

Research Article

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Functional stasis and changing habitat preferences among mammalian communities from the PETM of the Bighorn Basin, Wyoming

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Abstract

The transition between the Paleocene and Eocene epochs (ca. 56 Ma) was marked by a period of rapid global warming of 5 °C to 8 °C following a carbon isotope excursion (CIE) lasting 200 ky or less referred to as the Paleocene-Eocene Thermal Maximum (PETM). The PETM precipitated a significant shift in the composition of North American floral communities and major mammalian turnover. We explored the ecological impacts of this phenomenon by analyzing 173 mammal species from the Bighorn Basin, Wyoming, USA, including their associated body alongside a database of 30 palynofloral localities as proxies for habitat. For each time bin, we calculated mean and median differences in body mass and habitat preference between significantly aggregated and segregated mammal species. Aggregated species showed significant similarity in habitat preference only prior to the PETM, after which habitat preference ceased to be a significant factor in community assembly. Our measures of differences in body mass provide no evidence of a significant impact of competitive interactions on community assembly across the PETM, aligning with previous work. Our results indicate the persistence of a stable mammalian functional community structure despite taxonomic turnover, climate change and broadening habitat preferences.

Impact Statement

Here, we combine multiple measurements of niche occupation based on two different definitions of the niche concept to examine how terrestrial mammalian communities responded to climate change and range shifts in the past. We provide a framework for analyses of community paleoecology, which incorporates both environmental (i.e., habitat) and morphological estimates of niche occupation at a community scale. As a case study for this methodology, we examined mammalian communities from the Paleocene-Eocene Thermal Maximum. Our results show that, on intermediate timescales, the variation in functional traits exhibited between species in the same communities can be conserved, possibly enabled by increasing primary productivity. In the aftermath of climate change and introduction of immigrant fauna, habitat preferences broadened within communities and narrowed between communities. The results are communities dominated by immigrant taxa where habitat preference is roughly homogenous between segregated species, and no longer a factor in determining community assembly. Our findings echo observations of other modern and fossil range shift events, and, combined with our expanded methodology, may aid in predicting and understanding how mammalian communities respond to climatological perturbation in the absence of humans.

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Introduction

Anthropogenic climate change and species transplantation have driven significant changes in, and homogenization of, species composition (Vitousek et al., 1996; Vitousek et al., 1997; McKinney and Lockwood, 1999; Parmesan and Yohe, 2003; Olden et al., 2004; Parmesan, 2006; Chen et al., 2011; Fraser et al., 2022) as well as losses of functional diversity (Naem et al., 2012; Mouillot et al., 2013; Matuoka et al., 2020; Li et al., 2022) among modern and fossil terrestrial communities. Human activities have also driven significant changes in mammal community structure in the form of changes in species associations (Lyons et al., 2016; Tóth et al., 2019; Pineda-Munoz et al., 2020). Given that neontological research is hindered by the typically short time frames available for studies of community response to anthropogenic disturbance, the fossil record allows us to readily examine the long-term ecological and evolutionary impacts of similar perturbations in the past (Dietl et al., 2015; Barnosky et al., 2017).

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Understanding how communities respond to changes in climate, environment, community composition and species associations in the past can provide data on how modern communities may respond to the effects of ongoing anthropogenic change. In this context, one interval of highly comparable, though less rapid, climate change, is the Paleocene-Eocene Thermal Maximum (PETM) (Kennett and Stott, 1991; Koch et al., 1992; Zachos et al., 2005; Smith et al., 2009; Gingerich, 2019).

The PETM was a period of major climate change characterized by a large (5 °C–8 °C), temporary increase in global temperatures that resulted from the release of thousands of Pg of isotopically light carbon in a period of <10 ky, commonly known as the onset of the Carbon Isotope Excursion (CIE) (Kennett and Stott, 1991; Dickens et al., 1995). The main body of the CIE has been estimated to have a duration of ~115 ka, while the recovery from the excursion has been estimated to have an excursion of another ~42 ka (Aziz et al., 2008; McNerny and Wing, 2011). In the terrestrial realm, the PETM is particularly well represented in the Bighorn Basin of Northern Wyoming, which preserves both faunas, including mammals, and floras (Koch et al., 2003; Wing et al. 2005; Abels et al., 2016). Floral records from the Bighorn Basin show that the changing climate had profound impacts on plant communities; closed-canopy wetland floras were replaced by shrubs and trees characteristic of drier, more open environments (Wing et al., 2003; Wing and Curran, 2013; Korasidis et al., 2022a, 2022b). The mammal communities of the Bighorn Basin subsequently experienced turnover, coinciding with the onset of the PETM (Gingerich, 2003). Faunal turnover during the PETM has generally been interpreted as a mass immigration event, resulting in the local disappearance of plesiadapids and the arrival of Eurasian mammals, including primates, perissodactyls and artiodactyls (Bowen et al., 2002; Gingerich, 2006). The immigration of Eurasian mammals into North America and northward range shifts were accompanied by a sharp rise in species richness and evenness in the post-PETM communities (Clyde and Gingerich, 1998; Bowen et al., 2002; Burger, 2012). Rapid climate change and immigration during the PETM are also associated with transient dwarfing among several mammal genera (Gingerich, 2003; Burger, 2012; Secord et al., 2012) but minimal changes in community structure (i.e., phylogenetic community structure, body mass dispersion and beta diversity; Fraser and Lyons, 2020). Though the picture of ecological change during the PETM is becoming clearer, changes in mammal species associations and their comparative occupation of niche space have been little explored. We therefore ask: in terms of both ecological roles and environmental (i.e., habitat) preferences, are there observable changes in the niche occupation among co-occurring mammals across the PETM?

The basic conceptual models of community assembly and classical niche theory predict that community assembly mechanisms are reflected in the packing of coexisting species in niche space (MacArthur and Levins, 1967; MacArthur and Wilson, 1967; Hubbell, 2001). By quantifying changes in species associations and the ways those species divide niche space, we can better understand the drivers of ecological change. Traits (e.g., body mass, locomotor strategy and diet) are most often used as proxies for the functional role of a species (Bambach et al., 2007; Chen et al., 2019; Fraser and Lyons, 2020; Pineda-Munoz et al., 2020). Sharing and partitioning of niche space can be quantified using single functional trait axes (e.g., body mass; Pineda-Munoz et al. [2016]) or by constructing ecomorphospaces incorporating multiple functional trait axes (e.g., Bambach et al., 2007; Chen et al., 2019), both of which constitute estimates of functional richness (i.e., the total amount of occupied

niche space) following the definition by Legras et al. (2018) (e.g., Mason et al., 2005; Villéger et al., 2008). Similarly, calculations of total morphological disparity can be used as metrics for niche overlap (e.g., Bapst et al., 2012; Whittingham et al., 2020). Changes in the degree of overlap in trait space, whether univariate or multivariate, among coexisting species are then interpreted as changes in niche similarity, reflecting underlying assembly processes such as limiting similarity (MacArthur and Levins, 1967), competitive exclusion (Hardin, 1960) and environmental or habitat filtering (Soininen et al., 2007a, 2007b; Soininen, 2010). Given the abiotic and biotic changes that typified the PETM, we expect considerable changes in the ways coexisting species divided available niche space.

Herein, we analyze changes in species associations using the methods of Ulrich (2008), which involves the calculation of co-occurrence metrics (i.e., C-score) for each pair of species in each North American Land Mammal Age (NALMA) and comparing to an effect size generated using a null model approach. The result is a series of p-values indicating whether species are aggregated (i.e., are found together more frequently than expected by chance), segregated (i.e., found together less frequently than expected by chance) or randomly associated (i.e., indistinguishable from the null model). Changes in the proportions of species association types have been used as indicators of significant ecological change, such as following the arrival of humans in North America (Lyons et al., 2016; Pineda-Munoz et al., 2020). Species co-occurrences allow for the comparison of niche similarity among and between potentially interacting taxa, and enable us to examine the factors which determine community assembly (Blois et al., 2014). Thus, we compare the niche space occupation of species pairs (aggregations, segregations and random) using estimates of their Grinnellian and Eltonian niches (Grinnell, 1917; Elton, 1927; Hutchinson, 1978). The Grinnellian niche is defined by the environmental conditions (e.g., habitat, temperature, precipitation) in which an organism exists, independent of competition. The Eltonian niche is constructed based on the ways in which an organism interacts with and competes with other organisms along resource use axes (Soberón, 2007; Devictor et al., 2010), and can be approximated using functional traits (Chapin III et al., 2000; McGill et al., 2006; Dehling and Stouffer, 2018).

We estimate the realized Grinnellian niches of species using the palynofloral record of the Bighorn Basin. Floral species richness and functional diversity covary strongly with abiotic environmental factors (Mosbrugger and Utescher, 1997; Mosbrugger et al., 2005; Jackson and Blois, 2015). Angiosperm leaf morphology is useful as a proxy for paleotemperature and mean annual precipitation (Wolfe, 1979; Wolfe, 1995) and has been used specifically in the context of the Paleocene-Eocene Bighorn Basin (Fricke and Wing, 2004). By extension, changes in the taxonomic composition of floral communities are indirectly indicative of changes in paleoenvironments (Harbert and Nixon, 2015; Harbert and Nixon, 2018; Bashforth et al., 2021). Furthermore, mammals, which maintain relatively constant body temperatures, interact most directly with plant communities and their communities are shaped by surrounding plant biomes (Bond et al., 1980; MacCracken et al., 1985; Louys et al., 2011; Suchomel et al., 2014; Luiselli et al., 2015). Furthermore, mammalian species may show strong habitat associations (e.g. Mares and Willig, 1994; Martin and McComb, 2002; Stephens and Anderson, 2014). Thus, the plant communities represent a better measure of the habitats with which mammals most closely interact and a proxy for their environments. As such, variation in mammal community richness is often best predicted by measures

of mean annual precipitation, which can also predict plant community richness (Currie, 1991, 2001; Francis et al., 2003). By quantifying the diverse compositions of palynofloral communities, and associating those compositions with mammal occurrences, we thus approximate the realized Grinnellian niches of mammal species based on the range of plant communities with which they co-occur. We herein refer to those ranges of plant community co-occurrences for each mammal species as their habitat or environmental preferences (*sensu* Beyer et al., 2010), as they approximate the occupied subset of the sample of available environments. By comparing the realized Grinnellian niches of species pairs, we can assess the degree to which environment drove changes in patterns of species occurrence.

We then estimate a component of the Eltonian niches of species using body mass. Body mass is a fundamental mammalian trait, which is a major determining factor in a wide range of other niche characteristics (Peters, 1983; Brougham and Campione, 2020). Furthermore, the degree to which species overlap in body mass trait space appears to reflect community assembly mechanisms (Bowers and Brown, 1982; Brown, 1995; Lyons and Smith, 2013; Fraser and Lyons, 2017; Pineda-Munoz et al., 2020). Mammalian body mass also covaries with other functional traits such as locomotion, thermoregulation and life history (Western, 1979; Dobson and Oli, 2007; Sibly and Brown, 2007; Lovegrove and Mowoe, 2013; Sandel, 2013; Kohli and Rowe, 2019). The diversity of traits that covary with body mass means that body mass distributions can be explained by a wide variety of competing factors, making it difficult to infer specific mechanisms affecting community assembly from body mass alone but conversely makes body mass a useful metric for broadly estimating niche space occupation and niche breadth (Grossnickle, 2020; Slater, 2022). Functional traits such as diet and locomotion can also vary widely among mammals with similar body masses (e.g., a 130-kg lion and a 130-kg wildebeest have greatly dissimilar diets and locomotor modes, despite their

comparable masses). As such, ecological results on the basis of body mass, while likely reflective of broader trends in Eltonian niche space, are not guaranteed to be same as those derived from other functional traits. Given the rarity with which functional traits can be confidently and precisely assigned from the PETM mammalian record, body mass represents the broadest and most descriptive available metric for describing their niches.

Combining Grinnellian and Eltonian methods of niche estimation provides a useful basis for the examination of ecological change through the PETM. By using multiple measures to diversely describe the mammalian niche, we can investigate how changes in functional diversity and environmental and habitat constraints, either independently or in concert, might affect community assembly. This mix of methods may hopefully provide a template for more holistic studies of community ecology in the fossil record going forward.

Methods

Species occurrence and ecological data. Mammal data were acquired from 173 mammal species across 126 sites from the Paleocene and Eocene of the Bighorn Basin in Wyoming (Figure 1). The relatively limited geographic range of the localities ensures that we are examining community-scale assembly processes rather than broader continental-scale trends. The sites spanned three time bins correlated to biozones of the Clarkforkian and Wasatchian North American Land Mammal Ages (NALMAs) (Rose, 1981; Robinson et al., 2005; Secord et al., 2006), the Paleocene Clarkforkian 3 (ca. 56.2–55.8 Ma) and Eocene Wasatchian 0 (ca. 55.8–55.7 Ma) and Wasatchian 1–2 (ca. 55.7–54.8 Ma). The Wasatchian 0 encompasses the PETM. The Wasatchian 1 and 2 are combined, following Rankin et al. (2015) and Fraser and Lyons (2020). Mammal occurrences were downloaded from the Paleobiology Database using the group name “mammalia” and the following parameters: Paleocene

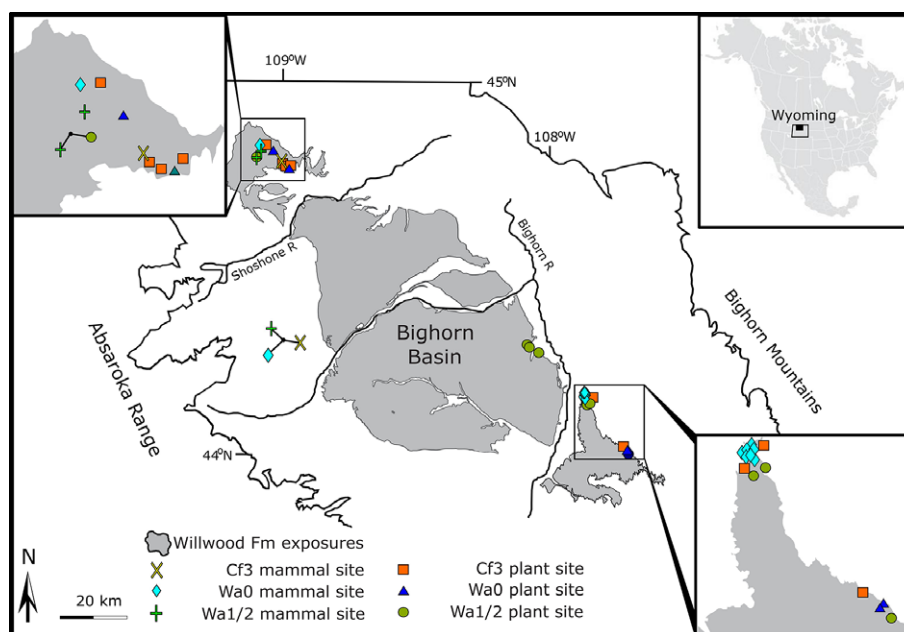


Figure 1. Map of the Bighorn Basin in Wyoming showing the locations of palynofloral- and mammal-bearing sites used in this study. Mammal sites are represented by three symbols corresponding to North American Land Mammal Ages: an X (Clarkforkian 3), a diamond (Wasatchian 0) and a plus sign (Wasatchian 1–2). Palynofloral sites are also represented by three symbols corresponding to North American Land Mammal Ages: a square (Clarkforkian 3), a triangle (Wasatchian 0) and a circle (Wasatchian 1–2). Black dots represent coordinates with multiple overlapping localities, which are indicated by attached black lines. Northwestern and Southeastern portions of the Basin are magnified for the sake of clarity. Exact locality information is provided in the [Supplementary Information B](#). Base map adapted from Baczynski et al. (2013).

and Eocene; region: North America; paleoenvironment: terrestrial (data sources available from the supplementary citation list of Fraser and Lyons, 2020). Mammalian site ages are defined by NALMA subdivisions following Gingerich et al. (1980), Gingerich (1989) and Gingerich (2001). For all mammals, taxonomy was standardized to the Paleobiology Database unless literature searches indicated names had been updated. Most importantly, we made significant efforts to account for splits and synonyms, which, unlike a name change (i.e., the name of a taxon is changed but the number of total species is unchanged), could affect the results of our various analyses.

Approximating mammal environmental niches. Palynological occurrence data were assembled by Korasidis and Wing (2023) from sites assigned to the Clarkforkian 3 (8 sites), Wasatchian 0 (13 sites) and Wasatchian 1 (9 sites) biozones from the Bighorn Basin, Wyoming. These sites were correlated to biozones by Korasidis et al. (2023). Palynofloras were assigned to the Clarkforkian 3 (palynofloral zone P6 of Nichols and Ott [1978]) based on the presence of *Aesculipollis wyomingensis*, *Caryapollenites inelegans*, *Caryapollenites wodehousei*, *Echitricolpites supraechinatus*, *Eucomia leopoldae*, *Intratrirporopollenites vespicipites*, *Momipites wyomingensis*, *Pistillipollenites mcgregorii* and *Rousea crassimurina* in addition to dominant *Caryapollenites veripites*. Palynofloras were assigned to the Wasatchian 0 (palynofloral zone E-0 of Korasidis et al. [2023]) based on the presence of *Friedrichipollis geminus*, *Platycarya platycaryoides*, *Retistephanocolporites pergrandis*, *Striatopollis calidarius* and *Striatricolporites astutus* and dominant *Areipites* spp. and *Aesculiidites circumstriatus*. Palynofloras were assigned to the Wasatchian 1 (palynofloral zone E of Nichols and Ott (1978) and Korasidis et al. [2023]) based on the presence of *Platycarya platycaryoides* and *Intratrirporopollenites instructus*.

A Jaccard distance matrix was constructed from the species composition of the palynofloral sites and examined using the Nonmetric Multi-Dimensional Scaling (NMDS) and PERMANOVA functions in PAST v4.13 (Hammer et al., 2001) to establish the similarity of palynofloral assemblages among sites. NMDS and PERMANOVA analyses of palynofloral sites were also conducted on the basis of a Cosine similarity matrix, producing near-identical results (see [Supplementary Information A](#)).

Environmental preferences for mammal species were quantified using their spatiotemporal associations with palynofloral assemblages. For each of the 126 mammal sites used, the geographically closest contemporaneous palynofloral site was determined using the earth.dist function in the R package fossil (Vavrek, 2011). Each mammal site was then assigned the same NMDS scores (NMDS 1 and 2) as the closest contemporaneous palynofloral locality. Absent greater stratigraphic detail, mammal and palynofloral sites from the same NALMA subdivisions are herein considered contemporaneous, thus limiting the temporal scale of results to that of the biozone. Each species was assigned an average of the NMDS scores for the sites at which they were found, thus allowing for a species-scale comparison of environmental preference across time bins. Mean environmental preferences were calculated for each time bin and compared between time bins via the ANOVA function in PAST v4.13 (Hammer et al., 2001).

Mammal ecomorphology. The niche space occupation of Paleocene-Eocene Bighorn Basin mammals was inferred via body mass. Body mass estimates are as in Fraser and Lyons (2020), which were compiled from Alroy (1998), Tomiya (2013), Smits (2015) and Smith et al. (2018) and ln-transformed. Body masses were based on specimen measurements and averaged within genera where direct measurements were unavailable. Mean body masses were

calculated for each time bin and plotted through time. Dietary and locomotor inferences were not included in this analysis of mammalian niche space, due to a rarity of clear associations between dental morphology and diet in Paleocene mammals, and similarly rarity of postcranial elements appropriate for locomotor inferences.

Species co-occurrence. Mammal assemblages from all three biozones were subjected to a PAIRS analysis using the R package cooccur (Griffith et al., 2016) following the methodology of Ulrich (2008), Blois et al. (2014), Lyons et al. (2016) and Pineda-Munoz et al. (2020). Briefly, we determined whether pairs of species were significantly aggregated (i.e., found together more frequently than by chance), segregated (i.e., found apart more frequently than by chance) or randomly associated within each biozone. To do so, we calculated a scaled C-score for each pair of species in the site-by-species occurrence matrix for each biozone. We used the following method of calculating C-scores: $C_{ij} = (R_i - D)(R_j - D)/R_iR_j$, where C_{ij} was the C-score for species pair i and j , R_i was the row total (the number of species occurrences) for species i , R_j was the row total for species j and D was the number of shared sites in which both species are present. For each species pair, C-score values range from 0.0 (complete aggregation) to 1.0 (complete segregation). To determine whether species were significantly aggregated or segregated, we calculated p-values, by constructing a null distribution of C-scores for each biozone by shuffling matrix elements, keeping row and column totals. Maintaining row and column totals ensures that differences in species occupancy (row totals) and sampling intensity between sites (column totals) are incorporated into the null distribution of C-scores for each species pair (Gotelli, 2000; Ulrich and Gotelli, 2010). Lyons et al. (2016) and Tóth et al. (2019) also showed that changes in the numbers of aggregated, segregated and randomly associated species pairs can be biased as a result of differences in collection mode, temporal grain, taphonomic biases, taxonomic resolution, differential sampling of abundant and rare species or differences in the spatiotemporal extents among time bins and localities, but that sampling biases can be mitigated by rigorous resampling (e.g. Tóth et al., 2019) or comparison to a null model (e.g. Lyons et al., 2016). We control for potential sampling and taphonomic biases by employing a null model, as described below. The R code used to produce the species pairs and null model is available here: <https://github.com/danielleleefraser/PETMpairs>.

Ecological differences. To test whether the ecomorphology and environmental preferences of species pairs changed through time, we followed a very similar methodology to Pineda-Munoz et al. (2020). For environment and body mass, we calculated absolute differences for all aggregated, segregated and randomly associated species pairs and took the average within each type for each biozone. Significant changes through time were assessed using randomly assembled mammal assemblages, as described below.

Null modeling. In the present study, we address whether the differences in environmental or habitat preferences and ecomorphology among significantly aggregated and segregated species pairs changed across the PETM. Linear regression cannot be used due to sample size limitations ($n = 3$ time bins) and a lack of statistical power. Furthermore, the metrics we employ herein may be sensitive to sampling intensity (i.e., number of samples, number of species and occupancy of sites) (Gotelli and Colwell, 2011; Ulrich et al., 2018). Thus, to assess the significance of change through time, we use a null model that randomizes the assignment of species among sites across all three biozones (Gotelli, 2000), preserving richness differences among sites and, thus, taphonomic differences. It thus randomizes patterns of species associations. We consider

this the appropriate null model for the present study due to our use of a co-occurrence metric, which calculated significant aggregation or segregation based on species occurrences across multiple sites. We then compared our observed environmental preferences and body masses to the null model using standardized effect sizes, specifically Cohen's D ($d = (\text{mean observed} - \text{mean null}) / \text{standard deviation of null}$). We considered absolute values of $d \leq 0.2$ small effect sizes (i.e., nonsignificant differences) and $d \geq 0.8$ large effect sizes (i.e., significant differences). The above null modeling approach also addresses the role of taphonomy because richness differences were preserved among sites, thus controlling for simple taphonomic biases that could generate heterogeneity in the number of species per site and number of sites per time bin.

Results

The total number of nonrandom and random species pairs increased from the Clarkforkian 3 to Wasatchian 0 (Figure 2), reflecting the increase in faunal species richness during the PETM (Woodburne et al., 2009; Chew and Oheim, 2013). The majority of significant pairs were aggregations; segregations were rare during the entire interval, consistent with previous results (Lyons et al., 2016; Pineda-Munoz et al., 2020). No segregated species pairs were discernible during the Wasatchian 0 biozone, precluding clear patterns from being discerned between segregated pairs.

The NMDS constructed from the 30 palynofloral localities revealed three distinct clusters of palynofloral communities along two NMDS axes. NMDS results returned a stress value of 0.1591, below the generally accepted stress limit of 0.2 in ecological research (Kruskal, 1964; Clarke, 1993; McCune and Grace, 2002). The three clusters of palynofloral communities correspond to each of the three studied time bins, these being the pre-CIE (Clarkforkian 3), CIE (Wasatchian 0) and post-CIE (Wasatchian 1) (Figure 3). These clusters showed minimal overlap in NMDS space, with all three showing significantly different compositions when analyzed by PERMANOVA (10,000 permutations, Bonferroni corrected

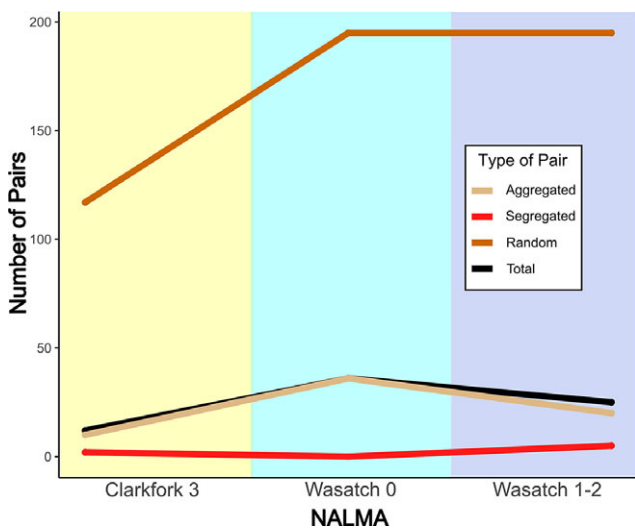


Figure 2. Quantities of mammal species pair types through the Clarkforkian 3 (ca. 56.2–55.8 mya), Wasatchian 0 (ca. 55.8–55.7 mya) and Wasatchian 1–2 (ca. 55.7–55.2 mya) biozones of the Bighorn Basin. Shown are numbers of significantly aggregated and segregated species pairs for each time bin, as determined through PAIRS analysis in the R package cooccur (Griffith et al., 2016). Total significant pairs (aggregated + segregated) and pairs that show no significant association or dissociation patterns (labeled here as “Random”) are also shown.

p -value differences between each cluster ≤ 0.0003). Pairwise F -values derived from PERMANOVA are as follows: Clarkforkian 3/Wasatchian 0 = 10.89, Clarkforkian 3/Wasatchian 1–2 = 5.608 and Wasatchian 0/Wasatchian 1–2 = 13.13. The Clarkforkian 3 and Wasatchian 1–2 biozones were almost exclusively differentiated from each other along NMDS coordinate 2, while the Wasatchian 0 was differentiated from both of the other two time bins primarily along NMDS coordinate 1. These results are nearly identical to those produced on the basis of a Cosine similarity matrix (see [Supplementary Information A](#)).

The mammal localities are limited in their geographic spread (Figure 1). As such, the 126 mammal sites were most closely geographically correlated to only five contemporaneous palynofloral localities. The Wasatchian 1–2 mammal sites were geographically associated with only one palynofloral site, while the Clarkforkian 3 and Wasatchian 0 mammal sites were associated with only two different palynofloral sites each (see [Supplementary Information B](#)). However, mammal species that spanned more than a single biozone were associated with multiple palynofloral sites, which were used to inform calculations of their Grinnellian niche.

The environmental preferences, as calculated using the average of the NMDS scores of associated palynofloral sites, among aggregated species are less similar than expected under a null model during the Clarkforkian 3 for both NMDS axes, increasing in dissimilarity between the Clarkforkian 3 and Wasatchian 0 time bins to fall in-line with null expectations (Table 1; Figure 4a,b). Differences in environmental preference between segregated species are not distinguishable from null expectations for NMDS coordinate 1, but significantly decrease with respect to palynofloral NMDS coordinate 2 (Figure 4c,d). The lack of change between segregated species along NMDS coordinate 1 is expected, as that axis primarily serves to describe the uniqueness of floral communities in the Wasatchian 0 time bin (Figure 3), a time bin in which there were no significantly segregated species pairs. Thus, differences in environmental preference among segregated species pairs are best described with respect to NMDS coordinate 2. Differences in environmental preference between randomly paired mammal species all fall within the standard deviation of the null model for both NMDS coordinates (Figure 4e,f). Across all species, mean environmental preferences also appear to change significantly between time bins along both NMDS coordinates (Figure 4g), with ANOVA results showing highly significant ($p < 0.0005$) Mann–Whitney pairwise differences in both NMDS values among all time bins with the exception the Wasatchian 0 and 1/2 time bins, which could be differentiated along NMDS coordinate 1, but not along NMDS coordinate 2 ($p = 0.6636$); these trends appear the same when means for each time bin are calculated only from taxa whose first occurrences fall within that time bin (Figure 4i–j). The range of mammalian environmental preferences appears expand from the Clarkforkian 3 (NMDS1 = 0.02219, NMDS2 = 0.0776) to the Wasatchian 0 (NMDS1 = 0.02576, NMDS2 = 0.100) and Wasatchian 1–2 (NMDS1 = 0.02587, NMDS2 = 0.0831), as appears to be the case in both the total set of mammalian taxa and the set only including first occurrences (Figure 4g–j). These results, combined with the palynofloral assemblage data, show an increase in the difference in environmental preference among commonly associated mammalian species over the studied interval in conjunction with progressive change in the environmental setting. That change is also accompanied by a greater similarity in the environmental preference among segregated species.

Mammalian species pairs showed minimal changes in the body mass components of Eltonian niche occupation (Figure 5). We

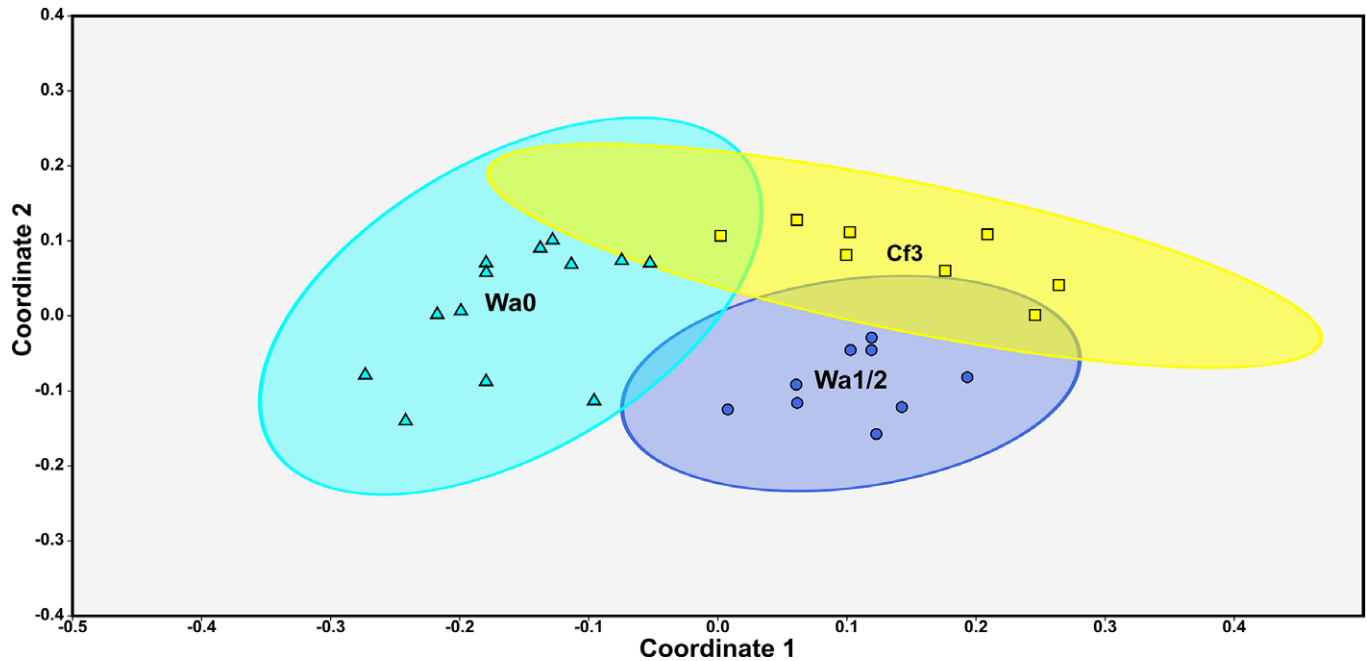


Figure 3. NMDS plot displaying the similarity in composition of palynofloral communities from each of the Clarkforkian 3 (Squares, Cf3), Wasatchian 0 (Triangles, Wa0) and Wasatchian 1–2 (Circles, Wa1–2) time bins. NMDS was produced based on a Jaccard similarity matrix comparing the taxonomic occurrences of all 30 palynofloral sites. NMDS is ordinated across 2 axes, returning a stress value of 0.1591. Palynofloral assemblage age assignments derived from Korasidis et al. (2023) and presence-absence data from Korasidis and Wing (2024). Ellipses represent 95% confidence intervals of the total assemblage space occupied in each time bin.

Table 1. Effect sizes of differences in climate preference between species pairs within each of the Clarkforkian 3 (ca. 56.2–55.8 mya), Wasatchian 0 (ca. 55.8–55.7 mya) and Wasatchian 1–2 (ca. 55.7–55.2 mya) biozones. Differences in climate preference are shown along each of the 2 palynofloral NMDS axes. Differences are shown separately among pairs of each type: aggregated (Agg.), segregated (Seg.), and random (Rand.). Segregated species pairs are not observed from the Wasatchian 0 biozone

Biozone	Agg. Diff. (NMDS1)	Seg. Diff. (NMDS1)	Rand. Diff. (NMDS1)	Agg. Diff. (NMDS2)	Seg. Diff. (NMDS2)	Rand. Diff. (NMDS2)
Clarkforkian 3	–1.042142	–0.951861	–0.936426	–1.035858	–0.682449	–0.937878
Wasatchian 0	–0.395042	NA	–0.195936	–0.760942	NA	–0.721962
Wasatchian 1–2	–0.551791	–0.845517	–0.606639	–0.653171	–0.953286	–0.501387

observe no change in body mass differences regardless of the type of species pair through the PETM (Figure 5a–c). We observed a slight, but statistically insignificant decrease in mean body mass across all taxa between the Clarkforkian 3 and Wasatchian 0 biozones, with ANOVA results showing no significant Mann–Whitney pairwise differences (p -values >0.61) in mean log body mass among any of the three time bins (Figure 5d), a pattern that is repeated (p -values >0.48) when looking only at the first occurrences (Figure 5e).

Discussion

The PETM in North America was characterized by rapid, short lived climate change, the arrival of Eurasian (i.e., artiodactyls, perissodactyls and primates) immigrants, and northward range expansions of endemic mammals that were not balanced by extinctions (Bowen et al., 2002; Gingerich, 2006; Burger, 2012; Fraser and Lyons, 2020). The results were richer mammal communities (i.e., greater γ and α diversity) and, potentially, changes in how communities were assembled (Burger, 2012; Fraser and Lyons, 2020). Today, the assembly of tropical and temperate mammal communities are driven by divergent processes; temperate mammal communities are subject to environmental filtering, a process

whereby species are sorted along abiotic and biotic gradients according to their environmental tolerances (Weiher et al., 1998; Soininen et al., 2007a; Soininen et al., 2007b; Kraft et al., 2015), to a greater degree than tropical communities (Hawkins et al., 2003; Currie et al., 2004; Helmus et al., 2007). The assembly of tropical mammal communities may be driven more by species–species interactions (i.e., resource competition) than their temperate counterparts, though this pattern may not always hold true (Safi et al., 2011; Fraser and Lyons, 2017). We therefore expected significant changes in the assembly of PETM mammal communities. The methods used herein can be useful tools for teasing apart the processes driving mammalian community assembly through the PETM (Blois et al., 2014; Tóth et al., 2019). Through identifying aggregated and segregated species pairs, we make fruitful comparisons of body masses and environmental preferences that enhance our ability to differentiate assembly processes such as environmental filtering and resource competition (Blois et al., 2014; Tóth et al., 2019; Pineda-Munoz et al., 2020).

The PETM was a rapid climate change event that may have changed the degree to which environmental filtering drove community assembly. Under an environmental filtering model, we expect species with similar environmental preferences to inhabit

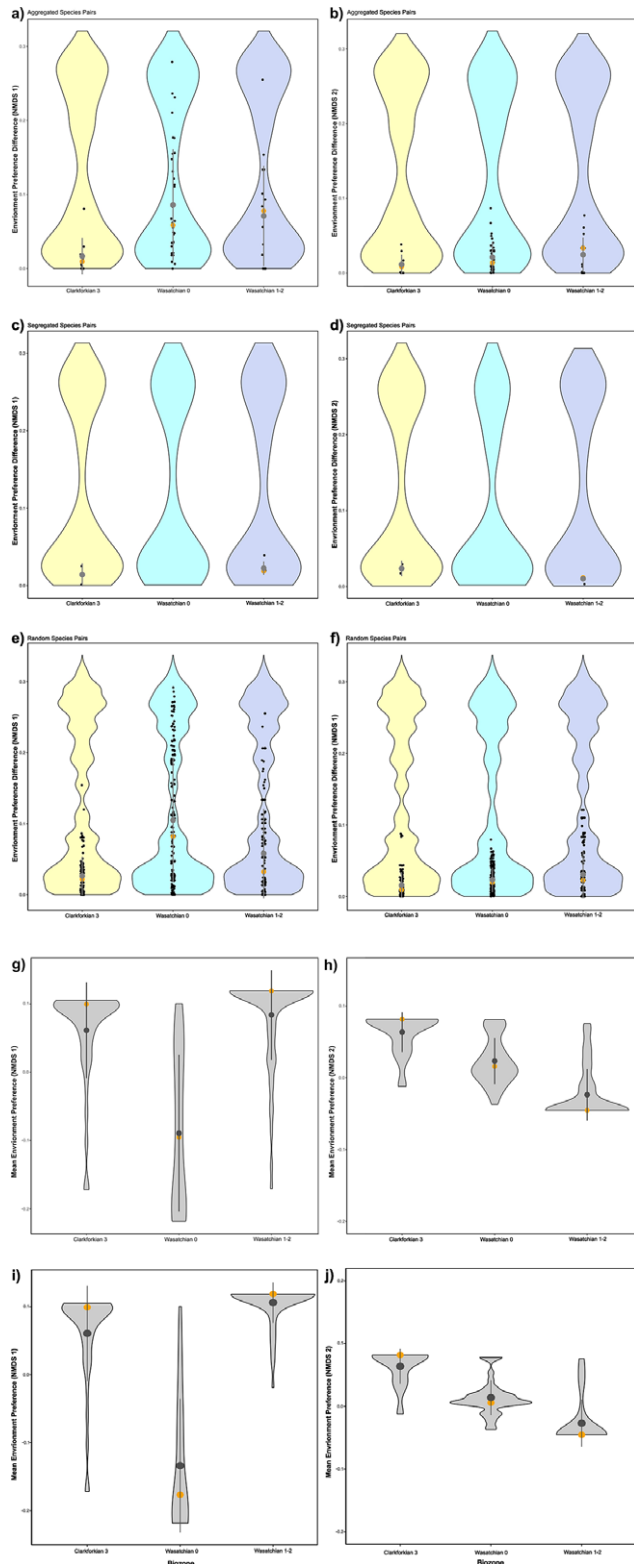


Figure 4. Mean differences in environmental preference between mammal species pairs and regional environmental distributions through the Clarkforkian 3 (ca. 56.2–55.8 mya), Wasatchian 0 (ca. 55.8–55.7 mya) and Wasatchian 1–2 (ca. 55.7–55.2 mya) biozones. Environmental preferences are here determined as a mean of the NMDS coordinates of the closest contemporaneous palynofloral sites for each mammal taxon. Mean and median differences in scores along NMDS coordinate 1 are shown for aggregated (a), segregated (c) and random (e) species pairs. Mean and median differences in scores along NMDS 2 coordinate 2 are likewise shown for aggregated (b), segregated (d) and random (f), species pairs. No differences in environmental

the same communities (Weiher et al., 1998; Kraft et al., 2015). Furthermore, those species should share traits that mediate their relationship with the environment (Weiher et al., 1998; Cornwell et al., 2006), in this case, body mass. Body mass may directly interact with climate through the laws of thermodynamics (Porter and Gates, 1969; Ahlborn, 2000; Gillooly et al., 2001) but is also correlated with many other fundamental components of mammalian niches (Western, 1979; Peters, 1983; Iriarte-Diaz, 2002; Dobson and Oli, 2007; Sibly and Brown, 2007; Lovegrove and Mowoe, 2013; Kohli and Rowe, 2019). In the context of species pairs, under an environmental filtering scenario, significantly aggregated species should be most similar in associated floral NMDS scores and body mass, while segregated species should be least similar in both categories (Blois et al., 2014).

We show that environmental preferences among aggregated species pairs were more similar than null expectations during the Clarkforkian 3 and that differences in environmental preferences became indistinguishable from the null during and after the PETM (Table 1; Figure 4a,b), which might indicate that community assembly may no longer have been driven by environmental filtering (sensu Blois et al., 2014). However, we find the same pattern for random and segregated (along NMDS 1) species pairs (Table 1; Figure 4a, b), suggesting that the observed change among aggregated pairs likely does not indicate a change in community assembly. Conversely, we show that differences in environmental preferences among segregated species along NMDS 2 were indistinguishable from null expectations until the Wasatchian 1–2 biozones, whereupon they become significantly similar (Figure 4d), evidencing a lack of an environmental filter with respect to paleofloral habitats. We also find a lack of significant change in comparative body masses among species pairs of all types (Figure 5a–c), in agreement with Fraser and Lyons' (2020) observations of static body mass dispersion through the same period. While we can only reject post-Clarkforkian environmental filtering of mammalian taxa through the lens of palynofloral communities, there is a strong correlation between changes in floral community composition and changes in abiotic environmental variables (e.g., mean annual precipitation, temperature and seasonality), both in general (Laughlin et al., 2011; Harbert and Nixon, 2015; Harbert and Nixon, 2018; Bashforth et al., 2021; Bricca et al., 2022) and in the specific case of the PETM in the Bighorn Basin (Fricke and Wing, 2004; Wing and Curran, 2013; Korasidis and Wing, 2023). Given the breadth of associations between plant community composition and the abiotic environment, we consider associations between mammals and palynofloral assemblages to be reflective of broader mammalian environmental preferences. Furthermore, while there are estimates of MAT for the Bighorn Basin during the PETM (e.g. Snell et al., 2013), mammals with their relatively constant body temperatures are expected to interact most directly with plant communities, apparent as significant correlations between

preference are shown between segregated species pairs in the Wasatchian 0 biozone as there were no significantly segregated species pairs determined from that interval. Differences in environmental preference values which fall within the expectations of our null model are shown by the colored violin plots. Distributions of environmental preferences among all Bighorn Basin mammals are shown in gray with means and medians along NMDS 1 (g and i) and NMDS 2 (h and j). We here show both mean palynofloral NMDS scores of all mammal taxa occurring within a given time bin (g and h), and mean scores for each time bin of only those mammal taxa which first occur in that time bin (i and j). In all cases, mean differences are shown as gray dots, while median differences are shown as orange dots, with 95% confidence intervals shown as orange bars. Regional environmental preference distributions were not compared to a null model.

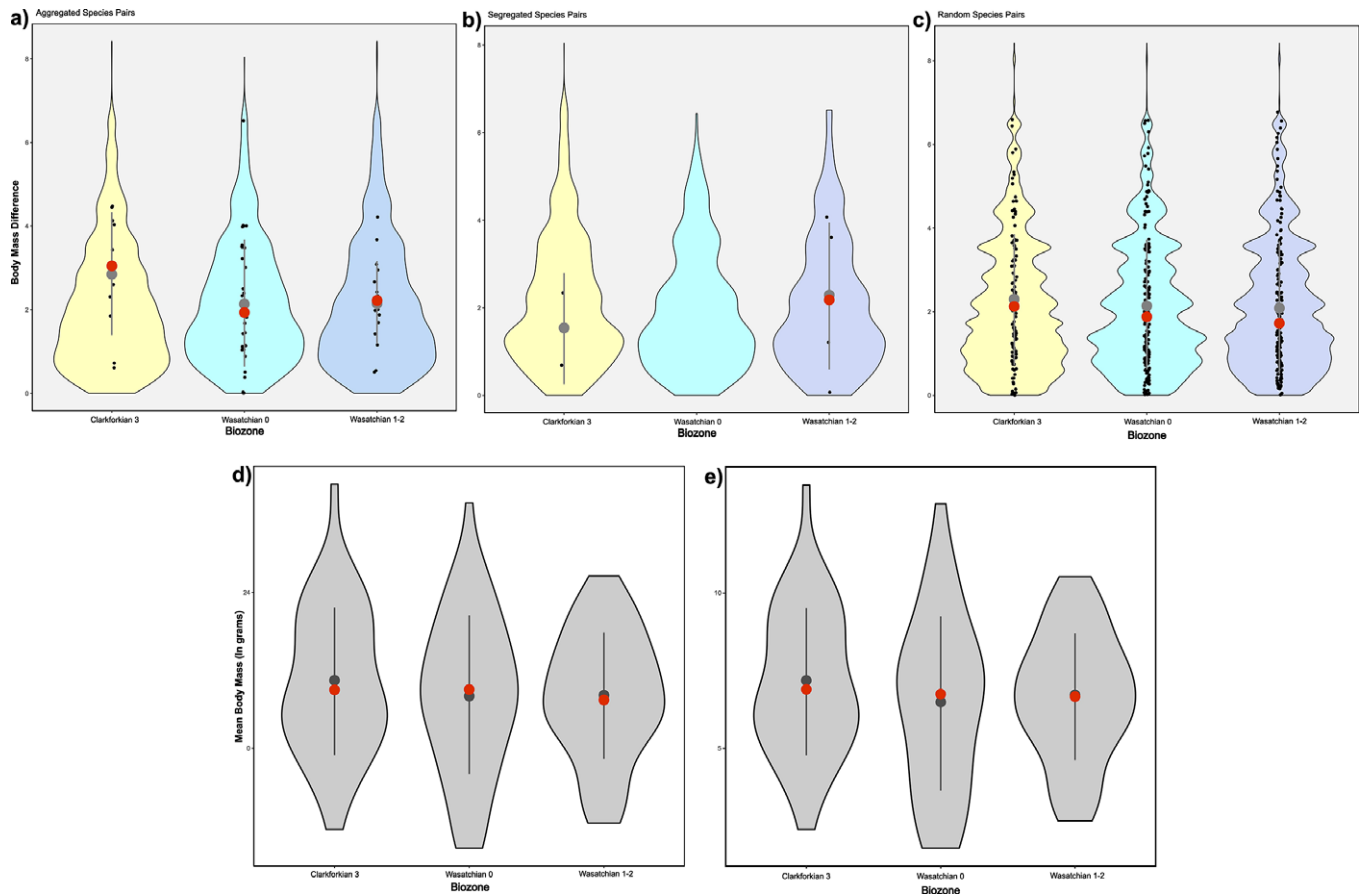


Figure 5. Mean differences in body mass between mammal species pairs and regional body mass distributions through the Clarkforkian 3 (ca. 56.2–55.8 mya), Wasatchian 0 (ca. 55.8–55.7 mya) and Wasatchian 1–2 (ca. 55.7–55.2 mya) biozones. Body mass estimates are here compiled from Alroy (1998), Tomiya (2013), Smits (2015) and Smith et al. (2018) and ln-transformed. Mean differences are shown for aggregated (A), segregated (B) and random (C) species pairs. No differences in body masses are shown between segregated species pairs in the Wasatchian 0 biozone as there were no significantly segregated species pairs determined from that interval. Differences in body mass which fall within the expectations of our null model are represented by colored violin plots. Distributions are shown for all body mass estimates from mammal taxa occurring within a given time bin (D), and for each time bin of only those mammal taxa which first occur in that time bin (E). In all cases, mean differences are shown as gray dots, while median differences are shown as red dots, with 95% confidence intervals shown as gray bars. Regional body mass distributions were not compared to a null model.

mammal richness and primary productivity or energy in both space and time (Currie, 1991; Fritz et al., 2016). There are also potentially unmeasured environmental variables for which correlations with PETM floral community structure are unknown, which may represent unexplored environmental filters. However, based on the analyses herein, we suggest that a change in the strength of environmental filtering was unlikely to have been a significant factor in the assembly of post-Clarkforkian mammalian communities.

A reduced role for environmental filtering in community assembly, specifically relating to the biotic and abiotic conditions created by plant assemblages, during and after the PETM could suggest either a change in the variance of mammal environmental/habitat preferences or spatial variability of environment (Peres-Neto et al., 2012; Blois et al., 2014; Daniel et al., 2019). An increase in the overall variance of preferred environments or habitats among mammal taxa (Figure 4g–h) could increase the similarity of environmental preferences among taxa, regardless of whether they are aggregated or segregated pairs, reducing the differentiability of the observed differences from the null model. Such a trend may have been a result of greater environmental generalism among newcomer taxa; taxa with first appearances in the Wasatchian 0 appear to be associated with a wider array of palynofloral assemblages (Figure 4j–i), though the same taxa only show a small apparent

increase in the variance of body masses (Figure 5e). Broader environmental preferences would have made the newcomer taxa more likely to successfully shift their ranges in a period of climatic upheaval like the PETM (Bergman, 1988; Parsons, 1994; Marvier et al., 2004; Richmond et al., 2005). However, taxa that survived through the Clarkforkian 3 into Wasatchian 0 also tended to possess wide environmental preferences (Figure 4g–h), likely reflecting persistence of taxa that could weather PETM climate change, as has been modeled and observed in environmental generalists with respect to modern climate change (e.g. Warren et al., 2001; Juilliard et al., 2004; Thomas et al., 2004).

Stability of individual species' Grinnellian niches (i.e., association with palynofloral assemblages) through time is an assumption that has allowed for the prediction of historical ranges (Svenning et al., 2011) and responses to climate change (e.g. Peterson, 2003; Tingley et al., 2009). Individual taxa can, however, undergo significant changes in their geographic distributions and, thus, environmental conditions in which they live. Over longer timescales, native taxa tend to constrict their realized Grinnellian niche space when faced with climate change and introduction of immigrant taxa (Peterson, 2011; Brame and Stigall, 2014; Stigall, 2014). Immigrant taxa also alter their Grinnellian niche occupation during range shift events over short timescales (e.g., Broennimann et al., 2007;

Early and Sax, 2014). We calculated species environmental preferences in a time transgressive manner, however. That is, environmental preferences for each taxon were calculated based on their occurrences across all three biozones, as a closer approximation of their long-term environmental preferences and, potentially, environmental tolerances. Furthermore, the spatially clustered nature of the palynofloral and mammal occurrences within each biozone means that the only way to capture variability in mammal environmental preferences is to compute means across time bins. Thus, the observed changes in mean environmental preference, variance and reduced similarity among species pairs must result from changes in species composition rather than shifts in the Grinnellian niches of individual taxa through time.

Enhanced spatial homogeneity of environment does not appear to explain the changes in the comparative environmental preferences among species pairs. Palynofloral and macrofloral communities do not appear to show significant changes in spatial variability through the PETM (Wing and Currano, 2013, Korasidis and Wing, 2023). Mammal communities also show either an increase (Darroch et al., 2014) or no change (Fraser and Lyons, 2020) in β diversity during the PETM, suggesting that enhanced environmental homogeneity did not drive the observed increase in environmental preference similarity among segregated species during the Wasatchian 1–2 biozones (Figure 4d).

Increases in mammal α and γ diversity during the PETM of North America (Gingerich, 2003; Darroch et al., 2014; Chew, 2015; Fraser and Lyons, 2020) may also have changed the competitive landscape; new arriving species, such as artiodactyls and perissodactyls, overlapped in stable isotope (i.e., $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and, thus, dietary and environmental niche space with endemic taxa (Secord et al., 2008), potentially enhancing the likelihood of interspecific resource competition. While species that immigrated into the Bighorn Basin during the PETM tended to be smaller (Figure 5e) than incumbent taxa (Bowen et al., 2002; Gingerich, 2006), this does not on its own provide significant evidence against enhanced resource competition among species.

The outcome of competitive interactions can include competitive exclusion or limiting similarity, phenomena for which we find no evidence with respect to body masses from the Clarkforkian 3 through Wasatchian 1–2, as they were not differentiable from null expectations (Figure 5a–c). These results complement those of Fraser and Lyons (2020), who suggested that the niche space of PETM mammalian communities in North America was unsaturated based on a lack of evidence for enhanced intraspecific interactions despite increased species richness. The principle of competitive exclusion posits that species with extremely similar or identical Eltonian niches may not coexist in the same community (Hardin, 1960). Limiting similarity predicts that there be an upper limit on the degree to which coexisting species can overlap in resource use (MacArthur and Levins, 1967; Abrams, 1983). Under both limiting similarity and competitive exclusion, we expect greater differences in body mass distributions among aggregated species pairs than the null expectation, and fewer differences among segregated species pairs than the null expectation (*sensu* Blois et al., 2014). However, the longer temporal scales averaged by paleontological data mean that significant aggregations or segregations may be products of environmental or taphonomic factors in addition to biotic interactions (Blois et al., 2014). If neither taphonomy nor environment can explain significant aggregations or segregations of species, then we can infer that biotic interactions played a role in community assembly. In the present case, interspecific interactions can be confidently invoked if species

associations are not already explained by differences in environmental preference and if differences in body masses among significantly aggregated or segregated species differ significantly from null expectations, which address taphonomic effects (see *Methods*). Likewise, competitive exclusion, predicted to manifest as significant similarity among segregated species pairs, may be less discernible with increasing spatial scale (Araújo and Rozenfeld, 2014), though some exceptions from both mammalian and avian ecology do show larger-scale discernibility of interactions (Gotelli et al., 2010; Safi et al., 2011; Fraser and Lyons, 2017). The spatial scale of the present study (~200 km) is comparatively small, thus enhancing the potential for detecting interspecific interactions, yet we were still unable to detect any evidence of body mass-mediated changes in community assembly among PETM mammals.

While body mass can account for a large part of an animal's Eltonian niche, it is not perfectly correlated with every other Eltonian niche metric. Body mass is broadly collinear with traits such as diet and locomotion (Western, 1979; Sibly and Brown, 2007; Lovegrove and Mowoe, 2013), but these traits may exhibit different patterns to that of body mass in mammalian communities through the PETM. There are changes documented in the diversity of locomotor modes between Clarkforkian and Wasatchian mammals resulting from the arrival of diverse digitigrade and unguligrade immigrants, among others (Rose, 1990; Gould, 2017). Dietary niche occupation, too, may have seen changes during the PETM (Stroik and Schwartz, 2018; Selig et al., 2021). However, there is not yet sufficiently detailed or abundant information on the locomotor or dietary habits of PETM Bighorn Basin mammals to support co-occurrence analyses like PAIRS.

In lieu of niche space expansion, stasis in the similarity of body mass space between species pairs during a period of increasing taxonomic diversity could be explained by enhanced primary productivity as competition for resources is relaxed (MacArthur, 1972; Strobeck, 1973; Lawlor, 1980). The Bighorn Basin experienced an increase in the abundance of nitrogen-fixing legumes during the PETM (Bruneau et al., 2008; Currano et al., 2016), conditions which are associated with increased primary productivity (Epihov et al., 2017). Mean annual precipitation, also considered a correlate of primary productivity (Chapin III et al., 2011), decreased at the beginning of the PETM, but rebounded by the end of the CIE body (i.e., roughly contemporaneous with the end of the Wasatchian 0 biozone) (Wing et al., 2005; Kraus and Riggins, 2007; Secord et al., 2012). It is therefore possible that, at least by the end of the Wasatchian 0, primary productivity had increased sufficiently to dampen competition for resources, though more direct estimates of regional primary productivity are needed to test this hypothesis. Were it to have occurred, increased primary productivity would represent a reasonable mechanism for the unsaturation of mammalian niche spaces interpreted by Fraser and Lyons (2020).

Climate change and range shift events like those seen in the modern are often associated with climatic generalism, particularly on the part of incoming immigrant taxa (Bergman, 1988; Vermeij, 1991; Marvier et al., 2004). Our results from the PETM of the Bighorn Basin indicate that such events may also broaden the range of environmental preferences exhibited by subsequent post-event communities as a whole, removing environmental preference as a determining factor in community assembly and homogenizing environmental preference across geography. These results are likely best compared to modern communities that are unsaturated in niche occupation or which occur in environments with increasing primary activity. Our observations of Grinnellian niche variance also indicate that assumptions of niche stability over time may not

be applicable at the community scale, as the predictive power of environmental preference on community assembly is lost with the onset of climate change and faunal turnover.

Conclusions

Our findings combine to depict a changing environment in the PETM of the Bighorn Basin, which features little to no change in the occupation of body mass space, despite dramatic taxonomic and environmental change. We find no evidence for changes in the degree to which community assembly was driven by environmental preferences or functional roles between the Wasatchian 0 and Wasatchian 1–2 biozones. The methods used herein demonstrate the utility of incorporating different distinct modes of niche quantification in elucidating the effects of environmental disturbance and range shifts on community structure. The decrease of differences in environmental preference between communities (shown here through segregated species pairs) additionally indicates that environmental preference was not only not a determining factor in the geographic separation of species, but that across geography species were significantly more homogeneous in their environmental preferences than expected. Given that body mass also does not appear to have an impact on community assembly during this time, we are left with no distinct drivers of species segregation. Our results appear to concur with the idea that the unsaturated nature of mammalian communities may have enabled functional stability during a period of climate change and faunal turnover.

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Data availability statement. The data that support the findings of this study are available from the corresponding author, M.A.J.B.W., upon reasonable request. R code used to produce mammal species pairs and null models is available here: <https://github.com/danielleleefraser/PETMpairs>.

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Author contribution. Conception and design of work: M.A.J.B.W., V.A.K. and D.F.; Data collection: M.A.J.B.W., V.A.K. and D.F.; Data analysis: M.A.J.B.W. and D.F. Drafting and revising: M.A.J.B.W., V.A.K. and D.F.

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Competing interest. The authors declare no competing interest.

References

- Abels HA, Lauretano V, van Yperen AE, Hopman T, Zachos JC, Lourens LJ, Gingerich PD and Bowen GJ (2016) Environmental impact and magnitude of paleosol carbonate carbon isotope excursions marking five early Eocene hyperthermals in the Bighorn Basin, Wyoming. *Climate of the Past* **12**, 1151–1163.
- Abrams P (1983) The theory of limiting similarity. *Annual Review of Ecology, Evolution, and Systematics* **14**, 359–376.
- Ahlborn BK (2000) Thermodynamic limits of body dimension of warm blooded animals. *Journal of Non-Equilibrium Thermodynamics* **25**, 87–102.
- Alroy J (1998) Cope's rule and the dynamics of body mass evolution in north American fossil mammals. *Science* **280**, 731–734.
- Araújo MB and Rozenfeld A (2014) The geographic scaling of biotic interactions. *Ecography* **37**, 406–415.
- Aziz HA, Hilgren FJ, van Luijk GM, Sluijs A, Kraus MJ, Pares JM and Gingerich PD (2008) Astronomical climate control on paleosol stacking patterns in the upper Paleocene-lower Eocene Willwood formation, Bighorn Basin, Wyoming. *Geology* **36**, 531–534.
- Baczynski AA, McInerney FA, Wing SL, Kraus MJ, Bloch JI, Boyer DM, Secord R, Morse PE and Fricke HC (2013) Chemostratigraphic implications of spatial variation in the Paleocene-Eocene thermal maximum carbon isotope excursion SE Bighorn Basin, Wyoming. *Geochemistry Geophysics, Geosystems* **14**, 4133–4152.
- Bambach RK, Bush AM and Erwin DH (2007) Autecology and the filling of ecospace: Key metazoan radiations. *Palaeontology* **50**, 1–22.
- Bapst D, Bullock P, Melchin M, Sheets H and Mitchell C (2012) Graptoloid diversity and disparity became decoupled during the Ordovician mass extinction. *PNAS* **109**, 3428–3433.
- Barnosky AD, Hadly EA, Gonzalez P, Head J, Polly PD, Lawing AM, Eronen JT, Ackerly DD, Alex K, Biber E, Blois J, Brashares J, Ceballos G, Davis E, Dietl GP, Dirzo R, Doremus H, Fortelius M, Greene HW, Hellmann J, Hickler T, Jackson ST, Kemp M, Koch PL, Kremen C, Lindsey EL, Looy CV, Marshall CR, Mendenhall C, Mulch A, Mychajliw AM, Nowak C, Ramakrishnan U, Schnitzler J, Das Shrestha K, Solari K, Stegner L, Stegner MA, Stenseth NC, Wake MH and Zhang Z (2017) Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787.
- Bashforth AR, DiMichele WA, Eble CF, Falcon-Lang HJ, Looy CV and Lucas SF (2021) The environmental implications of upper Paleozoic plant-fossil assemblages with mixtures of wetland and drought-tolerant taxa in tropical Pangea. *Geobios* **68**, 1–45.
- Bergman E (1988) Foraging ability and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *Journal of Animal Ecology* **57**, 443–453.
- Beyer HL, Haydon DT, Morales JM, Frair JL, Hebblewhite M, Mitchell M and Matthiopoulos M (2010) The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B* **365**, 2245–2254.
- Blois JL, Gotelli NJ, Behrensmayer AK, Faith JT, Lyons SK, Williams JW, Amatangelo KL, Bercovici A, Du A, Eronen JT, Graves GR, Jud N, Labandeira C, Looy CV, McGill B, Patterson D, Potts R, Riddle B, Terry R, Tóth A, Villaseñor A and Wing S (2014) A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen association across the late quaternary. *Ecography* **37**, 1095–1108.
- Bond W, Ferguson M and Forsyth G (1980) Small mammals and habitat structure along altitudinal gradients in the southern cape mountains. *South African Journal of Zoology* **15**, 34–43.
- Bowen GJ, Clyde WC, Koch PL, Ting S, Alroy J, Tsubamoto T, Wang Y and Wang Y (2002) Mammalian dispersal at the Paleocene-Eocene boundary. *Science* **295**, 2062–2065.
- Bowers MA and Brown JH (1982) Body size and coexistence in desert rodents: Chance or community structure? *Ecology* **63**, 391–400.
- Brame, H-MR and Stigall AL (2014) Controls on niche stability in geologic time: Congruent responses to biotic and abiotic environmental changes among Cincinnati (late Ordovician) marine invertebrates. *Paleobiology* **40**, 70–90.
- Bricca A, Di Musciano M, Ferrara A, Theurillat J-F and Cutini M (2022) Community assembly along climatic gradient: Contrasting pattern between- and within-species. *Perspectives in Plant Ecology, Evolution and Systematics* **56**, 125675.
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT and Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters* **10**, 701–709.
- Brougham T and Campione NE (2020) Body size correlates with discrete-character morphological proxies. *Paleobiology* **46**, 304–317.

- Brown JH** (1995) *Macroecology*. Chicago: University of Chicago Press.
- Bruneau A, Mercure M, Lewis GP and Herendeen PS** (2008) Phylogenetic patterns and diversification in the caesalpinoid legumes. *Botany* **86**, 679–718.
- Burger BJ** (2012) Northward range extension of a diminutive-size mammal (*Ectocion parvus*) and the implication of body size change during the paleocene-eocene thermal maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **363**–364, 144–150.
- Chapin III FS, Matson PA and Vitousek PM** (2011) *Principles of Terrestrial Ecology*. New York: Springer.
- Chapin III FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, and Díaz S** (2000) Consequences of changing biodiversity. *Nature* **405**, 234–242.
- Chen I-C, Hill JK, Ohlemüller R, Roy DB and Thomas CD** (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.
- Chen M, Strömberg CAE and Wilson GP** (2019) Assembly of modern mammal community structure driven by late cretaceous dental evolution, rise of flowering plants, and dinosaur demise. *PNAS* **116**, 9931–9940.
- Chew AE and Oheim KB** (2013) Diversity and climate change in the middle-late Wasatchian (early Eocene) Willwood formation, Central Bighorn Basin, Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology* **369**, 67–78.
- Chew AE** (2015) Mammal faunal change in the zone of the Paleogene hyperthermals ETM2 and H2. *Climate of the Past* **11**, 1223–1237.
- Clarke KR** (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecology* **18**, 117–143.
- Clyde WC and Gingerich PD** (1998) Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* **26**, 1011–1014.
- Cornwell WK, Schwikl DW and Ackerly DD** (2006) A trait-based test for habitat filter: Convex hull volume. *Ecology* **87**, 1465–1471.
- Currano ED, Laker R, Flynn AG, Fogt KK, Stradtman H and Wing SL** (2016) Consequences of elevated temperatures and pCO₂ on insect folivory at the ecosystem level: Perspectives from the fossil record. *Ecology and Evolution* **6**, 4318–4331.
- Currie DJ** (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist* **137**, 27–49.
- Currie DJ** (2001) Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. *Ecosystems* **4**, 216–225.
- Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E and Turner JRG** (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**, 1121–1134.
- Daniel J, Gleason JE, Cottenie K and Rooney RC** (2019) Stochastic and deterministic processes drive community assembly across a gradient of environmental filtering. *Oikos* **128**, 1158–1169.
- Darroch SAF, Webb AE, Longrich N and Belmaker J** (2014) Palaeocene-Eocene evolution of beta diversity among ungulate mammals in North America. *Global Ecology and Biogeography* **23**, 757–768.
- Dehling DM and Stouffer DB** (2018) Bringing the eltonian niche into functional diversity. *Oikos* **127**, 1711–1723.
- Devictor V, Clavel J, Juillard R, Lavergne S, Mouillot D, Thullier W, Venail P, Villager S and Mouquet N** (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology* **47**, 15–25.
- Dickens GR, O'Neil JR, Rea DK and Owen RM** (1995) Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene. *Paleoceanography* **10**, 965–971.
- Dietl GP, Kidwell SM, Brenner M, Burney DA, Flessa KW, Jackson ST and Koch PL** (2015) Conservation paleobiology: Leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences* **43**, 79–103.
- Dobson FS and Oli MK** (2007) Fast and slow life histories of mammals. *Ecoscience* **14**, 292–299.
- Early R and Sax DF** (2014) Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography* **23**, 1356–1365.
- Elton CS** (1927) *Animal Ecology*. Chicago: University of Chicago Press.
- Epihov DZ, Batterman SA, Hedin LO, Leake JR, Smith LM and Beerling DJ** (2017) N₂-fixing tropical legume evolution: A contributor to enhanced weathering during the Cenozoic? *Proceedings of the Royal Society B* **284**, 20170370.
- Francis AP, Currie DJ and Ritchie ME** (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist* **161**, 523–536.
- Fraser D and Lyons SK** (2017) Biotic interchange has structured Western hemisphere mammal communities. *Global Ecology and Biogeography* **26**, 1408–1422.
- Fraser D and Lyons SK** (2020) Mammal community structure through the Paleocene-Eocene thermal maximum. *American Naturalist* **196**, 271–290.
- Fraser D, Villaseñor A, Tóth AB, Balk MA, Eronen JT, Barr WA, Behrensmeyer AK, Davis M, Du A, Faith JT, Graves GR, Gotelli NJ, Jukar AM, Looy CV, McGill BJ, Miller JH, Pineda-Munoz S, Potts R, Shupinski AB, Soul LC and Lyons SK** (2022) Late quaternary biotic homogenization of north American mammalian faunas. *Nature Communications* **13**, 3940.
- Fricke HC and Wing SL** (2004) Oxygen isotope and paleobotanical estimates of temperature and δ18O-latitude gradients over North America during the early Eocene. *American Journal of Science* **304**, 612–635.
- Fritz SA, Eronen JT, Schnitzler J, Hof C, Janis CM, Mulch A, Böhning-Gaese K and Graham CH** (2016) Twenty-million-year relationship between mammalian diversity and primary productivity. *PNAS* **113**, 10908–10913.
- Gillooly JF, Brown JH, West GB, Savage VM and Charnov EL** (2001) Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.
- Gingerich PD** (1989) New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology* **28**, 1–97.
- Gingerich PD** (2001) Biostratigraphy of the continental Paleocene-Eocene boundary interval on polecat bench in the northern Bighorn Basin. In Gingerich PD (ed.), *Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming* pp. 37–71. Ann Arbor: University of Michigan Press.
- Gingerich PD** (2003) Mammalian responses to climate changes at the Paleocene-Eocene boundary: Polecat bench record in the northern Bighorn Basin, Wyoming. In Wing SL, Gingerich PD, Schmitz B and Thomas E (eds.), *Causes and consequences of globally warm climates in the Early Paleogene*. Boulder: Geological Society of America. Geological Society of America Special Paper **369**, 463–478.
- Gingerich PD** (2006) Environment and evolution through the Paleocene-Eocene thermal maximum. *TRENDS in Ecology and Evolution* **21**, 246–253.
- Gingerich PD** (2019) Temporal scaling of carbon emission and accumulation rates: Modern anthropogenic emissions compared to estimates of PETM onset accumulation. *Paleoceanography and Paleoclimatology* **34**, 329–355.
- Gingerich PD, Rose KD and Krause DW** (1980) Early Cenozoic mammalian faunas of the Clark's Fork Basin-polecat bench area, northwestern Wyoming. *University of Michigan Papers on Paleontology* **24**, 51–68.
- Gotelli NJ** (2000) Null model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621.
- Gotelli NJ, Graves GR and Rahbek C** (2010) Macroecological signals of species interactions in the Danish avifauna. *PNAS* **107**, 5030–5035.
- Gotelli NJ and Colwell RK** (2011) Estimating species richness. In Magurran E and McGill BJ (eds.), *Frontiers in Measuring Biodiversity*. New York: Oxford University Press. pp. 39–54.
- Gould FDH** (2017) Testing the role of cursorial specializations as adaptive key innovations in Paleocene-Eocene ungulates of North America. *Journal of Mammalian Evolution* **24**, 453–463.
- Griffith DM, Veech JA and Marsh CJ** (2016) Cooccur: probabilistic species co-occurrence analysis in R. R Package Version 2.6–2.
- Grinnell J** (1917) The niche-relationships of the California Thrasher. *The Auk* **34**, 427–433.
- Grossnickle DM** (2020) Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. *Evolution* **74**, 610–628.
- Hammer Ø, Harper D and Ryan P** (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**, 9 pp.

- Harbert RS and Nixon KC** (2015) Climate reconstruction analysis using coexistence likelihood estimation (CRACLE): A method for the estimation of climate using vegetation. *American Journal of Botany* **102**, 1277–1289.
- Harbert RS and Nixon KC** (2018) Quantitative late quaternary climate reconstruction from plant macrofossil communities in Western North America. *Open Quaternary* **4**, 8.
- Hardin G** (1960) The competitive exclusion principle. *Science* **131**, 1292–1297.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE and Turner JRG** (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–3117.
- Helmus MR, Savage K, Diebel MW, Maxted JT and Ives AR** (2007) Separating the determinants of phylogenetic community structure. *Ecology Letters* **10**, 917–925.
- Hubbell SP** (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton: Princeton University Press.
- Hutchinson GE** (1978) *An Introduction to Population Ecology*. New Haven: Yale University Press.
- Iriarte-Diaz J** (2002) Differential scaling of locomotor performance in small and large terrestrial mammals. *Experimental Biology* **205**, 2897–2908.
- Jackson ST and Blois JL** (2015) Community ecology in a changing environment: Perspectives from the quaternary. *PNAS* **112**, 4915–4921.
- Juilliard R, Jiguet F and Couvet D** (2004) Common birds facing global changes: What makes a species at risk? *Global Change Biology* **10**, 148–154.
- Kennett JP and Stott LD** (1991) Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Paleocene. *Nature* **353**, 225–229.
- Koch PL, Zachos JC and Gingerich PD** (1992) Correlation between isotope records in marine and continental carbon reservoirs near the Paleocene-Eocene boundary. *Nature* **358**, 319–322.
- Koch PL, Clyde WC, Hepple RP, Fogel ML, Wing SL and Zachos JC** (2003) Carbon and oxygen isotope records from paleosols spanning the Paleocene-Eocene boundary, Bighorn Basin, Wyoming. In Wing SL, Gingerich PD, Schmitz B and Thomas E (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. Boulder: Geological Society of America. pp. 49–64.
- Kohli BA and Rowe RJ** (2019) Beyond guilds: The promise of continuous traits for mammalian functional diversity. *Journal of Mammalogy* **100**, 285–298.
- Korasidis VA, Wing SL, Shields CA and Kiehl JT** (2022a) Global changes in terrestrial vegetation and continental climate during the Paleocene-Eocene thermal maximum. *Paleoceanography and Paleoclimatology* **37**, e2021PA004325.
- Korasidis VA, Wing SL, Nelson DM, Baczynski AA** (2022b) Reworked pollen reduces apparent floral change during the Paleocene-Eocene thermal maximum. *Geology* **50**, 1398–1402.
- Korasidis VA, Wing SL, Harrington G, Demchuk T, Gravendyck J, Jardine PE and Willard D** (2023) Biostratigraphically significant palynofloras from the Paleocene–Eocene boundary of North America. *Palynology* **47**, 2115159.
- Korasidis VA and Wing SL** (2023) Palynofloral change through the Paleocene-Eocene thermal maximum in the Bighorn Basin, Wyoming. *Paleoceanography and Paleoclimatology* **38**, e2023PA004741.
- Kraft NJB, Adler PB, Godoy O, James EC, Fuller S and Levine JM** (2015) Community assembly, coexistence, and the environmental filtering metaphor. *Functional Ecology* **29**, 592–599.
- Kraus MJ and Riggins S** (2007) Transient drying during the Paleocene-Eocene thermal maximum (PETM): Analysis of paleosols in the Bighorn Basin, Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology* **245**, 444–461.
- Kruskal JB** (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* **29**, 115–129.
- Laughlin DC, Fulé PZ, Huffman DW, Crouse J and Laliberté E** (2011) Climatic constraints on trait-based forest assembly. *Journal of Ecology* **99**, 1489–1499.
- Lawlor LR** (1980) Structure and stability in natural and randomly constructed competitive communities. *The American Naturalist* **116**, 394–408.
- Legras G, Loiseau N and Gaertner J-C** (2018) Functional richness: Overview of indices and underlying concepts. *Acta Oecologia* **87**, 34–44.
- Li X, Hu W, Bleisch WV, Li Q, Wang H, Lu W, Sun J, Zhang F, Ti B and Jiang X** (2022) Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conservation Biology* **36**, e13839.
- Louys J, Meloro C, Elton S, Ditchfield P and Bishop LC** (2011) Mammal community structure correlates with arboreal heterogeneity in faunally and geographically diverse habitats: Implications for community convergence. *Global Ecology and Biogeography* **20**, 717–729.
- Lovegrove B and Mowoe M** (2013) The evolution of mammal body sizes: Responses to Cenozoic climate change in north American mammals. *Journal of Evolutionary Biology* **26**, 1317–1329.
- Luiselli L, Amori G, Akani GC and Eniang EA** (2015) Ecological diversity, community structure and conservation of Niger Delta mammals. *Biodiversity and Conservation* **24**, 2809–2830.
- Lyons SK and Smith FA** (2013) Macroecological patterns of body size in mammals across time and space. In Smith FA and Lyons SK (eds.), *Animal Body Size: Linking Pattern and Process across Space and Time*. Chicago: University of Chicago Press. pp. 116–144.
- Lyons SK, Amatangelo KL, Behrensmayer AK, Bercovici A, Blois JL, Davis M, DiMichele WA, Du A, Eronen JT, Faith JT, Graves GR, Jud N, Labandeira C, Looy CV, McGill B, Miller JH, Patterson D, Pineda-Munoz S, Potts R, Riddle B, Terry R, Tóth A, Ulrich W, Villaseñor A, Wing S, Anderson H, Anderson J, Waller D and Gotelli NJ** (2016) Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529**, 80–83.
- MacArthur RH** (1972) *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper and Row.
- MacArthur RH and Levins R** (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* **101**, 377–385.
- MacArthur RH and Wilson EO** (1967) *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- MacCracken JG, Uresk DW and Hansen RM** (1985) Rodent-vegetation relationships in southeastern Montana. *Northwest Science* **59**, 272–278.
- Mares MA and Willig MR** (1994) Inferring biome associations of recent mammals from samples of temperate and tropical faunas: Paleoecological considerations. *Historical Biology* **8**, 31–48.
- Martin KJ and McComb WC** (2002) Small mammal habitat associations at patch and landscape scales in Oregon. *Forest Science* **48**, 255–264.
- Marvier M, Kareiva P and Neubert MG** (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multi-species metapopulation. *Risk Analysis* **24**, 869–878.
- Mason NWH, Mouillot D, Lee WG and Wilson JB** (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118.
- Matuoka MA, Benchimol M, del Almeida-Rocha JM and Morante-Filho JC** (2020) Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators* **116**, 106471.
- McCune B and Grace JB** (2002) *Analysis of Ecological Communities*. Glendened Beach: MjM Software Design.
- McGill BJ, Enquist BJ, Weiher E and Westoby M** (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–185.
- McInerney FA and Wing SL** (2011) The Paleocene-Eocene thermal maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual Review of Earth and Planetary Sciences* **39**, 489–516.
- McKinney ML and Lockwood JL** (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**, 450–453.
- Mosbrugger V and Utescher T** (1997) The coexistence approach – A method for quantitative reconstructions of tertiary terrestrial paleoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **134**, 61–86.
- Mosbrugger V, Utescher T and Dilcher DL** (2005) Cenozoic continental climatic evolution of Central Europe. *PNAS* **102**, 14964–14969.
- Mouillot D, Graham NAJ, Villéger S, Mason NWH and Bellwood DR** (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* **28**, 167–177.
- Naem S, Duffy JE and Zavaleta E** (2012) The functions of biological diversity in an age of extinction. *Science* **336**, 1401–1406.

- Nichols DJ and Ott HL** (1978) Biostratigraphy and evolution of the Momipites-Caryapollenites lineage in the early tertiary of the Wind River basin, Wyoming. *Palynology* **2**, 93–112.
- Olden JD, Poff NL, Douglas MR, Douglas ME and Fausch KD** (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19**, 18–24.
- Parmesan C** (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* **37**, 637–639.
- Parmesan C and Yohe G** (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Parsons PA** (1994) The energetic cost of stress. Can biodiversity be preserved? *Biodiversity Letters* **2**, 11–15.
- Peres-Neto PR, Leibold MA and Dray S** (2012) Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* **93**, S14–S30.
- Peters R H** (1983) *The Ecological Implications of Body Size*. New York: Cambridge University Press.
- Peterson AT** (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* **78**, 419–433.
- Peterson AT** (2011) Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography* **38**, 817–827.
- Pineda-Munoz S, Evans AR and Alroy J** (2016) The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42**, 659–669.
- Pineda-Munoz S, Jukar AM, Tóth AB, Fraser D, Wu A, Barr WA, Amatangelo KL, Balk MA, Behrensmeyer AK, Blois J, Davis M, Eronen JT, Gotelli NJ, Looy C, Miller JH, Shupinski AB, Soul LC, Villaseñor A, Wing S and Lyons SK** (2020) Body mass-related changes in mammal community assembly patterns during the late quaternary of North America. *Ecography* **43**, 1–11.
- Porter WP and Gates DM** (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs* **39**, 227–244.
- Rankin BD, Fox JW, Barrón-Ortiz CR, Chew AE, Holroyd PA, Luttke JA, Yang X and Theodor JM** (2015) The extended Price equation quantifies species selection on mammalian body size across the Paleocene/Eocene thermal maximum. *Proceedings of the Royal Society B* **282**, 20151097.
- Richmond CE, Breitbart DL and Rose KA** (2005) The role of environmental generalist species in ecosystem function. *Ecological Modelling* **188**, 279–295.
- Robinson P, Gunnell GF, Walsh SL, Clyde WC, Storer JE, Stucky RK, Froehlich DJ, Ferrusquía-Villafraña I and McKenna MC** (2005) Wasatchian through Duchesnean Biochronology. In Woodburne MO (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. New York: Columbia University Press, pp. 106–155.
- Rose KD** (1981) The Clarkforkian land mammal age and mammalian composition across the Paleocene-Eocene boundary. *University of Michigan Papers on Paleontology* **26**, 1–197.
- Rose KD** (1990) Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood formation, Bighorn Basin, Wyoming. *Geological Society of America Special Papers* **243**, 107–133.
- Safi K, Cianciaruso MV, Loyola RD, Brito D, Armour-Marshall K and Diniz-Filho JAF** (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B* **366**, 2536–2544.
- Sandel AA** (2013) Brief communication: Hair density and body mass in mammals and the evolution of human hairlessness. *American Journal of Physical Anthropology* **152**, 145–150.
- Secord R, Gingerich PD, Smith ME, Clyde WC, Wilf P and Singer BS** (2006) Geochronology and mammalian biostratigraphy of middle and upper Paleocene continental strata, Bighorn Basin, Wyoming. *American Journal of Science* **306**, 211–245.
- Secord R, Wing SL and Chew A** (2008) Stable isotopes in early Eocene mammals as indicators of forest canopy structure and resource partitioning. *Paleobiology* **34**, 282–300.
- Secord R, Bloch JI, Chester SGB, Boyer DM, Wood AR, Wing SL, Kraus MJ, McInerney FA and Krigbaum J** (2012) Evolution of the earliest horses driven by climate change in the Paleocene-Eocene thermal maximum. *Science* **335**, 959–962.
- Selig KR, Chew AE and Silcox MT** (2021) Dietary shifts in a group of early Eocene euarchontans (Microsypidae) in association with climate change. *Palaeontology* **64**, 609–628.
- Sibly RM and Brown JH** (2007) Effects of body size and lifestyle on evolution of mammal life histories. *PNAS* **104**, 17707–17712.
- Slater GJ** (2022) Topographically distinct adaptive landscapes for teeth, skeletons, and size explain the adaptive radiation of Carnivora (Mammalia). *Evolution* **76**, 2049–2066.
- Smith FA, Smith REE, Lyons SK and Payne JL** (2018) Body size downgrading of mammals over the late quaternary. *Science* **360**, 310–313.
- Smith JJ, Hasiotis ST, Lraus MJ and Woody DT** (2009) Transient dwarfism of soil fauna during the Paleocene-Eocene thermal maximum. *PNAS* **106**, 17655–17660.
- Smits PD** (2015) Expected time-invariant effects of biological traits on mammal species duration. *PNAS* **112**, 13015–13020.
- Snell KE, Thrasher BL, Eiler JM, Koch PL, Sloan LC and Tabor NJ** (2013) Hot summers in the Bighorn Basin during the early Paleogene. *Geology* **41**, 55–58.
- Soberón J** (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**, 1115–1123.
- Soininen J** (2010) Species turnover along abiotic and biotic gradients: Patterns in space equal patterns in time? *Bioscience* **60**, 433–439.
- Soininen J, Lennon JL and Hillebrand H** (2007a) A multivariate analysis of beta diversity across organisms and environments. *Ecology* **88**, 2830–2838.
- Soininen J, McDonald R and Hillebrand H** (2007b) The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.
- Stephens RB and Anderson EM** (2014) Habitat associations and assemblages of small mammals in natural plant communities of Wisconsin. *Journal of Mammalogy* **95**, 404–420.
- Stigall AL** (2014) When and how do species achieve niche stability over long time scales? *Ecography* **37**, 1123–1132.
- Strobeck C** (1973) N species competition. *Ecology* **54**, 650–654.
- Stroik LK and Schwartz GT** (2018) The role of dietary competition in the origination and early diversification of north American euprimates. *Proceedings of the Royal Society B* **285**, 20181230.
- Suchomel J, Purchart L, Čepelka L and Heroldová M** (2014) Structure and diversity of small mammal communities of mountain forests in Western Carpathians. *European Journal of Forest Research* **133**, 481–490.
- Svenning J-C, Flojgaard C, Marske KA, Nógues-Bravo D and Normand S** (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**, 2930–2947.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL and Williams SE** (2004) Extinction risk from climate change. *Nature* **427**, 145–148.
- Tingley MW, Monahan WB, Beissinger SR and Moritz C** (2009) Birds track their Grinnellian niche through a century of climate change. *PNAS* **106**, 19637–19643.
- Tomiya S** (2013) Body size and extinction risk in terrestrial mammals above the species level. *American Naturalist* **182**, E196–E214.
- Tóth AB, Lyons SK, Barr WA, Behrensmeyer AK, Blois JL, Bobe R, Davis M, Du A, Eronen JT, Faith D, Gotelli NJ, Graves GR, Jukar AM, Miller JH, Pineda-Munoz S, Soul LC, Villaseñor A and Alroy J** (2019) Reorganization of surviving mammal communities after the end-Pleistocene megafaunal extinction. *Science* **365**, 1305–1308.
- Ulrich W** (2008) Pairs – a FORTRAN program for studying pair-wise species associations in ecological matrices. Available at <http://www.keib.umk.pl/pairs/?lang=en>
- Ulrich W and Gotelli NJ** (2010) Null model analysis of species associations using abundance data. *Ecology* **91**, 3384–3397.
- Ulrich W, Kubota Y, Kusumoto B, Baselga A, Tuomisto H and Gotelli NJ** (2018) Species richness correlates of raw and standardized co-occurrence matrices. *Global Ecology and Biogeography* **27**, 395–399.
- Vavrek M** (2011) fossil: palaeoecological and palaeogeographical analysis tools. R Package Version 2.6–2. Available at <https://CRAN.R-project.org/package=fossil>
- Vermeij GJ** (1991) When biotas meet: Understanding biotic interchange. *Science* **253**, 1099–1104.
- Vitousek PM, D'Antonio CM, Loope LL and Westbrooks R** (1996) Biological invasions as global environmental change. *American Scientist* **84**, 468–478.

- Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M and Westbrooks R** (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1–16.
- Villéger S, Mason WH and Mouillot D** (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D and Thomas CD** (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.
- Weihner E, Clarke GDP and Keddy PA** (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* **81**, 309–322.
- Western D** (1979) Size, life history and ecology in mammals. *African Journal of Ecology* **17**, 185–204.
- Whittingham M, Radzevičius S and Spiridonov A** (2020) Moving towards a better understanding of iterative evolution: An example from the late Silurian Monograptidae of the Baltic Basin. *Palaeontology* **63**, 629–649.
- Wing SL, Harrington GJ, Bowen GJ and Koch PL** (2003) Floral change during the initial Eocene thermal maximum in the Powder River Basin, Wyoming. In Wing SL, Gingerich PD, Schmitz B, and Thomas E (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. Boulder, CO: Geological Society of America, Geological Society of America Special Paper **369**, pp. 425–440.
- Wing SL, Harrington GJ, Smith FA, Bloch JI, Boyer DM and Freeman KH** (2005) Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* **310**, 993–996.
- Wing SL and Currano ED** (2013) Plant response to a global greenhouse event 56 million years ago. *American Journal of Botany* **100**, 1234–1254.
- Wolfe JA** (1979) Temperature parameters of humid to Mesic forests of eastern Asia and relation of forests to forests of other regions of the northern hemisphere and Australasia. *Geological Survey of the USA Professional Paper* **1106**, 1–37.
- Wolfe JA** (1995) Paleoclimatic estimates from tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences* **23**, 119–142.
- Woodburne MO, Gunnell GF and Stuck RK** (2009) Climate directly influences Eocene mammal faunal dynamics in North America. *PNAS* **106**, 13399–13403.
- Zachos JC, Röhl U, Schellenberg SA, Sluijs A, Hodell DA, Kelly DC, Thomas E, Nicolo M, Raffi I, Lourens LJ, McCarren H and Kroon D** (2005) Rapid acidification of the ocean during the Paleocene-Eocene thermal maximum. *Science* **308**, 1611–1615.