich 2006, Burger 2012, Bowen 2014). The combined effects of invasion and rapid climate change were significant decreases in body size within and among mammal genera as well as considerable species turnover (Clyde and Gingerich 1998, Gingerich 2006, Woodburne et al. 2009, Secord et al. 2012, Rankin et al. 2015). However, changes in community assembly under the dramatic environmental and biotic changes of the PETM have hitherto not been explored. We therefore ask: Did the abiotic and biotic changes characteristic of the PETM alter the ways in which associations of species (nominally, communities) were assembled? Using a large dataset of mammal occurrences in the Big Horn and Clark Fork Basins in Wyoming (Gingerich et al. 1980, Gingerich 1989, 2001), we test for changes in community structure before, during, and after the PETM. Given the considerable change in the composition of the regional species pool through the PETM, we expect significant change in multiple aspects of community structure.

The appearance and loss of species via speciation, extinction, and immigration/emigration determine the size and composition of the regional pool of species available to colonize local sites (Rosenzweig 1995). Partitioning of species from the regional pool among local assemblages then occurs *via* the various processes that comprise community

assembly. In general, the makeup of local assemblages is determined by the size and composition of the regional species pool as well as the outcomes of both species-species and species-environment interactions (Rosenzweig 1995, Caley and Schluter 1997, Whittaker et al. 2001, Kraft et al. 2015). Due to divergent phylogenetic ancestry and evolutionary histories, species differ in their environmental tolerances, food preferences, and competitive abilities (Rosenzweig 1995, Pavoine and Bonsall 2010, Kraft et al. 2015). Species are therefore differently able to colonize the same sites and, thus, the composition of local species assemblages varies among sites typified by different biotic and abiotic conditions. Depending on *inter alia* the steepness of environmental gradients, competitive factors, and rates of dispersal, local assemblages can differ markedly or little in species composition (Leibold et al. 2004, Turner 2004, Cottenie 2005, Badgley 2010, Kraft et al. 2011, Baselga et al. 2012, Dobrovolski et al. 2012, Qian and Xiao 2012, Cadotte et al. 2013). At the local scale, classical niche theory predicts that the ways in which species are packed into physical and niche (i.e., trait and phylogenetic) space reflect assembly mechanisms (MacArthur and Levins 1967, Webb 2000, Losos 2008, Cavender-Bares et al. 2009). By quantifying changes in regional and local scale diversity as well as niche division, we can therefore infer changes in community assembly during the PETM.

The turnover, phylogenetic, and functional components of diversity are used as proxies for community assembly and are extensively studied in modern contexts (Webb et al. 2002, Graham and Fine 2008, Vamosi et al. 2009, Buckley et al. 2010, Davies and Buckley 2011, Swenson 2011, Cadotte et al. 2013). They are complementary measures of community assembly because they quantify the degree to which species share the landscape and available resources. Typically, the turnover component (often referred to as β diversity) is measured as an average difference in species composition among sites using one of a variety of dissimilarity metrics

(Baselga 2010, Qian and Xiao 2012) and is highest when environmental gradients are steep (Buckley and Jetz 2008). The functional (i.e., trait) and phylogenetic components of diversity are measures of niche space division that have been variously related to climate (Eronen et al. 2010a, Eronen et al. 2010b, Polly 2010, Qian et al. 2013, Fraser and Lyons 2017), competitive interactions (Schoener 1974, Connor and Simberloff 1979, Mayfield and Levine 2010, Safi et al. 2011, Fraser and Lyons 2017), speciation and extinction dynamics (Huang et al. 2011, Razafindratsima et al. 2012, Fraser et al. 2015), and biogeographic history (Fraser and Lyons 2017, Lawing et al. 2017). Traits, e.g., body mass, locomotor strategy, and diet, are most often used as proxies for the functional role of a species in a community (Oliveira et al. 2016). Phylogenetic distances among species (e.g., mean pairwise distances on the tree) are used to approximate unmeasured niche dimensions under the assumption that niches are phylogenetically conserved (Ricklefs 2010). Because the turnover, phylogenetic, and functional components of diversity vary in ways that are indicative of changes in the underlying ecology, they are useful measures of assessing changes in community assembly across the PETM.

Given the considerable climatological, morphological, and taxonomic changes that characterized the PETM, we expect that the ways species interacted with each other and their external environment also changed, resulting in changes to community assembly. Today, communities with the most species, typically those found in the tropics, are characterized by patterns of high taxonomic turnover among communities, phylogenetic evenness (the exclusion of closely-related species from the same community), and ecological redundancy. In contrast, species poor communities tend to be comprised of phylogenetically closely-related species with high morphological disparity and little taxonomic turnover from one community to another (Buckley and Jetz 2008, Safi et al. 2011, Oliveira et al. 2016, Fraser and Lyons 2017). The

differences in community assembly among species rich and species poor communities appear to relate to differences in climate (insofar as climate impacts the energy available to species), rates of species immigration, and rates of resource competition (Buckley and Jetz 2008, Safi et al. 2011, Oliveira et al. 2016, Fraser and Lyons 2017). Making a space-for-time substitution, we predict that the rapid warming, species immigration, and increasing species richness that typified the PETM led the structure of mammal assemblages to more closely resemble modern, species rich communities, such as those in the neotropics. Therefore, we expect to see an increase in β diversity, phylogenetic evenness, and lower morphological disparity during and potentially after the PETM.

Herein, we test for changes in regional and local species richness as well as rates of mammal first and last appearances during the late Paleocene and earliest Eocene of the Bighorn and Clark Fork basins in North America. We then quantify the functional, phylogenetic, and turnover components of assemblage structure to infer changes in the formation of species assemblages before, during, and after the PETM.

MATERIALS AND METHODS

Our dataset spans the latest Tiffanian (~57.3 Ma) to earliest Wasatchian (~55.5 Ma) North American land mammal ages (NALMAs) and includes the vast majority of mammal species that occur during the Paleocene-Eocene Thermal Maximum (PETM) in North America (Table S2). Mammal occurrences were downloaded from the Paleobiology Database using the group name “mammalia” and the following parameters = Paleocene and Eocene, region = North America, paleoenvironment = terrestrial (see supplementary citation list for data sources). Occurrences were vetted and taxonomy was standardized to Janis et al. (1998) and Janis et al. (2008). We

included only species occurring in localities from Wyoming (Bighorn and Clarks Fork Basins). Wyoming is the only region in North America within which mammal-bearing localities of PETM age are definitive and thoroughly studied. The localities are therefore found in a relatively geographically restricted region (Fig. S1). As such, inferred assembly processes should be due to biotic interactions and regional scale differences in abiotic factors rather than broad-scale (e.g., continental-scale) differences in climate and habitat. Localities were assigned to NALMA subdivisions (Tiffanian 6, Clarkfork 1, Clarkfork 2, Clarkfork 3, Wasatch 0, and Wasatch 1-2) based on Gingerich (1989), Gingerich (2001), and Gingerich et al. (1980). Wasatch 0 encompasses the PETM. As in Rankin et al. (2015), we combine Wasatch 1 and 2. We calculated both gamma (regional) and alpha (local) diversity for each NALMA using the first-order Jackknife species estimator in the fossil R package (Heltshe and Forrester 1983, Smith and Belle 1984, Walther and Morand 1998, Vavrek 2012). We also calculated mean taxonomic differences using the Jaccard index between temporally adjacent time bins as a test of how much the taxonomic identity of species changed through the PETM.

Estimating rates of first and last appearances

To test whether invasion and rapid climate change increased rates of extinction or extirpation amongst North American mammals during the PETM, we estimated rates of first and last appearances throughout the interval. Herein, we use the terms first and last appearances because we recognize that many first appearances are a result of dispersal events (rather than true origination) both from Eurasia and northward from southern latitudes.

We created a NALMA subdivision by mammal species occurrence matrix for the Bighorn Basin of Wyoming (data described in earlier sections). To estimate rates of first and last

appearances we used a capture-recapture model known as the Pradel seniority model (Pradel, 1996). We have chosen to use the Pradel model because it accounts for heterogenous and incomplete sampling (Liow & Nichols, 2010). The Pradel model simultaneously fits five model parameters including survival probability (the probability that a species survives into interval $i + 1$), probability of extinction ($1 - \text{survival probability}$), seniority (the probability that an extant species was also extant in interval $i - 1$), net per capita diversification rate (the product of survival probability and the ratio of the number of new species appearing in interval $i + 1$ to the number of species present at interval i), and sampling probability (the probability that an extant species is actually sampled in interval i).

It is important to simultaneously estimate the sampling probability because the fossil record is characterized by presences and absences that are influenced by sampling effort as well as biotic and abiotic taphonomic processes. As a result, the first observation of a fossil species is unlikely to be the true time of appearance; there is some probability that the species originated in preceding intervals. The same is true of species last appearances dates. That is, species have some probability of having gone extinct following their apparent last appearance in the fossil record (Liow and Nichols 2010). We therefore estimated species first appearances, last appearances, and sampling probabilities using MARK (White and Burnham 1999) executed via RMark (Laake 2013). We selected the best fitted model (the full model having time varying origination, extinction, and sampling parameters) using AICc. A model with time varying origination and sampling parameters and a constant rate of extinction was best fit (Table 1).

Semiformal Supertree

We created a semi-formal supertree for all mammals crossing the Paleocene-Eocene Thermal Maximum in our dataset, which includes 96% of species occurring in Wyoming from Tiffanian 6 to Wasatch 1 and 2 (Appendix I). We have also included species from before and after the PETM because their exclusion would bias the phylogenetic tip dating methods described below. Our approach is similar to that used by Smits (2015). The backbone of the mammal phylogeny is based on Tarver et al. (2016) and intergeneric relationships presented by Halliday et al. (2015). For genera not found in the recent phylogeny of Halliday et al. (2015), we used taxonomy as a guide; we assumed species from the same genus were sister taxa except where Janis et al. (1998, 2008) suggests otherwise. We also assume that genera were closely related to species in the same clade except where the clade was known to be polyphyletic (e.g., “condylarths”). Although our supertree may contain as of yet unknown polyphyletic genera, it reflects the current state of knowledge. All uncertain interfamilial and inter-generic relationships were represented by polytomies. Almost all inter-species relationships were represented by polytomies, given that comprehensive, species-level phylogenies do not exist for most Paleocene-Eocene mammals. Polytomies are not problematic for the types of analyses used herein (Finarelli and Badgley 2010, Raia 2010, Fraser et al. 2015, Fraser and Lyons 2017). As described below, we control for the alternative ways in which polytomies may be resolved using posterior distributions of tree topologies. Even though the phylogenetic trees used herein were not derived cladistically, they still represent testable phylogenetic hypotheses. Furthermore, use of taxonomy can yield similar results to using a phylogeny (Soul and Friedman 2015), so we do not expect systematic bias in our results.

We scaled the branch lengths of the phylogeny to reflect time in millions of years using species first and last appearance dates. We binned first and last occurrence dates into NALMA

subdivisions because many of the dates are based on localities that are dated by biostratigraphy rather than direct dating methods (i.e., the dates can be constrained only to dates associated with the NALMA to which fossil localities can be referred). Dates for the NALMA subdivisions are based on paleomagnetism (Secord et al. 2006). We used several time scaling methods available in the paleotree R package (Bapst 2012) including the all branches additive or aba (Brusatte et al. 2008, Lloyd et al. 2012), minimum branch lengths or mbl (Laurin 2004), and cal3 dating methods (Bapst 2013). The aba method scales nodes to be as old as the first appearance of their oldest descendent and adds a user input time variable to every branch, which we set to 1 Ma. The mbl method scales all branches of a tree so that they are greater than or equal to the time variable of 1 Ma while subtracting time added to later diverging branches from earlier diverging branches to maintain the proper temporal order of speciation events (Laurin 2004, Bapst 2012). The cal3 method requires estimates of instantaneous per-capita rates of speciation and extinction (Bapst 2013), which we calculated by estimating the sampling probability per bin using a likelihood function (`make_durationFreqDisc` in Paleotree) and converting to instantaneous or per capita rates (`sProb2sRate` in Paleotree) as per the example provided in the Paleotree documentation (Bapst 2012). The cal3 method then stochastically timescales trees using a probability distribution (gamma distribution with a shape parameter of two) of waiting times between speciation and first appearance in the fossil record (Bapst 2013).

For all time scaling methods, we generated posterior distributions of 1000 trees because all three methods allow for the random resolution of polytomies and, in the case of cal3, stochastic estimation of branch lengths based on sampling and rate estimates. We therefore performed all further analyses using the entire posterior distributions of tree topologies. Thus, the precise number of polytomies present in our supertree is unimportant.

Community Structure through Time

To assess changes in mammal community assembly across the PETM, we used metrics of community structure including mean phylogenetic pairwise distance (MPD), the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) (Webb et al. 2002, Webb and Donaghue 2005, Qian et al. 2013), body mass dispersion (mean body mass difference among co-existing species; BM_{dist}) (Fritz and Purvis 2010, Fraser and Lyons 2017), body mass distributions (Brown and Nicoletto 1991, Bakker and Kelt 2000, Kelt and Meyer 2009, Lyons and Smith 2013, Smith and Lyons 2013), and multivariate dispersion (Anderson 2006, Anderson et al. 2006) as measures of phylogenetic diversity, functional diversity, and mean taxonomic dissimilarity, respectively.

We first created locality-by-species occurrence matrices for each NALMA subdivision, limiting our sample to include only localities with 5 or more species occurrences. Our sample therefore includes 809 individual occurrences of 144 unique mammal species (Table S2). Individual fossil localities are treated as individual communities assembled from a regional pool of species (i.e., all species present in a given time interval). We quantified each metric both with and without species whose first appearances occur during the PETM (Table S1). Excepting Artiodactyla, Perissodactyla, and Primates, we have no way of differentiating invasions from southern latitudes from true speciation events. For each metric, we then evaluated the degree of observed change between consecutive NALMAs using Cohen's D (Cohen's $D = (\text{mean observed first NALMA} - \text{mean observed second NALMA}) / \text{pooled standard deviation}$). We consider absolute values of $d \leq 0.2$ small effect sizes and $d \geq 0.8$ large effect sizes, in keeping with convention (Cohen, 1988).

Phylogenetic Community Structure

Using the semiformal supertree, we first calculated mean pairwise phylogenetic distances for the regional species pools in each time bin (Table S4) as a measure of how the phylogenetic-relatedness of species assemblages changed, given invasion from Eurasia, northward range shifts, and speciation events.

We calculated the Net Relatedness Index (NRI) for each NALMA subdivision using the *picante* R package (Webb 2000, Webb et al. 2002, Kembel et al. 2014). NRI is a standardized measure of mean pairwise phylogenetic distances among co-occurring species. We have chosen NRI from among the several available metrics for phylogenetic diversity because it shows less co-linearity with species richness (Oliveira et al. 2016). Furthermore, NRI outperforms other similar metrics such as the Nearest Taxon Index at detecting environmental filtering (Freilich and Connolly 2015). The Net Relatedness Index is calculated as:

$$NRI = \frac{-1 * MPD_{obs} - mean(MPD_{exp})}{std(MPD_{exp})} \quad (\text{Equation 1})$$

where MPD_{obs} is the observed mean pairwise distance among species in the observed community and MPD_{exp} is calculated from a large sample of randomly drawn communities (Webb 2000). Positive values of NRI indicate that species in an assemblage (i.e. species that co-occur within a specific community) are more closely related than expected by chance (phylogenetically clustered). Negative values of NRI indicate that species in an assemblage are more distantly related than expected by chance (phylogenetically even). NRI values of zero indicate phylogenetic randomness (Webb 2000, Webb et al. 2002, Raia 2010).

We also calculated the Nearest Taxon Index (NTI) for each NALMA subdivision using the *picante* R package (Webb 2000, Webb et al. 2002, Kembel et al. 2014). NTI is a standardized measure of mean nearest taxon phylogenetic distances among co-occurring species. We have

chosen to also include NTI because it outperforms NRI at detecting limiting similarity (Freilich and Connolly 2015), but opted to include NRI also because the two metrics are useful for detecting different assembly processes. The Nearest Taxon Index is calculated as:

$$NTI = \frac{-1 * MNTD_{obs} - mean(MNTD_{exp})}{std(MNTD_{exp})} \quad (\text{Equation 2})$$

where $MNTD_{obs}$ is the observed mean nearest taxon distance among species in the observed community and $MNTD_{exp}$ is calculated from a large sample of randomly drawn communities (Webb 2000). Positive values of NTI indicate that species in an assemblage (i.e. species that co-occur within a specific community) are more closely related than expected by chance (phylogenetically clustered). Negative values of NTI indicate that species in an assemblage are more distantly related than expected by chance (phylogenetically even). NTI values of zero indicate phylogenetic randomness (Webb 2000, Webb et al. 2002, Raia 2010).

NRI and NTI must be standardized using null models because they are intended as measures of phylogenetic separation among species in the same community relative to a random selection of species in the regional pool (Webb 2000). NRI and NTI are only meaningful if the pool from which random assemblages of species are drawn are potential colonizers of any given site. Using a species pool that combines all time periods would randomly place taxa that never co-occurred in time in the same communities, inflating the denominator of each metric and reducing NRI and NTI. Therefore, a null model comprised of temporally-separated species is not useful for the purpose of calculating such community assembly metrics. Although a null model combining all time periods would scale phylogenetic diversity in the different NALMAs allowing for comparison of relative levels of phylogenetic diversity across time, it would not address the question we are asking, which concerns inferring community assembly processes given patterns of regional-scale phylogenetic diversity. By asking how clustered or even

community phylogenetic diversity is given the available regional species pool for a time period, we are asking about the relative importance of processes that can be inferred from these metrics (e.g., environmental filtering and limiting similarity) within each NALMA.

We chose to generate randomized communities for NRI and NTI calculation from the regional species pool for each time bin using a simple null model in which site richness is held constant but species occupancy is not (herein termed taxon shuffling) (Kembel 2009). For comparison, we also use the independent swap algorithm of (Gotelli 2000, Kembel and Hubbell 2006, Hardy 2008) because null models that maintain both grid cell richness and species occupancy yield the most reasonable rates of both Type I and Type II error (Kembel 2009). Swap algorithms start with the original occurrence matrix and involve randomly choosing submatrices with adjacent 1's and 0's then swapping them while retaining the row and column totals (Gotelli 2000, Gotelli and Entsminger 2001). However, we opted to present the results of the taxon shuffling model in the main text because the swap algorithm deals poorly with a nested occurrence matrix (those in which richness changes among sites and sites are occupied by subsets of the same species).

To test the degree to which our results are dependent on tree topology and resolution, we systematically degraded the phylogeny by collapsing increasing proportions (25% & 50%) of the phylogeny into polytomies using the `degradeTree` function in `paleotree` (Bapst 2012). The function randomly selects nodes in the phylogeny to collapse. We performed tree degradation 1000 times across a single phylogeny that was dated using the `cal3` method and re-calculated NRI and NTI. To reduce computation time, we did not perform the tree degradation analysis for all dated trees in this study (i.e., we did not perform tree degradation using the maximum length

branches and all branches additive dated trees nor across the entire posterior distribution of 1000 cal3 dated trees).

Body mass dispersion

Mammal body mass estimates were drawn from multiple literature sources (Alroy 1998a, Tomiya 2013, Smits 2015, Smith et al. 2018). Species for which body mass data were unavailable were assigned an average for their respective genus. Body mass estimates were therefore derived for 100% of taxa in our dataset (144 species). All body mass estimates were \log_{10} transformed.

We use body mass as the functional trait of interest because mammalian body size is a determinant of many niche characteristics including *inter alia* geographic range size, population density, dispersal ability, life history, metabolism, and the thermal niche (Peters 1983). Furthermore, body mass is collinear with many of the additional traits (e.g., diet) included in the calculation of functional diversity (Pineda-Munoz et al. 2016) and is a highly heritable trait in mammals (Smith et al. 2004). As a result, studies that include additional functional variables such as broad dietary category diet (e.g., herbivore, carnivore) do not yield patterns of functional diversity different from those expected for body mass dispersion alone (e.g., functional clustering in the tropics) (Safi et al. 2011, Oliveira et al. 2016, Fraser and Lyons 2017, Mazel et al. 2017, Fraser et al. 2018), suggesting that body mass does capture the major axes of niche variation (Rowan et al. 2016). Furthermore, inclusion of a large number of functional traits becomes redundant with phylogenetic diversity (Tucker et al. 2018).

Body Mass Distributions

To assess possible changes in the regional species pool, we compared the shape of body mass distributions among the six different North American Land Mammal Ages used herein. Histograms were constructed for each NALMA using all species present. The shapes of the distributions were compared using Kolmogorov-Smirnov two sample tests. Because we compared all pairwise combinations of NALMAs, we applied a Bonferroni correction.

Mean Taxonomic Dissimilarity

We calculated mean taxonomic dissimilarity using multivariate dispersion (Anderson et al. 2006, Fraser et al. 2014) for each NALMA subdivision and the Jaccard and Bray-Curtis faunal dissimilarity metrics. We then subject the dissimilarity values amongst sites in each NALMA to principal coordinates analysis (PCoA). We calculated Euclidean distances in PCoA space of all localities from the centroid using the R package *vegan* (Oksanen et al. 2012). Larger distances from the centroid indicate greater faunal dissimilarity among localities. We did not regress the Bray-Curtis or Jaccard index values against distance (i.e. distance decay of similarity), as has been used for modern species (Qian et al. 2009), because we have found such an approach to be highly influenced by species-area relationships, changes in distances among localities, and the number of taxa in the sample (results not shown).

Testing for significant change in community assembly through time

The core question of the present paper pertains to whether community assembly changed across the PETM. Regression analyses (i.e., linear regression) of community structure versus time are problematic because the sample size ($n=6$) is too small and thus lacks power.

Furthermore, we show that taxonomic similarity among NALMAs is low, signifying high rates of turnover among time bins across the entire interval (Fig. 1A). Because biodiversity metrics can be sensitive to sampling intensity, including the number of samples (Gotelli and K. Colwell 2011), the number of species (Ulrich et al. 2018), and the occupancy or fill of the species-by-site occurrence matrix (Ulrich and Gotelli 2007a, b), we used a null model, which randomizes the assignment of each site to a particular time bin (Gotelli 2000). The model preserves species associations at each site (i.e., co-occurrence at the same site), the total number of species occurrences, as well as the number of sites per time bin. However, the model reshuffles patterns of species association that change among the time bins. All community structure metrics were then compared to this null model through calculation of standardized effect sizes (Cohen's $D = (\text{mean observed} - \text{mean null}) / \text{standard deviation of null}$) to assess whether observed change among the time bins was more or less than expected based on changes in sampling intensity, number of sites, number of species, and matrix fill among bins. We consider absolute values of $d \leq 0.2$ small effect sizes and $d \geq 0.8$ large effect sizes.

The null model we employ to test for differences among time bins necessarily differs from the null model we use during the calculation of NRI and NTI. The former is used to help differentiate significant from non-significant differences among time bins. The latter is used to assess community-scale clustering and evenness relative to random sample of species from the regional pool.

Modern Comparison

We downloaded spatially referenced geographic range data for modern non-volant Western Hemisphere mammals (Patterson et al. 2007), which uses the taxonomy of Wilson and

Reeder (2005). The dataset includes 1366 species after the exclusion of a small number of unreadable or corrupted files. The Western Hemisphere mammal dataset has been used in other recent studies of community structure (Fraser and Lyons 2017, Polly et al. 2017). We sampled the ranges of extant Western Hemisphere mammals using a Behrmann equal area projection as per (Faurby and Svenning 2015) and 100 km by 100 km grid cells because smaller grid cell sizes are subject to bias (Hurlbert and Jetz 2007). We considered grid cells to be occupied by a species if the center of the cell intersected with its geographic range (Safi et al. 2011, Faurby and Svenning 2015). The result was a species by grid cell occurrence matrix, which we used for further analyses. We downloaded body size data for 1070 western hemisphere mammal species from the PanTHERIA database (Jones et al. 2009). Body masses were ln transformed before further analysis.

For each grid cell, we calculated the Net Relatedness Index using the modern mammal phylogeny of (Fritz et al. 2009), BM_{dist} , and β diversity. For NRI and NTI, we constructed randomized communities using the independent swap and taxon shuffling algorithms, as with the fossil communities. For β diversity we used the R function `spDistsN1` to calculate the great circle distances amongst grid cells. To calculate multivariate dispersion, we used a spatial window of 1000km and subsampled grid cells using the inverse of the great circle distance as the probability of selection (similar to the approach of (Buckley and Jetz 2008)). For each subsampled group of grid cells, we then performed the multivariate dispersion analysis and extracted the average distance of the focal grid cell from the centroid in PCoA space. For all three metrics, we plotted the values back onto projected maps of the Western Hemisphere under a Behrmann equal area projection.

RESULTS

There is considerable turnover in community composition and increasing phylogenetic diversity (measured as mean pairwise distances) of the regional species pool through the sampled interval (Fig. 1A-B), which reflects lengthening of branches due to evolutionary time as well as first and last appearances (invasions and speciation). High rates of mammal first appearances (speciation plus northward range shifts and invasions) during the PETM are not matched by increasing extinction/extirpation, leading to both increased γ (regional richness; Fig. 1C) and α diversity (local richness; Fig. 1D). Because our data record the high rate of species first appearances in North America during the PETM, despite declining sampling rate (Fig. 1C; purple dotted line), we reject data insufficiency as a driving factor for any of the patterns observed herein.

Except for the comparison between the Tiffanian 6 and Wasatch 1-2, the shape of the mammal body mass distribution is unchanged through the PETM (Clakfork 3 through Wasatch 0; $p > 0.05$; Table 2 & Fig. 2;), suggesting little change in the functional composition of the regional species pool, despite considerable taxonomic turnover; Fig. 1A). All observed changes should therefore reflect changes in community assembly rather than functional changes in the regional species pool.

North American Paleocene-Eocene mammal communities show lower mean taxonomic dissimilarity and higher phylogenetic diversity than most modern temperate mammal assemblages (Fig. 3) and are most comparable to modern assemblages at subtropical latitudes and the southeastern United States (Fig. S2 & Fig. S3). However, PETM mammal communities are more functionally homogenous than modern tropical assemblages (Fig. S3A), likely reflecting the smaller maximum body sizes of Paleocene through early Eocene mammals (Alroy

1998a, Smith et al. 2010). It is well-documented that the fossil record is biased against species of small body size but, because PETM communities are dominated by relatively small species, further sampling is likely only to strengthen this result.

We observe increases in the Net Relatedness and Nearest Taxon Indices during the PETM (Fig. 3A-B; Table 3). Under null expectations, however, both the NRI and NTI of PETM mammal communities decline (Fig. 3A-B), thus yielding large values of Cohen's D (calculated as the standardized difference between the observed and null; Table 4). We interpret NRI as indicating a shift from marginally phylogenetically even to marginally clustered and NTI as indicating a shift from evenness to indistinguishable from random because they are centered on zero (Fig. 3A-B). The effect sizes for differences among the earliest NALMAs (e.g., Tiffanian 6 – Clarkfork 1) are low and sample sizes are low, suggesting low statistical power. The effect sizes for change from Clarkfork 3 through Wasatch 0 (the PETM; primary focus of the present study) are >0.8 , indicating large mean differences (Table 3) and sufficient statistical power, given that both NALMAs are represented by >20 fossil sites. When comparing the changes in NRI and NTI across the PETM to spatial patterns of phylogenetic relatedness for modern Western Hemisphere mammals, however, we find that the change is similar in magnitude to variation observed within the same region (Fig. S2); the mean value of NRI changes from ~ -0.55 to 0.64, which is equivalent to the difference between northern Massachusetts and Nova Scotia (Fig. S2). Similarly, the change in NTI is equivalent to the difference between southern Florida and northern Florida. In neither case, do the mammal faunas vary considerably in richness or composition among the compared regions. We therefore suggest that the comparatively large effect sizes for Clarkfork 3 and Wasatch 0 are not indicative of biologically meaningful differences nor of low statistical power.

The patterns we observe for the NRI and NTI are invariant to phylogenetic time-scaling technique and the loss of up to 50% of phylogenetic resolution (Fig. S4-5), suggesting that even major changes in tree topology would not fundamentally alter our results. Change in NRI and NTI are comparatively muted when using the independent swap algorithm to calculate within-bin null models (Fig. S6) because it is a conservative null model algorithm. That is, our findings related to NRI and NTI appear to depend on the null model of choice; use of the independent swap algorithm suggests that both NRI and NTI are inconsistent with phylogenetic clustering and evenness (Fig. S6). For NRI, the finding of marginally increased clustering is therefore equivocal.

Mean body mass dispersion declines slightly through the PETM (Fig. 3C) and effect sizes for change among NALMAs are moderate across the PETM (Table 3) but the standardized differences between null and observed values are low, indicating that the observed change is within null expectations (Table 4). Thus, observed change in body mass dispersion likely only reflects the well-documented decline in the body mass of some mammal species (Secord et al. 2012) and not a change in community assembly processes. Mean taxonomic dissimilarity increases from the latest Tiffanian to earliest Wasatchian but the change is similarly indistinguishable from null expectations (Fig. 3D; Table 4) although standardized effect sizes are moderate to high (Table 3). These non-significant findings are unlikely to be due to low statistical power, given that the PETM is well sampled (>20 sites) and we employed 1,000 iterations of each null model.

All community assembly metrics show approximately the same pattern of change when species that first occur during the PETM (putative immigrants and new species) are excluded (Fig. S7).

DISCUSSION

During the Paleocene-Eocene Thermal Maximum (PETM), invasion by entirely new orders of mammals (Primates, Artiodactyla, and Perissodactyla) and range expansions among endemic North American mammals (Bowen et al. 2002, Gingerich 2006) led to increasing γ (regional richness; Fig. 1C; black dotted line) and α diversity (local richness; Fig. 1D). From Clarkfork 3 (latest Paleocene) to Wasatch 0 (PETM), mean α diversity increased by ~30%. Following the PETM, there was an additional 15% increase (Wasatch 1 and 2; Fig. 1C). Increases in α and γ diversity are consistent with our finding of an enhanced rate of first appearances that is not matched by an enhanced rate of extinction (Fig. 1C). The changes in γ diversity led to an overall decrease in taxonomic similarity (Fig. S1A) as well as increasing phylogenetic diversity of the regional species pool (Fig. 1B), which reflects a combination of evolutionary time and invasions.

The assembly of local communities is determined by a combination of the size and composition of the regional species pool as well as the outcomes of species-species and species-environment interactions (Rosenzweig 1995, Caley and Schluter 1997, Whittaker et al. 2001, Kraft et al. 2015). Therefore, given the rapid abiotic and biotic changes of the PETM, we expected change in multiple dimensions of community structure. Using a space-for-time substitution, we predicted that the structure of PETM and early Eocene communities would resemble modern species rich communities, which are typified by phylogenetic evenness, ecological redundancy, and high turnover of species from one community to another (Buckley and Jetz 2008, Safi et al. 2011, Oliveira et al. 2016, Fraser and Lyons 2017), more than Paleocene communities. Aside from a statistically poorly supported increase in the Net Relatedness Index during the PETM, suggesting a small degree of phylogenetic clustering, we

find little evidence for any marked changes in community structure, whether measured in using phylogenetic, trait-based, or β diversity methods (Fig. 3). Contrary to our expectation and despite changes in richness and the taxonomic composition of the regional species pool (Fig. 1A-B), community assembly was relatively unchanged through the PETM.

Resource competition is a commonly invoked biotic driver of community assembly and an oft cited explanation for the structure of modern species rich communities, such as those in the modern neotropics (but see Fraser & Lyons, 2017) (Buckley and Jetz 2008, Safi et al. 2011, Oliveira et al. 2016). At the regional scale, enhanced competition may translate to depressed rates of diversification or increased rates of extinction due to interspecific interactions resulting from increased overlap in resource use (i.e., niche saturation) (Gould 1980, Benton 1987, Raia et al. 2006, Liow and Stenseth 2007, Liow et al. 2015, Žliobaitė et al. 2017). At the local scale, competition due to niche similarity may drive the degree to which species can coexist, which species do coexist, and how coexisting species share the available niche space (Schoener 1974). Given phylogenetic niche conservatism, competition for resources is expected to be particularly intense among closely-related species (Brown 1984, Webb et al. 2002, Wiens and Graham 2005, Losos 2008, Cavender-Bares et al. 2009, Ricklefs 2010) (Mayfield and Levine 2010). Theoretically, communities dominated by interspecific competition may show increased rates of competitive exclusion (partitioning of physical space) (Hardin 1960, Cavender-Bares et al. 2006, Cavender-Bares et al. 2009) or character displacement (partitioning of trait space or limiting similarity) (Schoener 1974, Ricklefs 2010). The phylogenetic evenness and high taxonomic turnover among modern neotropical communities have been used to suggest competitive exclusion in the face of high species richness and ecological redundancy (Safi et al. 2011, Oliveira et al. 2016, Fraser and Lyons 2017) .

Our finding of similarity in community structure across the PETM is therefore particularly unexpected because the ecologies of the invading and resident taxa appear to have been similar. Both residents and invaders were comprised of numerous ungulate-like (“Condylarths” and artiodactyls, respectively) and arboreal mammals (e.g., multituberculates and primates, respectively) with similar body masses, dietary, and locomotor characteristics, suggesting general ecological similarity (McNab 1979, Peters 1983, McNab 1989, Kelt and Van Vuren 1999, Freckleton et al. 2003, Eronen et al. 2010a, Eronen et al. 2010b, Polly 2010, Polly et al. 2011). Invading primates, for example, shared locomotor (i.e., arboreality) and tooth shape characteristics with endemic North American mammals such as members of the Plesiadapiformes (Stroik and Schwartz 2018). Furthermore, immigrant taxa overlapped significantly in isotopic niche space with endemic clades (Secord et al. 2008), likely due to similarly C₃-dominated, folivorous diets. Mixing of immigrant and endemic congeneric species (those with similar niches and thus resource preferences), such as is apparent during the PETM, may have provided ample opportunity for interspecific resource competition (Cavender-Bares et al. 2004, Cavender-Bares et al. 2006, Cavender-Bares et al. 2009, Faurby and Svenning 2016, Fraser and Lyons 2017). Yet we find that, despite the increased regional and local richness during the PETM, community-scale measures of phylogenetic diversity, body mass dispersion, and β diversity were relatively unchanged, suggesting either that species did not experience significant resource competition or varied ecologically in ways that are not captured by the ecological proxies discussed here.

Abiotic factors such as climate also influence rates of diversification and community assembly through the process of environmental filtering. Environmental filtering is a process whereby species are sorted along abiotic gradients according to their environmental tolerances

(Soininen et al. 2007a, Soininen et al. 2007b, Soininen 2010), which, provided niches are phylogenetically conserved, may result in clustering of species in physical, niche, and phylogenetic space (MacArthur and Levins 1967, Lamanna et al. 2014). Environmental filtering is thought to be the dominant process responsible for the assembly of modern species poor communities such as those in the Canadian Arctic, which are characterized by phylogenetic clustering of species in communities and low taxonomic turnover from one community to the next (Safi et al. 2011, Fraser and Lyons 2017). Given that the PETM is characterized by significant and rapid climate warming of as much as 8°C over 21 ky, our expectation of community structure becoming more similar to that of modern neotropical communities may have been incorrect; perhaps, climate filtering was more important. However, we do not find changes in community assembly consistent with enhanced environmental filtering, as we might expect if PETM community assembly was similar to modern species poor communities.

Although it is difficult to infer process from pattern, if the events that characterize the PETM led to higher rates of resource competition, enhanced environmental filtering, or some combination thereof, we would expect significant changes in community structure as quantified using one or more of the metrics employed herein. What factors may have led to little change in community structure amongst mammal assemblages, despite the considerable biotic and abiotic perturbation typical of the PETM? We propose two possible explanations, i) the timescales over which we have evaluated the resilience of PETM mammal communities are sufficiently large to have masked short-term eco-evolutionary changes and ii) available niches were not entirely saturated, allowing for new species to exploit unfilled niche space.

The timescales over which modern studies of invasion are carried out are typically on the order of years or decades (Dietl et al. 2015). However, paleontological studies, such as ours,

encompass thousands to millions of years. Even competitively-dominated communities may not show hard limits to richness over such evolutionary timescales (Cornell and Lawton 1992) (but see Alroy (1998b), Benson et al. (2016), and Close et al. (2019)) because they exist in a state of shifting dominance among the processes of speciation, extinction, dispersal, invasion, and disturbance. Furthermore, thousands to millions of years may allow for the regional species pool to replenish communities from which endemics have been extirpated and for significant evolutionary change to facilitate the coexistence of endemics and invaders; extirpations and replenishment of local communities may have occurred on timescales shorter than the resolution of the PETM record in Wyoming. Although there may have been short-term eco-evolutionary changes that we cannot observe at the current temporal resolution, our results indicate that mammal communities do not show long-term changes (> one million years) in community assembly during the PETM.

Niche filling is the degree to which the available niche space is occupied by species in a community (Schoener 1974, Brown 1984, Walker and Valentine 1984, Cornell and Lawton 1992, Wiens and Graham 2005, Clarke and Gaston 2006). Saturation of niche space, theoretically, leads to depressed rates of diversification, as available niche space is depleted (Moen et al. 2014). Invasion of such saturated communities, those where all available niche space is filled, is thought to result in enhanced resource competition and, potentially, the displacement or extinction of endemic species (Brown and Sax 2004, Qian and Ricklefs 2006, Sax and Gaines 2008, McCreless et al. 2016). The assembly of communities may also change as niches become saturated, resulting in character displacement and/or competitive exclusion (Dayan and Simberloff 1994, Dayan and Simberloff 1996, Dayan and Simberloff 1998). Therefore, the degree of niche filling plays an important role in community assembly by setting

rates of speciation and extinction (Alroy 1998b) and determining community-scale responses to biotic perturbation such as invasion (Gill 1974, Cornell and Lawton 1992, Roopnarine and Angielczyk 2015). Over the past 66 million years, mammal communities show evidence of equilibrium diversity dynamics, suggesting that niche saturation is a common occurrence (Alroy 1998b, Benson et al. 2016, Close et al. 2019).

We find that high rates of mammal first appearances (speciation plus northward range shifts) and species invasion are not matched by high rates of extinction or extirpation, leading to both increased γ and α diversity (Fig. 1B). Furthermore, we find no evidence of the long-term changes expected for accommodation of new species by a saturated, competitively-dominated communities amongst Paleocene-Eocene mammal communities (Fig. 1-3). That is, we find none of the changes in niche or physical space division that are predicted for modern communities and expected for the accommodation of new species if communities are saturated.

Unsaturated communities can result from a variety of factors including abiotic perturbations that reduce population levels, niche conservatism, and niche contraction (Chesson and Warner 1981, Price 1984, Cornell and Lawton 1992, Darroch et al. 2014). Both widespread environmental perturbation (e.g., warming, reduced Net Primary Productivity) and narrowing of niches (i.e., mammal body size reduction) are characteristic of the PETM in North America (Clyde and Gingerich 1998, Gingerich 2006, McInerney and Wing 2011, Secord et al. 2012, Rankin et al. 2015). Furthermore, unsaturated communities may be a common phenomenon resulting from the fact that local communities exist in a state of flux due to the processes of invasion, dispersal, extirpation, and disturbance (Mateo et al. 2017). The possible commonness of unsaturated communities is exemplified by the numerous modern colonization events that have resulted in a higher richness than prior to the invasion (Sax and Brown 2000, Sax et al.

2002, Fridley et al. 2007, Jackson and Sax 2010, Dornelas et al. 2014, Tóth et al. 2014). We suggest, therefore, that PETM mammal communities in North America may have been unsaturated, at least at the timescale and spatial resolution of the current study, reducing the need for compensatory changes in community assembly despite increasing species richness.

Conclusions

Throughout the history of life, species invasions have occurred numerous times, although episodically (Simpson 1947). Invasion may be an ecological rule (Vermeij 2005). Furthermore, numerous modern ecological studies show that invasions do not necessarily lead to declining local richness but rather to increasing turnover of the species that occupy invaded local communities (Sax and Brown 2000, Sax et al. 2002, Fridley et al. 2007, Jackson and Sax 2010, Dornelas et al. 2014, Tóth et al. 2014); although invasion may lead to replacement of endemics by invaders, richness and local productivity may be retained. Herein, we show that North American mammal community assembly was relatively unchanged despite the rapid climate changes and invasion of Eurasian and southern-latitude species that typified the PETM. Although the species composition of the regional species pool certainly changed and the regional and local species richness increased, we find none of the eco-evolutionary changes expected for the accommodation of invading species by communities in which niches are saturated. If most communities exist below the level of niche saturation (Vermeij, 1991a; Ricklefs 2004) due to extirpation, dispersal, invasion, and disturbance that prevent communities from ever reaching carrying capacity, they may ultimately be able to absorb invading species.

Our findings are consistent with modern studies that show little impact of invasion on local-scale species richness (Sax and Brown 2000, Sax et al. 2002, Fridley et al. 2007, Jackson

and Sax 2010, Dornelas et al. 2014, Tóth et al. 2014), but differ from those that show changes in other aspects of community structure such as β diversity (e.g., Tóth et al., 2014). Further, they point to long-term robustness of past terrestrial mammal communities in the absence of anthropogenic influences. What remains unknown is whether the long-term robustness of mammalian communities is retained in the modern. Will anthropogenic global landscape modification ultimately limit the robustness of communities to human-assisted species translocation and climate change? Although rates of invasion and global extinctions are not yet unprecedented (Vermeij 1991, 2005, Barnosky et al. 2011), landscape modification may be the deciding factor in whether communities retain their richness and ecological functions.

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Author Contributions

DF conceptualized the study, acquired and organized data, carried out all data analyses excepting analysis of body size distributions, wrote the original draft of the manuscript, and reviewed and edited all iterations of the manuscript. SKL carried out the analysis of body size distributions,

wrote the related methods and results sections of the manuscript, and reviewed and edited all iterations of the manuscript. Both authors contributed to the ideas herein.

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TABLES

TABLE 1. Model fit statistics from the Pradel Seniority capture-recapture models.

Model	N parameters	AICc	Δ AICc	Akaike Weight	Deviance
extinction(~1) + sampling(~time) + origination(~time)	12	877.16	0.00	0.62	45.59
extinction(~time) + sampling(~time) + origination(~time)	16	878.18	1.01	0.38	37.64
extinction(~time) + sampling(~1) + origination(~time)	11	893.17	16.01	0.00	63.80
extinction(~1) + sampling(~time) + origination(~1)	8	897.41	20.25	0.00	74.52
extinction(~1) + sampling(~1) + origination(~time)	7	902.79	25.62	0.00	82.03
extinction(~time) + sampling(~time) + origination(~1)	12	904.32	27.16	0.00	72.75
extinction(~time) + sampling(~1) + origination(~1)	7	913.44	36.27	0.00	92.68
extinction(~1) + sampling(~1) + origination(~1)	3	914.62	37.46	0.00	102.21

Extinction refers to last appearances due to extinction or extirpation from the Bighorn Basin.

Origination refers to first appearances due to speciation or invasion. ~1 denotes time constant while ~time denotes time variable model terms.

Table 2. Results of Kolmogorov-Smirnov tests comparing the body size distributions of each time interval.

	Tiffanian 6	Clarkfork 1	Clarkfork 2	Clarkfork 3	Wasatch 0	Wasatch 1-2
Tiffanian 6		D = 0.494 p = 0.008	D = 0.307 p = 0.060	D = 0.423 p = 0.003	D = 0.376 p = 0.006	D = 0.403 p = 0.002
Clarkfork 1			D = 0.242 p = 0.473	D = 0.169 p = 0.881	D = 0.202 p = 0.664	D = 0.248 p = 0.380
Clarkfork 2				D = 0.161 p = 0.652	D = 0.110 p = 0.934	D = 0.153 p = 0.584
Clarkfork 3					D = 0.127 p = 0.844	D = 0.128 p = 0.967
Wasatch 0						D = 0.091 p = 0.967

D = Kolmogorov-Smirnov test statistic, p = p value. A Bonferroni correction was applied for multiple comparisons giving an $\alpha \leq 0.002$ for significance. Significant comparisons are in bold.

Table 3. Standardized differences of observed values between successive North American Land Mammal Ages for all community assembly metrics calculated using Cohen’s D.

	Metric	NALMAs	Mean Change	Effect Size	Upper 95% CI	Lower 95% CI
(A)	NRI	Tiffanian 6 - Clarkfork 1	-0.44	-0.35	-4.69	3.98
		Clarkfork 1 - Clarkfork 2	0.30	0.32	-1.17	1.81
		Clarkfork 2 - Clarkfork 3	-0.28	-0.29	-0.84	0.26
		Clarkfork 3 - Wasatch 0	1.19	1.44	0.76	2.12
		Wasatch 0 - Wasatch 1/2	-0.48	-0.73	-1.47	0.01
	NTI	Tiffanian 6 - Clarkfork 1	-0.95	-0.50	-4.87	3.87
		Clarkfork 1 - Clarkfork 2	-0.09	-0.09	-1.68	1.50
		Clarkfork 2 - Clarkfork 3	-0.21	-0.23	-0.89	0.43
		Clarkfork 3 - Wasatch 0	0.82	0.88	0.25	1.52
		Wasatch 0 - Wasatch 1/2	-0.14	-0.13	-0.85	0.59
	BM _{dist}	Tiffanian 6 - Clarkfork 1	-0.31	-2.68	-8.61	3.25
		Clarkfork 1 - Clarkfork 2	0.63	1.03	-0.60	2.66
		Clarkfork 2 - Clarkfork 3	-0.19	-0.40	-1.07	0.27
		Clarkfork 3 - Wasatch 0	-0.34	-0.75	-1.38	-0.12
		Wasatch 0 - Wasatch 1/2	0.19	0.37	-0.36	1.09
	β diversity	Tiffanian 6 - Clarkfork 1	-0.08	-0.68	-2.02	0.65
		Clarkfork 1 - Clarkfork 2	0.05	0.47	-0.14	1.08
		Clarkfork 2 - Clarkfork 3	-0.01	-0.12	-0.55	0.31
		Clarkfork 3 - Wasatch 0	0.08	0.82	0.40	1.23
		Wasatch 0 - Wasatch 1/2	-0.02	-0.19	-0.71	0.32
(B)	NRI	Tiffanian 6 - Clarkfork 1	-0.44	-0.35	-4.69	3.98
		Clarkfork 1 - Clarkfork 2	0.30	0.31	-1.28	1.91
		Clarkfork 2 - Clarkfork 3	-0.28	-0.28	-0.94	0.38
		Clarkfork 3 - Wasatch 0	1.12	1.39	0.71	2.07
		Wasatch 0 - Wasatch 1/2	-0.63	-1.02	-1.78	-0.26
	NTI	Tiffanian 6 - Clarkfork 1	-0.95	-0.50	-4.87	3.87
		Clarkfork 1 - Clarkfork 2	-0.09	-0.09	-1.68	1.50
		Clarkfork 2 - Clarkfork 3	-0.21	-0.23	-0.89	0.43
		Clarkfork 3 - Wasatch 0	0.84	0.96	0.32	1.61
		Wasatch 0 - Wasatch 1/2	-0.37	-0.39	-1.11	0.34
	BM _{dist}	Tiffanian 6 - Clarkfork 1	-0.31	-2.68	-8.61	3.25
		Clarkfork 1 - Clarkfork 2	0.63	1.03	-0.60	2.66

	Clarkfork 2 - Clarkfork 3	-0.19	-0.40	-1.07	0.27
	Clarkfork 3 - Wasatch 0	-0.32	-0.65	-1.27	-0.02
	Wasatch 0 - Wasatch 1/2	0.12	0.22	-0.50	0.94
β diversity	Tiffanian 6 - Clarkfork 1	-0.08	-0.68	-2.02	0.65
	Clarkfork 1 - Clarkfork 2	0.05	0.47	-0.14	1.08
	Clarkfork 2 - Clarkfork 3	-0.01	-0.12	-0.55	0.31
	Clarkfork 3 - Wasatch 0	0.08	0.84	0.42	1.26
	Wasatch 0 - Wasatch 1/2	0.01	0.18	-0.36	0.72

(A) With (B) without taxa that first occur during the PETM (Wasatch 0). Gray cells represent comparisons before and during the PETM.

Table 4. Standardized difference between the among-bin null and observed values for all community assembly metrics calculated using Cohen’s D. Among-bin null models were generated by shuffling sites equiprobably among time bins. (A) With (B) without taxa that first occur during the PETM (Wasatch 0). Gray cells represent the PETM.

	Metric	NALMA	Effect Size	Upper 95% CI	Lower 95% CI
(A)	NRI	Tiffanian 6	-16.07	-18.72	-13.43
		Clarkfork 1	-12.62	-14.87	-10.37
		Clarkfork 2	-3.96	-4.59	-3.33
		Clarkfork 3	-2.82	-3.40	-2.24
		Wasatch 0	5.71	4.84	6.58
		Wasatch 1/2	3.31	2.58	4.04
	NTI	Tiffanian 6	-6.03	-7.67	-4.38
		Clarkfork 1	-10.43	-12.45	-8.40
		Clarkfork 2	-5.43	-6.32	-4.55
		Clarkfork 3	-3.31	-3.93	-2.69
		Wasatch 0	2.42	1.85	2.99
		Wasatch 1/2	1.94	1.30	2.58
	BM _{dist}	Tiffanian 6	0.00	-1.39	1.39
		Clarkfork 1	0.00	-1.39	1.39
		Clarkfork 2	0.00	-0.49	0.49
		Clarkfork 3	0.00	-0.41	0.41
		Wasatch 0	-0.02	-0.45	0.40
		Wasatch 1/2	0.10	-0.45	0.64
β diversity	Tiffanian 6	0.41	-0.72	1.54	
	Clarkfork 1	-1.25	-1.73	-0.78	
	Clarkfork 2	-0.90	-1.25	-0.56	
	Clarkfork 3	-1.09	-1.34	-0.84	
	Wasatch 0	-0.24	-0.55	0.06	
	Wasatch 1/2	-0.35	-0.76	0.05	
(B)	NRI	Tiffanian 6	-16.55	-19.24	-13.85
		Clarkfork 1	-9.67	-11.63	-7.72
		Clarkfork 2	-4.66	-5.47	-3.85
		Clarkfork 3	-1.99	-2.51	-1.47
		Wasatch 0	5.79	4.91	6.66
		Wasatch 1/2	2.06	1.42	2.70
	NTI	Tiffanian 6	-6.03	-7.67	-4.38
		Clarkfork 1	-10.43	-12.45	-8.40

	Clarkfork 2	-5.43	-6.32	-4.55
	Clarkfork 3	-3.31	-3.93	-2.69
	Wasatch 0	2.70	2.12	3.29
	Wasatch 1/2	1.45	0.83	2.06
BM _{dist}	Tiffanian 6	0.00	-1.39	1.39
	Clarkfork 1	0.00	-1.39	1.39
	Clarkfork 2	0.00	-0.49	0.49
	Clarkfork 3	0.00	-0.41	0.41
	Wasatch 0	-0.23	-0.66	0.19
	Wasatch 1/2	0.02	-0.52	0.56
β diversity	Tiffanian 6	0.41	-0.72	1.55
	Clarkfork 1	-1.18	-1.66	-0.70
	Clarkfork 2	-0.87	-1.22	-0.52
	Clarkfork 3	-1.04	-1.29	-0.79
	Wasatch 0	-0.22	-0.52	0.09
	Wasatch 1/2	0.02	-0.41	0.45

Figure Legends

FIGURE 1. (A) Pairwise taxonomic similarity (Jaccard similarity) among temporally adjacent North American Land Mammal Ages. (B) Mean pairwise phylogenetic distances among species in the regional pool for each North American Land Mammal Age. Estimates of first and last appearance rates of Paleocene-Eocene mammals in the Bighorn Basin of Wyoming using Pradel Seniority capture-recapture models (CMR) including gamma diversity (black dotted line) (C) and alpha diversity +/- the standard deviation (D). The best fit CMR model was one holding extinction constant with time variable rates of first appearance and sampling or preservation. The Paleocene-Eocene Thermal Maximum is highlighted in dark gray. Tiff 6 = Tiffanian 6, CF1 = Clarkfork 1, CF2 = Clarkfork 2, CF3 = Clarkfork 3, Was0 = Wasatch 0, Was1-2 = Wasatch 1-2.

FIGURE 2. Body mass frequency distributions of Paleocene-Eocene mammals of North America. Kolmogorov-Smirnov two-sample tests indicate no significant change in the shape of the body mass distributions before and after the PETM (i.e., Clarkfork 3 vs. Wasatch 0 (PETM), $D = 0.127$, $p = 0.84$; see Table 2 for all pairwise comparisons among NALMAs).

FIGURE 3. Change in phylogenetic diversity measured using the Net Relatedness Index (NRI; A) and Nearest Taxon Index (NTI; B), functional diversity measured using body mass dispersion (C), and mean taxonomic dissimilarity (D) of North American mammals across the Paleocene-Eocene Thermal Maximum (PETM; delineated by gray shading) in Wyoming. The tree used to calculate the NRI and NTI was dated using the cal3 method. NRI and NTI were calculated as the mean pairwise distance and nearest taxon distance, respectively, for all localities across the 1000 trees in the posterior distribution standardized to 1000 iterations of taxa shuffled equiprobably among sites within each time bin. Box plots therefore represent the distribution of 1000 values of NRI and NTI per site. Black horizontal lines indicate the expected

mean of zero for the randomizations within each time bin. Taxonomic similarity was calculated as the mean distance from the PCoA centroid using the Jaccard Index. For body mass dispersion and taxonomic similarity, the box plots represent the distribution of values calculated for each locality. Gray circles with light gray bars show the mean of the null models where sites were shuffled among time bins +/- their standard deviation. *d* represents the value of Cohen's D for the main comparison, pre-PETM and PETM NALMAs. Other values for *d* for comparisons between NALMAs can be found in Table 3. Tiff 6 = Tiffanian 6, CF1 = Clarkfork 1, CF2 = Clarkfork 2, CF3 = Clarkfork 3, Was0 = Wasatch 0, Was1-2 = Wasatch 1-2.

Appendix I. 1000 time-scaled phylogenetic trees constructed using the cal3 method in the paleotree R package (Bapst, 2012).

Figure 1

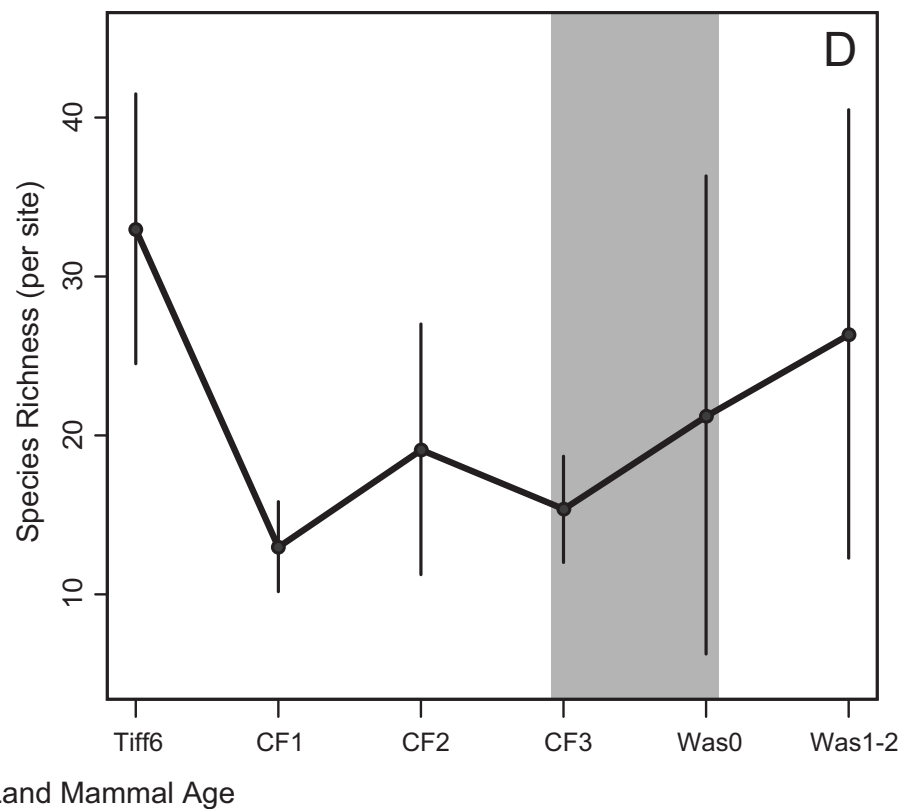
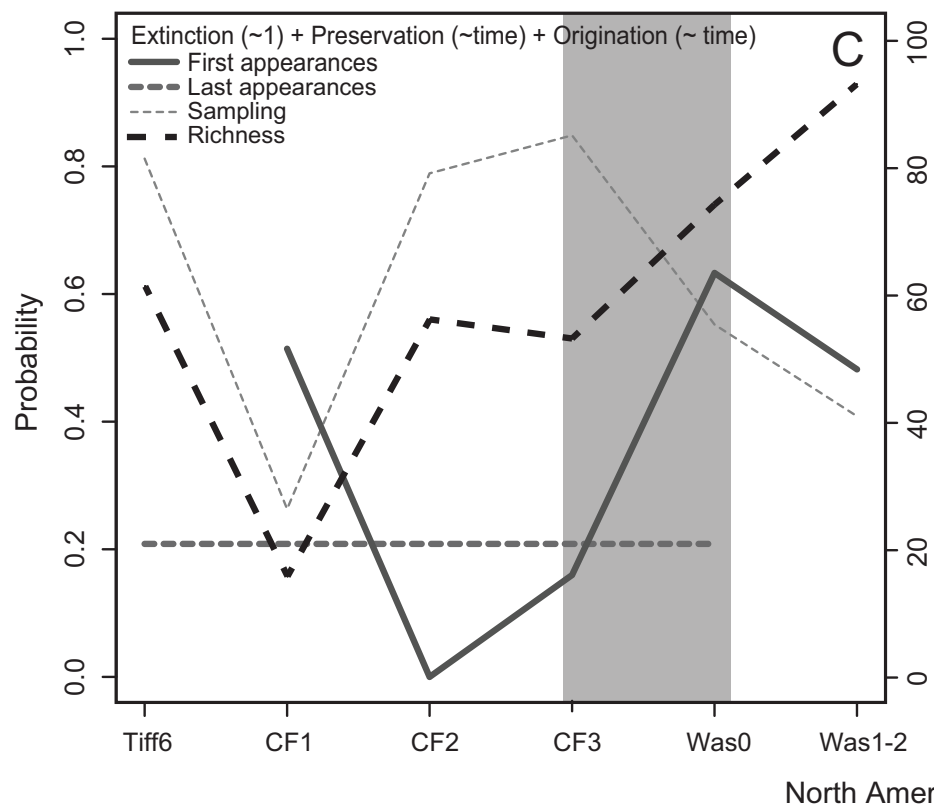
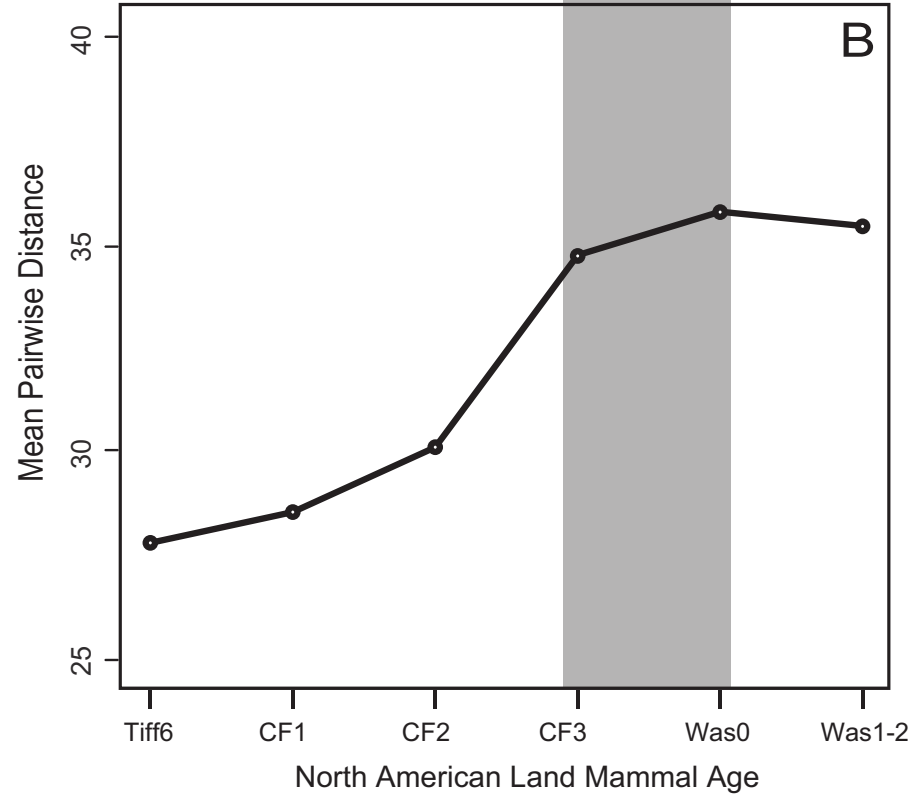
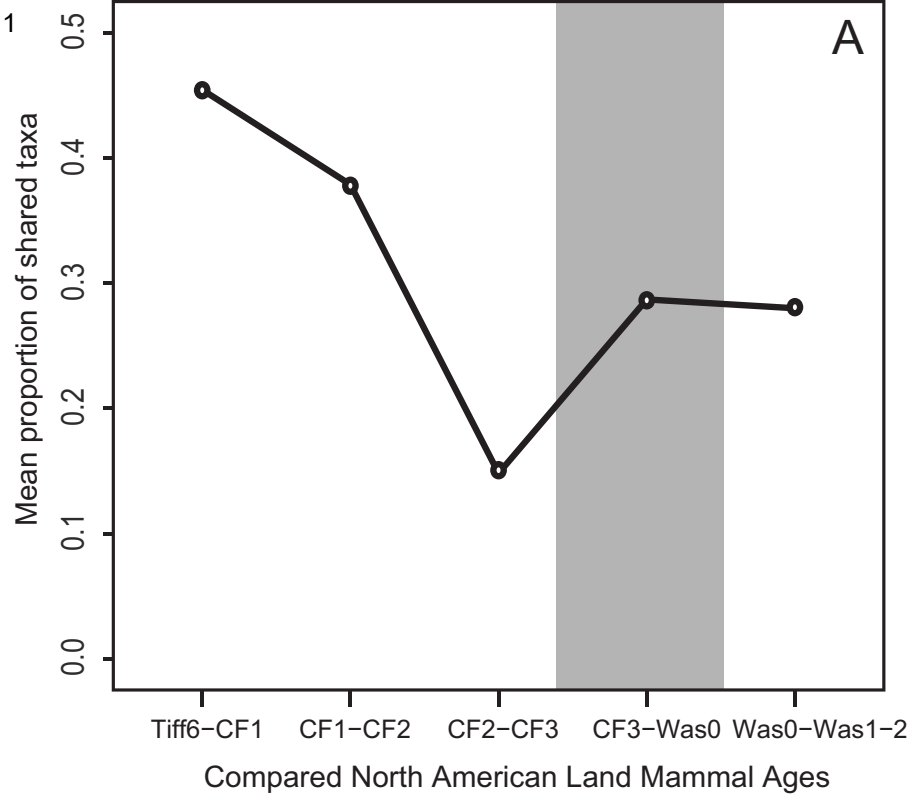


Figure 2

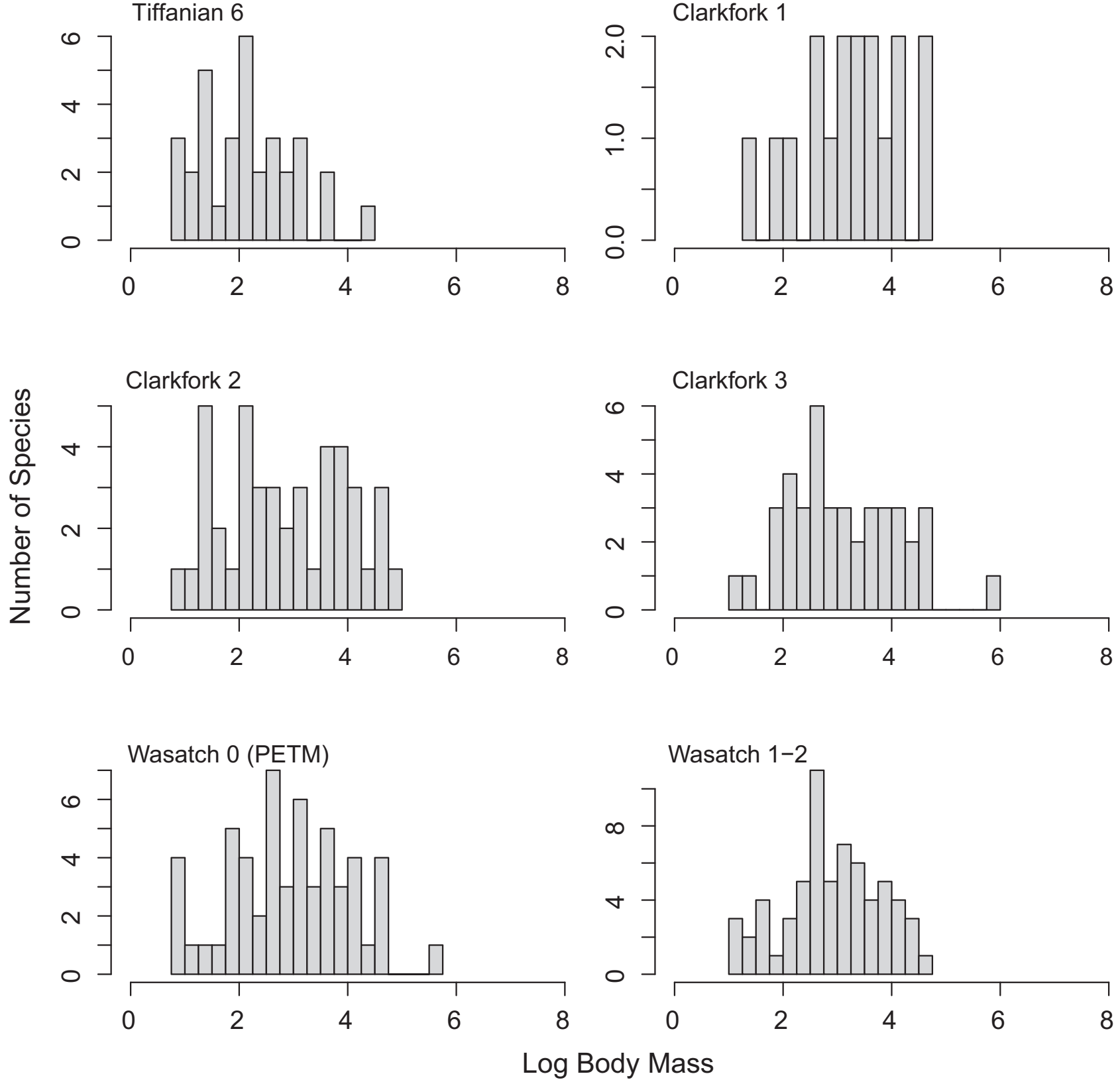
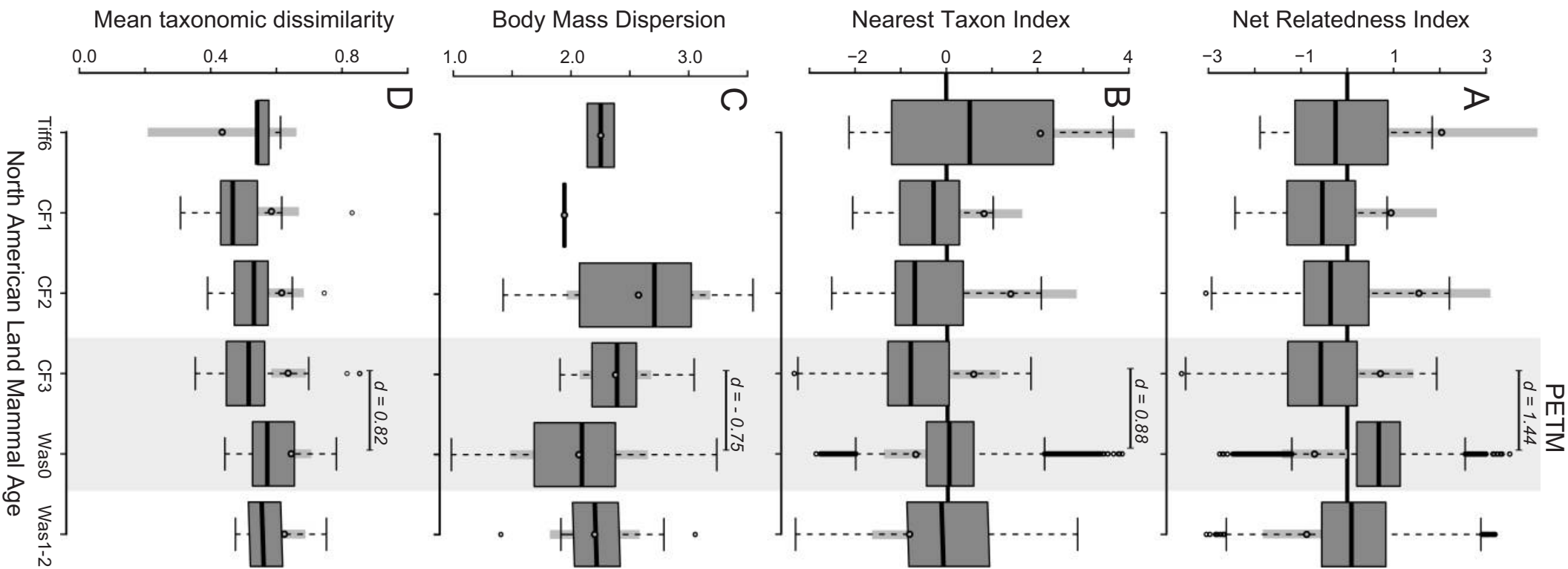


Figure 3



PETM Mammal Community Structure

The American Naturalist

Mammal community structure through the Paleocene-Eocene Thermal Maximum

Keywords: invasion, mammals, phylogenetic community structure, body size, beta diversity

Danielle Fraser^{1,2,3,*} and S. Kathleen Lyons⁴

Affiliations: ¹ Palaeobiology, Canadian Museum of Nature, PO Box 3443 Stn “D”, Ottawa ON
K1P 6P4

² Biology & Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario,
Canada K1S 5B6

³ Department of Paleobiology, Smithsonian Institution, National Museum of Natural History, 10th
and Constitution NW, Washington, DC 20560-0121

⁴ School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE, 68502 USA

*Dfraser@nature.ca

SUPPLEMENTAL TABLES

Table S1. Species with first occurrences during Wasatch 0 (PETM).

Species	Clade
<i>Chriacus gallinae</i>	Arctocyonidae
<i>Bunophorus robustus</i>	Artiodactyla
<i>Diacodexis metsiacus</i>	Artiodactyla
<i>Simpsonodus chacensis</i>	Artiodactyla
<i>Miacis exiguus</i>	Carnivora
<i>Barylambda faberi</i>	Cimolesta
<i>Esthonyx bisulcatus</i>	Esthonychidae
<i>Prototomus martis</i>	Hyaenodontidae
<i>Prototomus secundarius</i>	Hyaenodontidae
<i>Hyopsodus loomisi</i>	Hyopsodontidae
<i>Hyopsodus lysitensis</i>	Hyopsodontidae
<i>Hyopsodus powellianus</i>	Hyopsodontidae
<i>Hyopsodus simplex</i>	Hyopsodontidae
<i>Palaeictops bicuspis</i>	Leptictidae
<i>Parectypodus lunatus</i>	Multituberculata
<i>Palaeosinopa incerta</i>	Pantolestidae
<i>Peradectes elegans</i>	Paradectidae
<i>Simpsonlemur jepseni</i>	Paraomyidae
<i>Cardiolphus radinskyi</i>	Perissodactyla
<i>Sifrhippus grangeri</i>	Perissodactyla
<i>Xenicohippus grangeri</i>	Perissodactyla
<i>Copecion brachypternus</i>	Phenacodontidae
<i>Cantius abditus</i>	Primates
<i>Cantius frugivorus</i>	Primates
<i>Microsyops latidens</i>	Primates
<i>Tetonius matthewi</i>	Primates
<i>Lophiparamys debequensis</i>	Rodentia
<i>Paramys copei</i>	Rodentia
<i>Paramys taurus</i>	Rodentia
<i>Thisbemys perditus</i>	Rodentia
<i>Talpavoides dartoni</i>	Tribosphenida
<i>Viverravus lutosus</i>	Viverravidae

PETM Mammal Community Structure

Table S2. Occurrence summary for each NALMA and species.

NALMA	N Sites (>4 occurrences)	N Species	Species	Occupancy
Tiffanian 6	2	32	<i>Aletodon gunnelli</i>	1
			<i>Apheliscus nitidus</i>	1
			<i>Arctodontomys simplicidens</i>	1
			<i>Carpolestes nigridentis</i>	1
			<i>Carpolestes simpsoni</i>	1
			<i>Chiromyoides major</i>	1
			<i>Diacocherus minutus</i>	1
			<i>Dillerlemur pagei</i>	1
			<i>Ectocion osbornianus</i>	2
			<i>Ectypodus laytoni</i>	1
			<i>Ectypodus powelli</i>	2
			<i>Haplomyilus simpsoni</i>	1
			<i>Ignacius graybullianus</i>	1
			<i>Labidolemur kayi</i>	1
			<i>Leipsanolestes siegfriedti</i>	1
			<i>Microcosmodon rosei</i>	1
			<i>Microparamys cheradius</i>	1
			<i>Neoliotomus conventus</i>	1
			<i>Niptomomys doreenae</i>	1
			<i>Peradectes chesteri</i>	1
			<i>Peradectes protinnominatus</i>	1
			<i>Phenacolemur praecox</i>	1
			<i>Phenacolemur simonsi</i>	1
			<i>Plagioctenodon rosei</i>	1
			<i>Plagiomene accola</i>	1
			<i>Plesiadapis cookei</i>	1
			<i>Plesiadapis dubius</i>	1
			<i>Prochetodon taxus</i>	1
			<i>Uintacyon rudis</i>	1
			<i>Viverravus rosei</i>	1
			<i>Worlandia inusitata</i>	1
			<i>Wyonycteris chalice</i>	1
Clarfork 1	2	10	<i>Apheliscus nitidus</i>	1
			<i>Dipsalidictis krausei</i>	1
			<i>Ectocion osbornianus</i>	2
			<i>Neoliotomus conventus</i>	1
			<i>Phenacodus intermedius</i>	2

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			<i>Plesiadapis dubius</i>	2
			<i>Plesiadapis gingerichi</i>	2
			<i>Probathyopsis praecursor</i>	1
			<i>Thryptacodon antiquus</i>	1
			<i>Viverravus politus</i>	1
Clarkfork 2	16	43	<i>Acidomomys hebeticus</i>	1
			<i>Aletodon gunnelli</i>	3
			<i>Apheliscus nitidus</i>	3
			<i>Arctodontomys simplicidens</i>	1
			<i>Arctostylops steini</i>	2
			<i>Azygonyx ancylion</i>	10
			<i>Azygonyx xenicus</i>	1
			<i>Carpolestes simpsoni</i>	5
			<i>Ceutholestes dolosus</i>	1
			<i>Chiromyoides potior</i>	2
			<i>Cyriacotherium psamminum</i>	1
			<i>Diacocherus minutus</i>	1
			<i>Didymictis protenus</i>	3
			<i>Didymictis proteus</i>	10
			<i>Dillerlemur pagei</i>	9
			<i>Dipsalidictis aequidens</i>	7
			<i>Dipsalidictis krausei</i>	1
			<i>Dipsalidictis platypus</i>	1
			<i>Dipsalodon matthewi</i>	2
			<i>Dissacus praenuntius</i>	6
			<i>Ectocion osbornianus</i>	16
			<i>Ectypodus powelli</i>	3
			<i>Haplomylys simpsoni</i>	5
			<i>Ignacius clarkforkensis</i>	1
			<i>Ignacius graybullianus</i>	3
			<i>Labidolemur kayi</i>	2
			<i>Leipsanolestes siegfriedti</i>	1
			<i>Microcosmodon rosei</i>	2
			<i>Palaeoryctes punctatus</i>	1
			<i>Peradectes protinnominatus</i>	3
			<i>Phenacodus intermedius</i>	15
			<i>Phenacodus vortmani</i>	4
			<i>Plagioctenodon rosei</i>	1
			<i>Plesiadapis cookei</i>	12
			<i>Princetonia yalensis</i>	2
			<i>Probathyopsis praecursor</i>	5
			<i>Prodiacodon tauricinerei</i>	1
			<i>Thryptacodon antiquus</i>	2

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			<i>Titanoides nanus</i>	2
			<i>Tythaena lichna</i>	2
			<i>Uintacyon rudis</i>	3
			<i>Viverravus laytoni</i>	2
			<i>Viverravus politus</i>	3
Clarkfork 3	21	37	<i>Aletodon gunnelli</i>	7
			<i>Apheliscus nitidus</i>	9
			<i>Arctodontomys simplicidens</i>	1
			<i>Arctodontomys wilsoni</i>	1
			<i>Arctostylops steini</i>	1
			<i>Azygonyx ancylion</i>	2
			<i>Azygonyx grangeri</i>	12
			<i>Cyriacotherium psamminum</i>	2
			<i>Diacocherus minutus</i>	1
			<i>Didymictis protenus</i>	14
			<i>Didymictis proteus</i>	4
			<i>Dillerlemur pagei</i>	1
			<i>Dipsalidictis aequidens</i>	1
			<i>Dipsalidictis krausei</i>	1
			<i>Dipsalidictis platypus</i>	1
			<i>Dissacus praenuntius</i>	6
			<i>Ectocion osbornianus</i>	23
			<i>Haplomylus simpsoni</i>	17
			<i>Ignacius graybullianus</i>	1
			<i>Mimoperadectes labrus</i>	1
			<i>Niptomomys doreenae</i>	1
			<i>Palaeonodon parvulus</i>	1
			<i>Palaeonictis peloria</i>	3
			<i>Phenacodus intermedius</i>	19
			<i>Phenacodus vortmani</i>	7
			<i>Phenacolemur praecox</i>	7
			<i>Plagioctenodon rosei</i>	1
			<i>Plagiomene accola</i>	3
			<i>Plesiadapis dubius</i>	4
			<i>Princetonia yalensis</i>	1
			<i>Probathyopsis praecursor</i>	11
			<i>Prodiacodon tauricinerei</i>	1
			<i>Thryptacodon antiquus</i>	5
			<i>Uintacyon rudis</i>	5
			<i>Viverravus acutus</i>	2
			<i>Viverravus politus</i>	10
			<i>Worlandia inusitata</i>	1
Wasatch Zero	22	55	<i>Acarictis ryani</i>	1

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<i>Acritoparamys atwateri</i>	3
<i>Arctodontomys wilsoni</i>	5
<i>Arfia junnei</i>	14
<i>Cantius torresi</i>	5
<i>Chriacus badgleyi</i>	13
<i>Copecion davisi</i>	16
<i>Coryphodon eoacenus</i>	1
<i>Diacodexis ilicis</i>	11
<i>Didymictis leptomytus</i>	9
<i>Didymictis proteus</i>	1
<i>Dipsalidictis platypus</i>	2
<i>Dipsalidictis transiens</i>	1
<i>Dissacus praenuntius</i>	4
<i>Ectocion osbornianus</i>	2
<i>Ectocion parvus</i>	16
<i>Ectoganus bighornensis</i>	5
<i>Ectoganus lodbelli</i>	2
<i>Ectypodus tardus</i>	2
<i>Esthonyx gunnelli</i>	3
<i>Esthonyx spatularius</i>	1
<i>Gracilocyon rosei</i>	1
<i>Gracilocyon winkleri</i>	1
<i>Herpetotherium innominatum</i>	1
<i>Hyopsodus loomisi</i>	15
<i>Ignacius graybullianus</i>	1
<i>Leptacodon donkroni</i>	1
<i>Macrocranion junnei</i>	4
<i>Miacis deutschii</i>	1
<i>Mimoperadectes labrus</i>	10
<i>Nanomomys thermophilus</i>	1
<i>Niptomomys doreenae</i>	2
<i>Palaeonodon nievelti</i>	5
<i>Palaeonictis wingi</i>	1
<i>Palaeosinopa lutreola</i>	2
<i>Paramys taurus</i>	3
<i>Peradectes protinnominatus</i>	3
<i>Phenacodus intermedius</i>	5
<i>Phenacodus vortmani</i>	2
<i>Phenacolemur praecox</i>	1
<i>Plagioctenoides microlestes</i>	1
<i>Plagioctenoides tombowni</i>	1
<i>Princetonina yalensis</i>	1
<i>Prolimmocyon eerius</i>	2

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			<i>Prototomus deimos</i>	3
			<i>Sifrhippus grangeri</i>	2
			<i>Sifrhippus sandrae</i>	15
			<i>Teilhardina brandti</i>	8
			<i>Thryptacodon barae</i>	1
			<i>Tuscahomys major</i>	7
			<i>Tuscahomys worlandensis</i>	2
			<i>Uintacyon gingerichi</i>	6
			<i>Viverravus acutus</i>	5
			<i>Viverravus politus</i>	2
			<i>Viverravus rosei</i>	1
Wasatch one-two	13	63	<i>Acarictis ryani</i>	1
			<i>Apheliscus chydaeus</i>	10
			<i>Arctodontomys wilsoni</i>	9
			<i>Arenahippus aemulor</i>	1
			<i>Arenahippus pernix</i>	1
			<i>Arfia opisthotoma</i>	1
			<i>Arfia shoshoniensis</i>	6
			<i>Arfia zeke</i>	4
			<i>Azygonyx grangeri</i>	1
			<i>Cantius mckennai</i>	2
			<i>Cantius ralstoni</i>	3
			<i>Cardiolphus radinskyi</i>	8
			<i>Chalicomomys willwoodensis</i>	2
			<i>Copacion brachypternus</i>	1
			<i>Deltatherium absarokae</i>	1
			<i>Didymictis leptomyus</i>	5
			<i>Didymictis protenus</i>	3
			<i>Dipsalidictis platypus</i>	1
			<i>Dipsalidictis transiens</i>	4
			<i>Ectocion osbornianus</i>	3
			<i>Ectypodus simpsoni</i>	1
			<i>Ectypodus tardus</i>	3
			<i>Eoryctes melanus</i>	3
			<i>Esthonyx spatularius</i>	3
			<i>Galecyon mordax</i>	1
			<i>Gracilocyon winkleri</i>	1
			<i>Hapalodectes anthracinus</i>	1
			<i>Haplomyus scottianus</i>	2
			<i>Haplomyus speirianus</i>	3
			<i>Homogalax protapirinus</i>	1
			<i>Hyopsodus loomisi</i>	3
			<i>Hyopsodus simplex</i>	1

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<i>Ignacius graybullianus</i>	3
<i>Miacis deutschii</i>	1
<i>Miacis exiguus</i>	1
<i>Micromomys antelucanus</i>	2
<i>Microparamys hunterae</i>	1
<i>Microsypops angustidens</i>	1
<i>Neoliotomus ultimus</i>	7
<i>Oxyaena gulo</i>	2
<i>Palaeonodon nievelti</i>	7
<i>Palaeonictis occidentalis</i>	1
<i>Parapternodus antiquus</i>	1
<i>Parectypodus lunatus</i>	1
<i>Phenacodus vortmani</i>	1
<i>Plagiomene accola</i>	1
<i>Plagiomene multicuspis</i>	1
<i>Prolimmocyon atavus</i>	1
<i>Prolimmocyon haematus</i>	5
<i>Prototomus deimos</i>	1
<i>Prototomus martis</i>	6
<i>Prototomus phobos</i>	5
<i>Pseudotetonius ambiguus</i>	1
<i>Sifrihippus grangeri</i>	11
<i>Teilhardina americana</i>	2
<i>Tetonius matthewi</i>	1
<i>Thryptacodon antiquus</i>	3
<i>Tinimomys graybullianus</i>	1
<i>Uintacyon massetericus</i>	2
<i>Viverravus acutus</i>	9
<i>Viverravus politus</i>	5
<i>Viverravus rosei</i>	3
<i>Wyolestes apheles</i>	1

SUPPLEMENTAL FIGURES

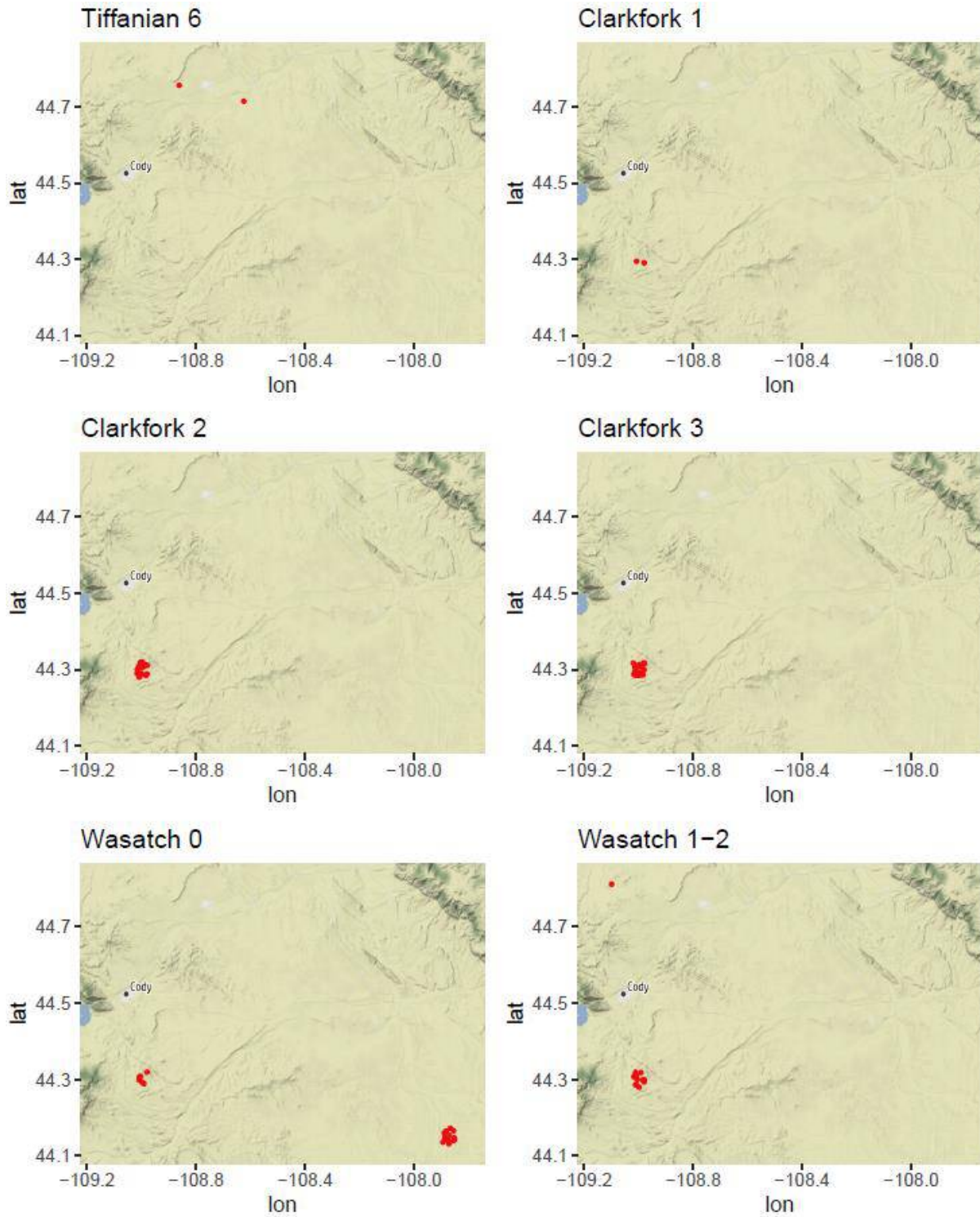


Figure S1. Geographic locations for all sites in the present study.

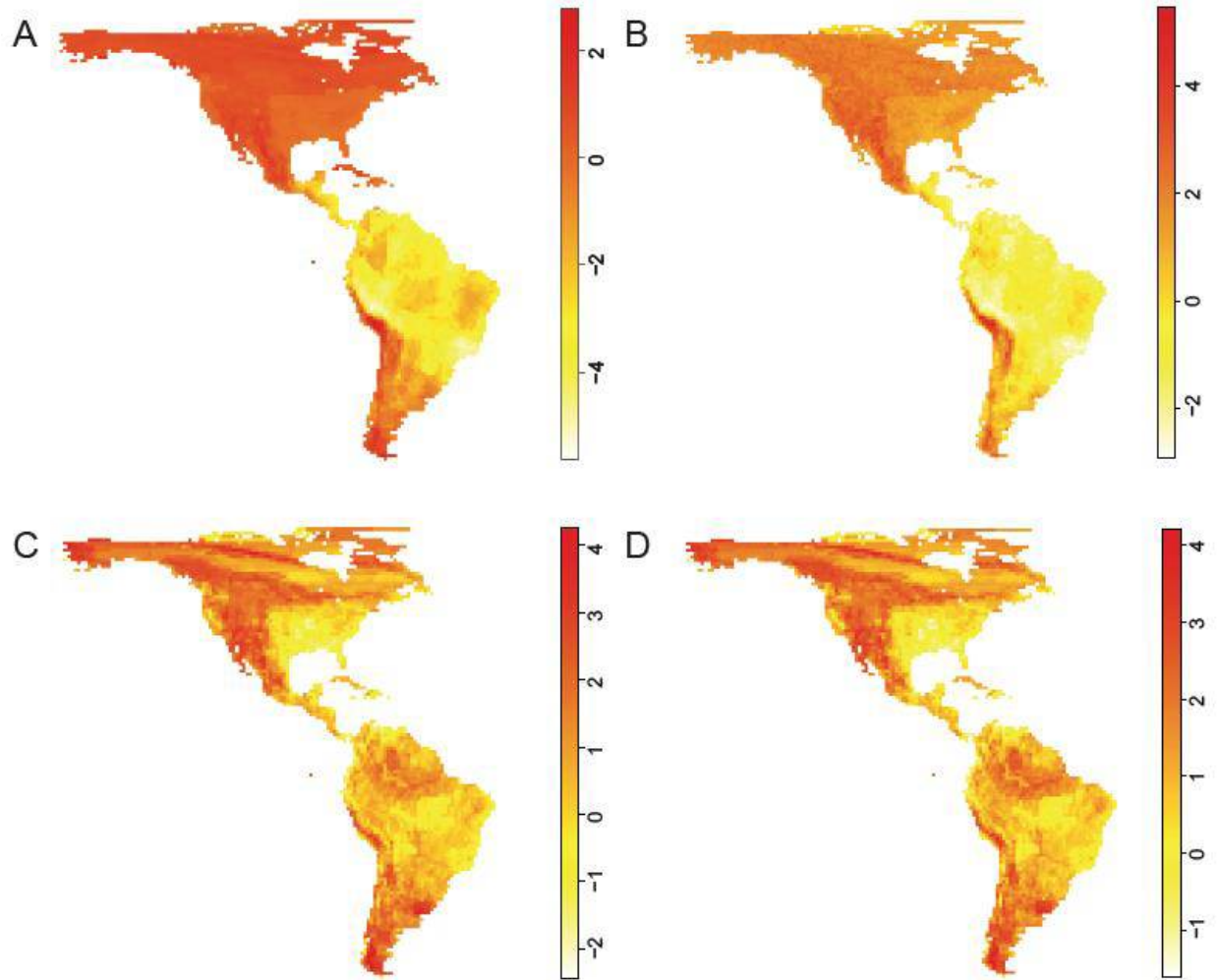


FIGURE S2. Latitudinal patterns of phylogenetic diversity for modern Western Hemisphere non-volant mammals. (A) Net Relatedness Index (NRI) using a simple taxon shuffling algorithm to generate null species assemblages, (B) NRI using the independent swap algorithm, (C) Nearest Taxon Index (NTI) using a simple taxon shuffling algorithm, and (D) NTI using the independent swap algorithm.

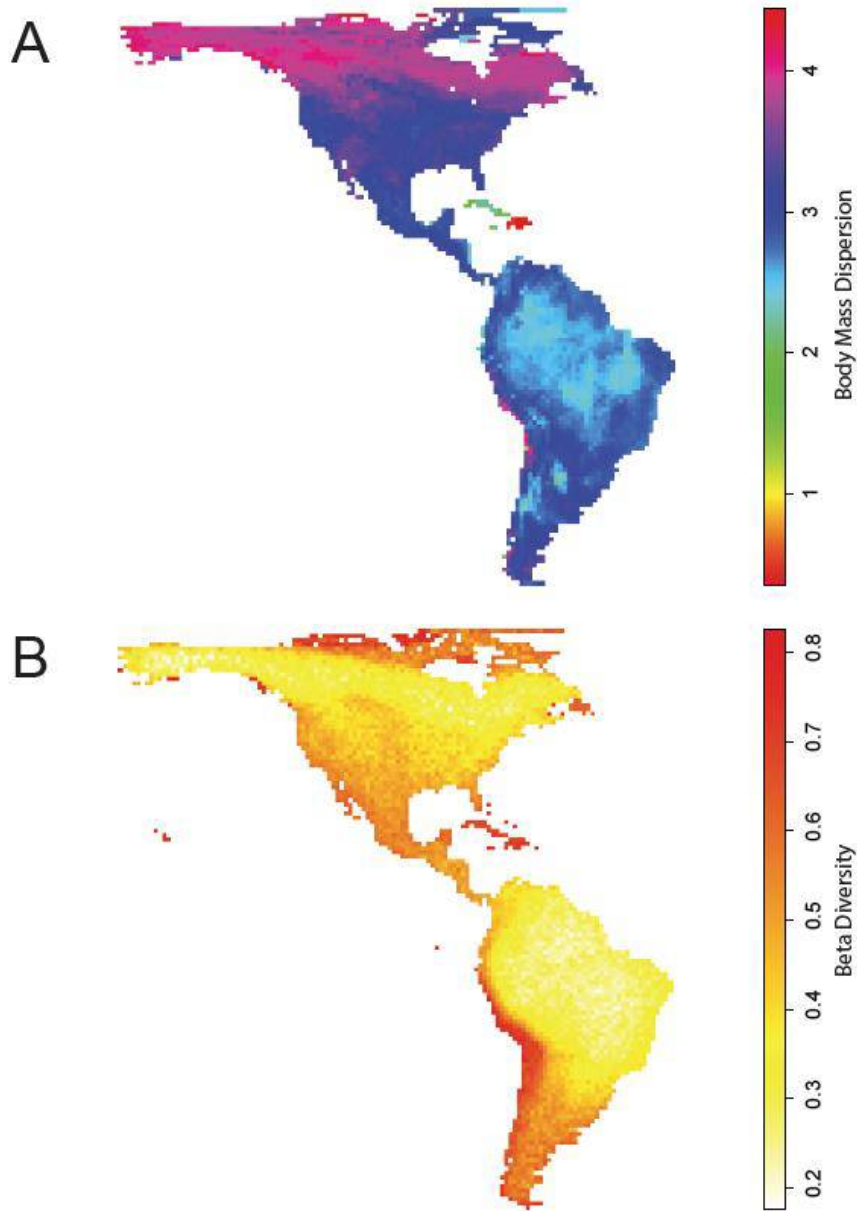


FIGURE S3. Latitudinal patterns of body mass dispersion (A), and β diversity (B) for modern Western Hemisphere non-volant mammals. β diversity was calculated using the Jaccard Index.

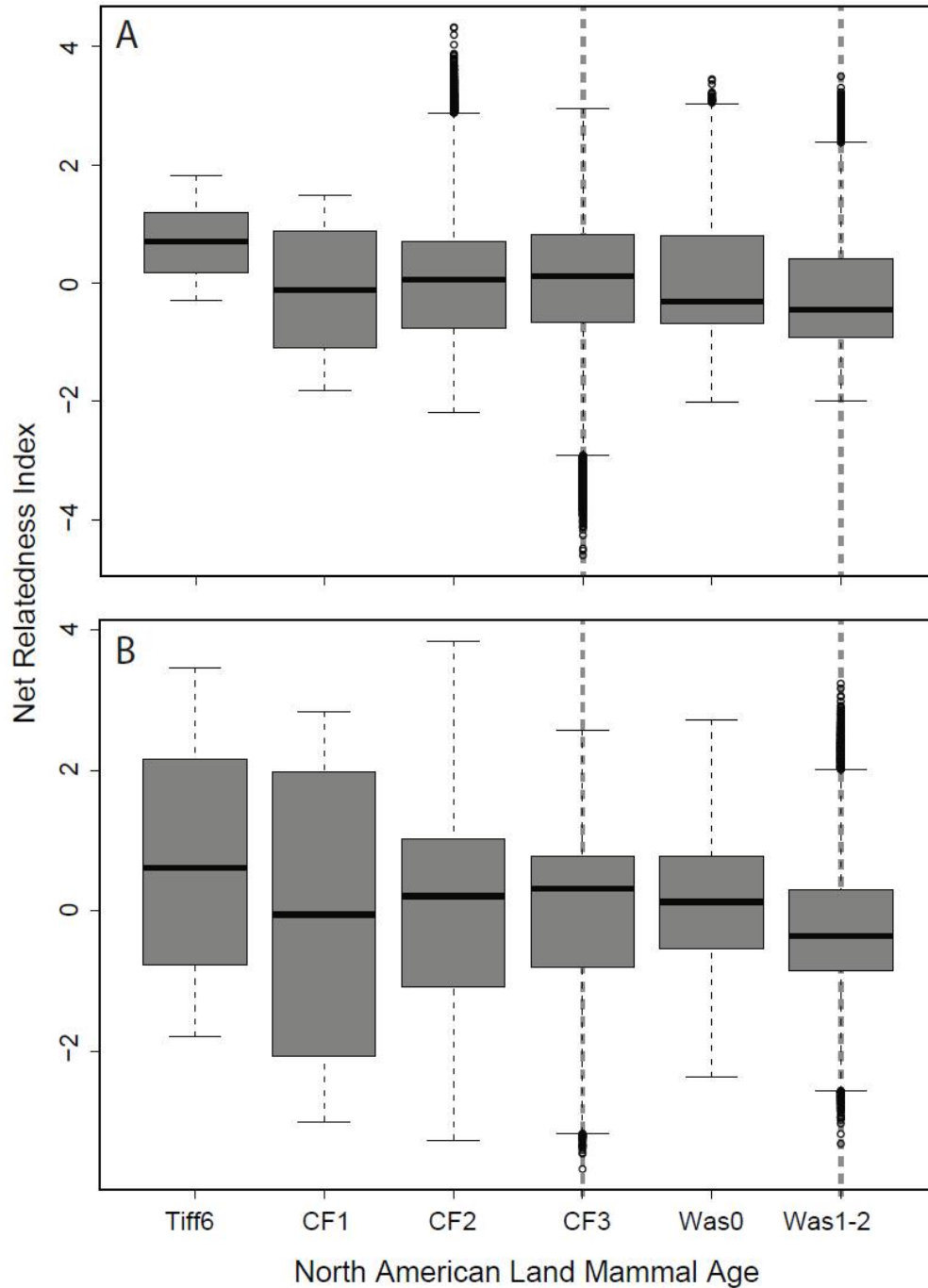


FIGURE S4. Change in mammal phylogenetic diversity (Net Relatedness Index) the late Paleocene to early Eocene in Wyoming (PETM is delineated by dotted lines) as calculated using the minimum branch length dated phylogenies (A) and all branches additive dated phylogenies (B). NRI and NTI were calculated as the mean pairwise distance and nearest taxon distance,

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respectively, for all localities across the 1000 trees in the posterior distribution standardized to 1000 iterations of taxa shuffled equiprobably among sites within each time bin. Box plots therefore represent the distribution of 1000 values of NRI and NTI per site.

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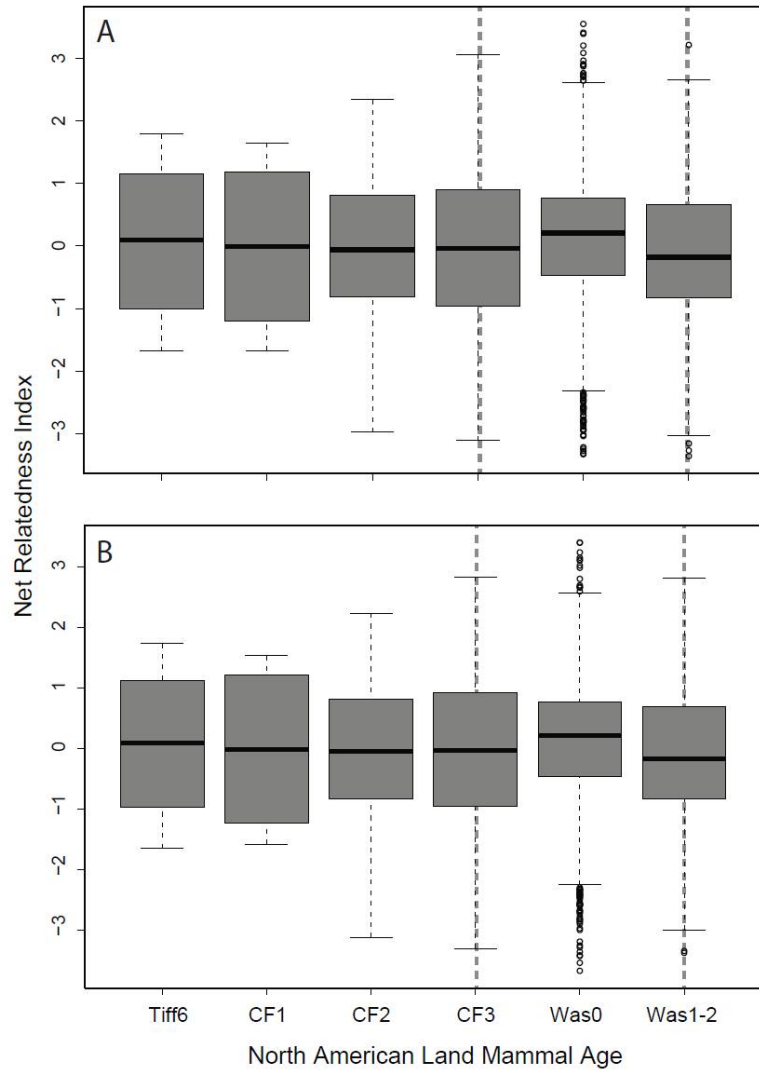


FIGURE S5. Change in mammal phylogenetic diversity (Net Relatedness Index) from the late Paleocene to early Eocene in Wyoming (PETM is delineated by dotted lines) as calculated after degrading one of the cal3 dated phylogenies by 25% (A) and 50% (B). NRI and NTI were calculated as the mean pairwise distance and nearest taxon distance, respectively, for all localities across the 1000 trees in the posterior distribution standardized to 1000 iterations of taxa shuffled equiprobably among sites within each time bin. Box plots therefore represent the distribution of 1000 values of NRI and NTI per site.

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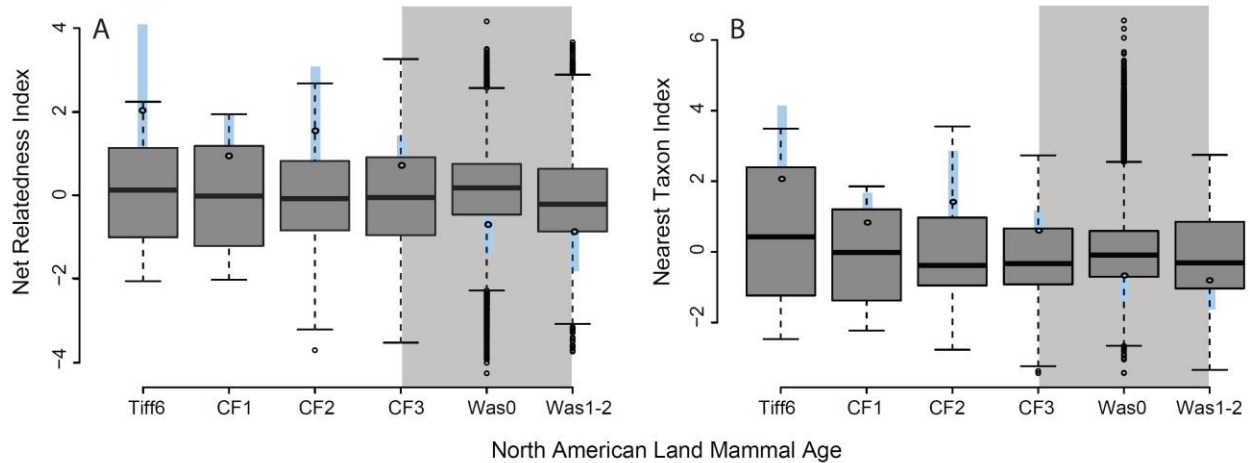


FIGURE S6. Change in phylogenetic diversity measured using the Net Relatedness Index (NRI; A) and Nearest Taxon Index (NTI; B) of North American mammals across the Paleocene-Eocene Thermal Maximum (PETM; delineated by gray shading) in Wyoming. NRI and NTI were calculated as the mean pairwise distance and nearest taxon distance, respectively, for all localities across the 1000 trees in the posterior distribution standardized to 1000 iterations of the independent swap algorithm within each time bin. Box plots therefore represent the distribution of 1000 values of NRI and NTI per site. Gray circles with blue bars show the mean of the null models where sites were shuffled among time bins +/- their standard deviation. The tree used to calculate the NRI and NTI was dated using the cal3 method. Tiff 6 = Tiffanian 6, CF1 = Clarkfork 1, CF2 = Clarkfork 2, CF3 = Clarkfork 3, Was0 = Wasatch 0, Was1-2 = Wasatch 1-2.

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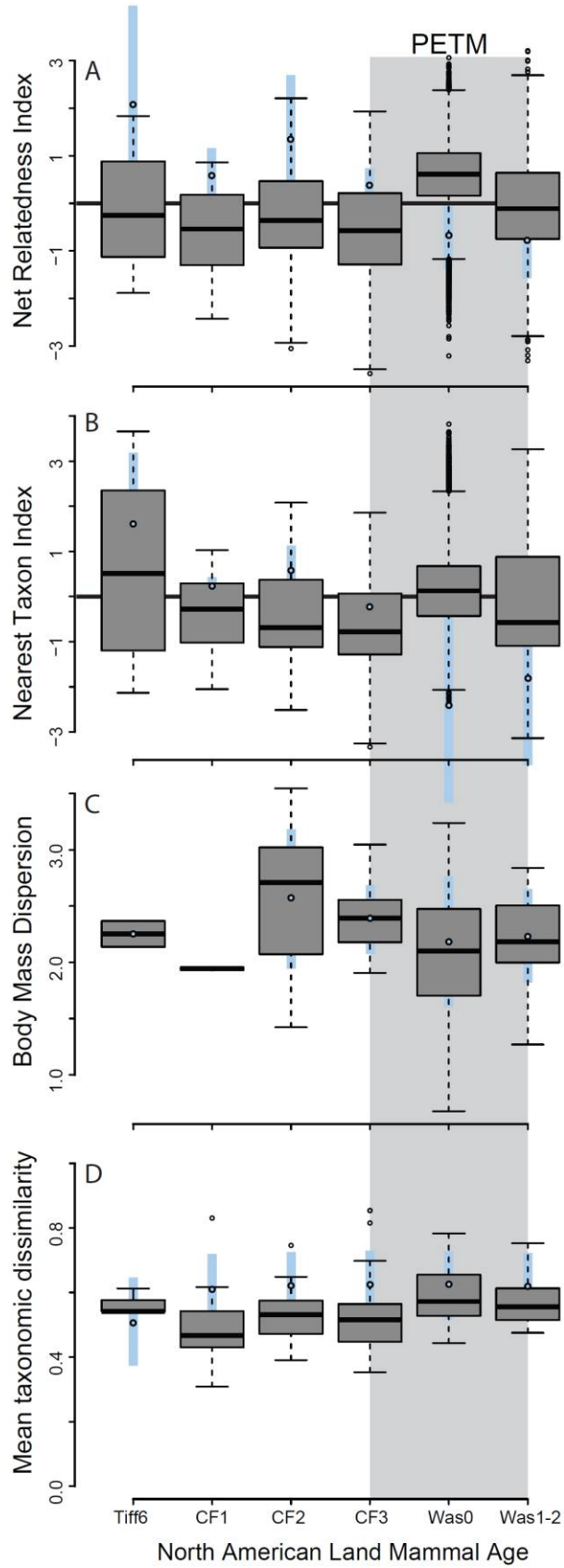


Figure S7. Change in phylogenetic diversity measured using the Net Relatedness Index (NRI; A) and Nearest Taxon Index (NTI; B), functional diversity measured using body mass dispersion (C), and mean taxonomic dissimilarity (D) of North American non-immigrant mammals across the Paleocene-Eocene Thermal Maximum (PETM; delineated by gray shading) in Wyoming. The tree used to calculate the NRI and NTI was dated using the cal3 method. NRI and NTI were calculated as the mean pairwise distance and nearest taxon distance, respectively, for all localities across the 1000 trees in the posterior distribution standardized to 1000 iterations of taxa shuffled equiprobably among sites within each time bin. Box plots therefore represent the distribution of 1000 values of NRI and NTI per site. Taxonomic similarity was calculated as the mean distance from the PCoA centroid using the Jaccard Index. Black horizontal lines indicate the value at which NRI and NTI are indistinguishable from within-bin null expectations. For body mass dispersion and taxonomic similarity, the box plots represent the distribution of values calculated for each locality. Gray circles with blue bars show the mean of the null models where sites were shuffled among time bins +/- their standard deviation.. Tiff 6 = Tiffanian 6, CF1 = Clarkfork 1, CF2 = Clarkfork 2, CF3 = Clarkfork 3, Was0 = Wasatch 0, Was1-2 = Wasatch 1-2.