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Unique functional diversity during early Cenozoic mammal radiation of North America

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Mammals influence nearly all aspects of energy flow and habitat structure in modern terrestrial ecosystems. However, anthropogenic effects have probably altered mammalian community structure, raising the question of how past perturbations have done so. We used functional diversity (FD) to describe how the structure of North American mammal palaeocommunities changed over the past 66 Ma, an interval spanning the radiation following the K/Pg and several subsequent environmental disruptions including the Palaeocene–Eocene Thermal Maximum (PETM), the expansion of grassland, and the onset of Pleistocene glaciation. For 264 fossil communities, we examined three aspects of ecological function: functional evenness, functional richness and functional divergence. We found that shifts in FD were associated with major ecological and environmental transitions. All three measures of FD increased immediately following the extinction of the non-avian dinosaurs, suggesting that high degrees of ecological disturbance can lead to synchronous responses both locally and continentally. Otherwise, the components of FD were decoupled and responded differently to environmental changes over the last ~56 Myr.

1. Introduction

Understanding the consequences of major ecological disruptions on community structure represents an important intersection between macroecological and macroevolutionary theory. Communities are dynamic entities whose membership is determined by assembly processes that might both shape and be shaped by taxonomic and morphological evolution [1–3]. However, ecological processes governing the way species assemble differ across spatial scales, making it difficult to disentangle the role of individual processes [3–5]. For example, local-scale diversity reflects the level of resource distribution and can be affected by different intensities of competition and niche packing [6]. In contrast, environmental variability and climate become increasingly important at larger spatial scales [6–8]. Although identifying general rules in community assembly is complicated by the fact that these processes act on various scales across space and time [9], trying to do so is important both for understanding Phanerozoic history and because preserving ecosystem functions is increasingly recognized as an important goal of conservation efforts [10].

Previous work measured community responses to biotic and abiotic changes using taxonomic diversity (i.e. numbers of species or genera) and/or morphological disparity (e.g. range of anatomical types) [11,12]. Although we expect the diversity of ecological roles to increase as taxonomic diversity increases [13], this relationship can vary across space and time [14]. Thus, taxonomic diversity does not always provide adequate information about community dynamics or function [15]. An alternative approach to infer processes driving community structure uses functional diversity (FD) [16], a 'taxon-free' method that ordinates species in multidimensional trait space. Evaluating changes in multidimensional trait space can be beneficial because the changes in community structure are more directly associated with ecosystem functioning [11–13,16–18]. Functional traits directly correspond to the role of a species in the community. The composition of functional traits within a community determines the ecological services it provides. FD not only allows us to map functional trait distributions in multidimensional space, but it also allows us to disentangle community structure into different structural components: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). Measuring changes across multiple indices allows us to capture more subtle changes that may not be detected using other methods. However, without a baseline understanding of mammal community dynamics, it is difficult to interpret changes in FD, as current communities reflect thousands of years of anthropogenic manipulation, complicating our ability to discern the effects of human activity on community assembly processes.

The fossil record provides a history of how the mammal community FD was influenced by the biotic and abiotic environment prior to large-scale impacts by humans. For example, over the Cenozoic, mammals underwent major faunal transitions, immigration events and significant reorganizations of palaeocommunities [9,19–21], beginning with the diversification of mammals triggered by the extinction of non-avian dinosaurs [22,23]. Moreover, the Cenozoic (66–0 Ma) was also marked by a variety of climatic and environmental changes (figure 1) [24,25]. While climate cooled overall during this period, this was interspersed with periods of rapid global warming, resulting in a transition from high-latitude subtropical forests in North America at the Palaeocene–Eocene boundary (~56 Ma) [26] to cyclical glaciation periods by the Early-Middle Pleistocene (EMPT, ~800 ka) [27]. The changing climate led to more open habitats and the expansion of grasslands; North America was dominated by grasslands by the middle-to-late Miocene [27]. By 2.7 Ma, the onset of glacial cycles in North America began [27], resulting in ice sheets and boreal forests. This combination of abiotic and biotic shifts over the Cenozoic provides the opportunity to evaluate the responses of mammal communities to both ecological and environmental change.

Here, we calculated the FD of North American mammals across the last 66 Myr to evaluate mammal community evolution. We measured FD on the local and continental scales to individually analyse the effect of ecological, environmental and climatic shifts and investigate the relationship between local and continental FD. Furthermore, we assessed the effect of multiple biotic and abiotic variables on FD through time as North American mammals experienced a plethora of ecological, environmental and climatic events. Our approach provides a deeper understanding of how community structure changed across evolutionary timescales and the influence of spatial scale.

2. Material and methods

(a) Data

FD, a taxon-free approach that focuses on species traits, provides a quantitative framework to explore the relationship between species diversity and ecosystem functioning [28]. Here, we assessed changes in the FD of mammal palaeocommunities across the Cenozoic. We used presence–absence data for 264 North American palaeocommunities encompassing 2462 species taken from the Paleobiology Database (PBDB; Datafile1, electronic supplementary material, figure S1) and vetted for taxonomic errors. A palaeocommunity was defined in our study as a single excavated fossil locality. We applied a series of taphonomic filters to reduce the effects of biases in the fossil record (see electronic supplementary material). Palaeocommunities were only included if they contained a minimum of 15 species that encompassed multiple orders and trophic levels. When possible, we refined PBDB locality dates based on faunal zone and local stage names (see electronic supplementary material). Owing to the extensive geographic and temporal range included, we had to address multiple possible biases. First, it was possible that the 264 palaeocommunities varied in the spatial extent they represented. Indeed, determining the precise spatial extent or excavation extent of a fossil locality is difficult and often essential information is lacking. However, we believe that such variability did not drive our results. Rather, we would expect the random variation in spatial extent among palaeocommunities to create noise, minimizing patterns and the significance of FD shifts. In addition, larger spatial extents might well contain higher species richness; we examined the possible issue of variable species richness (see methods in electronic supplementary material: Sensitivity Analyses). Second, the number of palaeocommunities included in our analyses changed over time. If a time interval with a smaller number of palaeocommunities by chance did not appropriately represent the entire range of FD present, it is possible that such variation could influence FD estimates. To explore this potential issue, we ran a sub-sampling routine (see electronic supplementary material, Sensitivity Analyses).

We collected data on species traits commonly used in studies of extant mammalian FD (i.e. body mass, locomotion, diet and life habit) [29,30] from the primary literature and online databases (electronic supplementary material, table S1). Diet categories were restricted to those we could most accurately distinguish in the fossil record. Some diet categories used in our databases were combined to limit diet uncertainties in earlier or rarer species (electronic supplementary material, table S1); granivores were combined with frugivores and piscivores were considered carnivores. When body mass was not available, body mass was averaged at the lowest available taxonomic level (genus, family and order). In this study, we address possible concerns with calculating FD using averaged body masses based on higher taxonomic levels and combining continuous and categorical variables (see electronic supplementary material, Sensitivity Analyses).

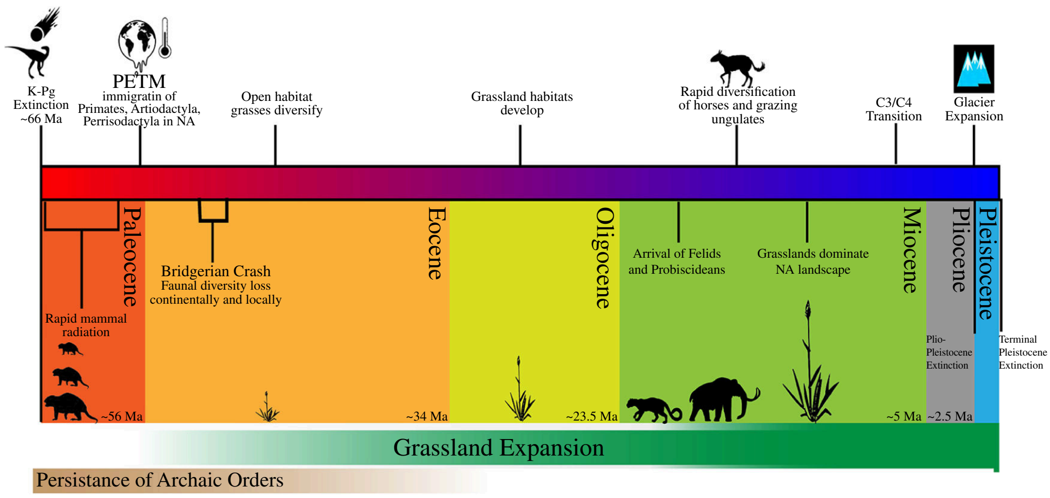

Figure 1. Cenozoic timeline of abiotic and biotic factors influencing North American mammal palaeocommunity structure.

(b) FD analyses

We calculate three FD indices using the R package 'FD' [31,32], functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve), chosen owing to their independence from one another (electronic supplementary material, table S2). FD was calculated for the whole North American fauna in 1 Myr bins and each of our 264 communities (see electronic supplementary material). Functional richness is the volume of trait space occupied, functional evenness represents how evenly species occupy the trait space, and functional divergence measures the degree of divergence of species traits relative to the centroid of trait space. These metrics are largely independent of one another compared with other FD metrics and demonstrate the possible variation in the extent and distribution of community functional space [17]. However, functional richness is often highly correlated with species richness owing to the greater likelihood that there will be unique ecological roles with more species, while functional evenness and functional divergence are not dependent on species richness [17]. We assessed the possible effect of variation in species richness on functional richness patterns. We used linear regressions to identify the threshold at which species richness is no longer significantly associated with functional richness. We then subsetted the data to remove all palaeocommunities that drive the relationship between functional richness and species richness and replotted the data to examine changes in the results (see electronic supplementary material: Sensitivity Analyses).

To calculate FD, we created a trait matrix that included species names and four traits (i.e. locomotion, body mass, life habit and diet). Previous studies suggest that combining categorical and numerical traits may impact results owing to magnitude variation between trait types [33]. We addressed this possible issue in our study (see electronic supplementary material: Sensitivity Analyses). We converted the trait matrix into a distance matrix using Gower's dissimilarity metric [34] and then ordinated species in multidimensional space using principal coordinates analysis (PCoA) on the distance matrix, with a square root correction applied to our non-Euclidean data. The convex hull volumes for each palaeocommunity were based on the first five PCoA axes. FD was calculated for each palaeocommunity across the Cenozoic, and we also calculated the FD of the continental fauna in 1 Myr time bins (electronic supplementary material, data files 1–3).

(c) Breakpoint analysis

A breakpoint analysis was used to identify periods during the Cenozoic when the slope of the relationship between FD and time significantly shifted. A breakpoint represents the start or end of a decline or increase in FD. We identified the location and number of significant shifts in FD using the R package 'breakpoint' and 'segmented'. The R package 'breakpoint' was used to estimate the approximate location and estimated number of breakpoints for each FD metric [35]. This method requires *a priori* specification of the maximum number of breakpoints possible. Initially, we allowed the analysis to estimate up to 10 breakpoints. The maximum number returned was four. Thus, we set the maximum number allowed to four. Breakpoints were then estimated four times for each FD metric, controlling for the maximum number of breakpoints. For each iteration, we increased the maximum number of breakpoints allowed up to the limit of four breakpoints, beginning with one breakpoint; resulting breakpoint estimates were entered into the segmented function of the R package 'segmented' [36]. The segmented function uses the estimated breakpoint to identify the exact location and standard error of each breakpoint. AICc values were used to determine the best-fit model of the four runs for each FD metric at the continental and local scale (electronic supplementary material, tables S3–S8). To demonstrate changes in FD, we conducted median line regressions for each FD metric at both spatial scales. We used the breakpoints to divide data. Median line regressions were applied to before, after and between breakpoints to visually represent the shift in FD. The median line regressions were added to figure 2 using the 'geom_quantile' function in the R package 'ggplot2' [37].

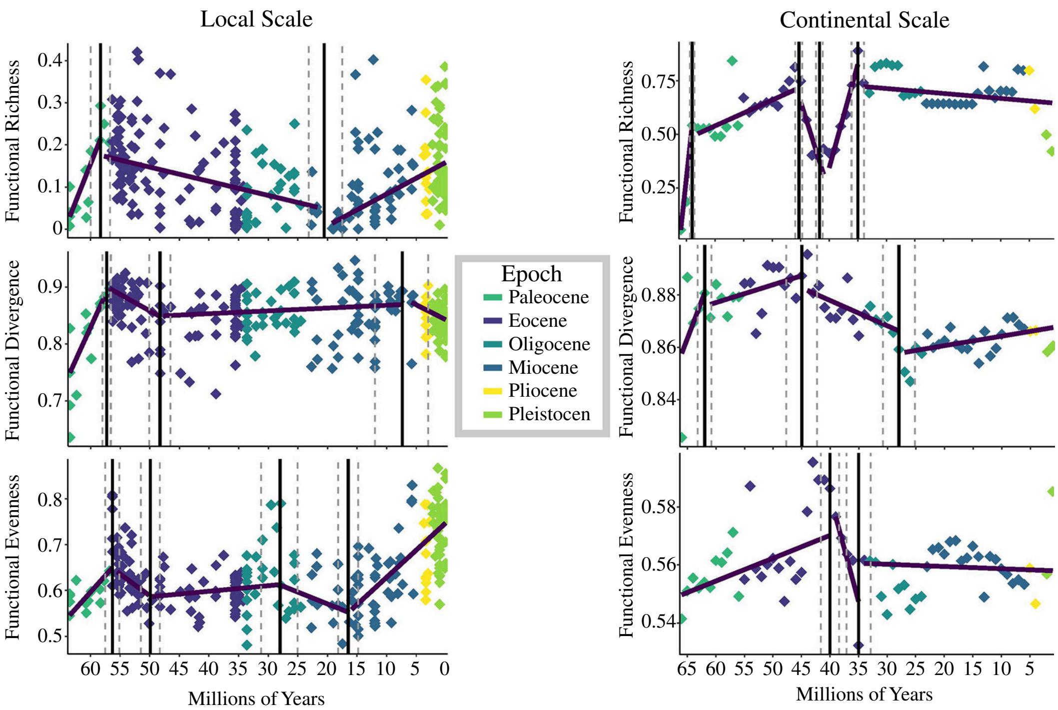

Figure 2. Changes in FD indices through the Cenozoic on the continental and local spatial scale. On the local-scale graphs, each datum represents a palaeocommunity, which is colour-coded by epoch. FD for the North American mammal continental fauna was plotted in 1 Myr time bins. Each point represents a 1 Myr time bin. Dotted lines indicate confidence intervals and solid lines represent breakpoints. Median line regressions were used to represent the direction of change in FD before, after and between breakpoints to provide a visible representation of the significance identified by the breakpoints.

(d) Abiotic and biotic variables

We ran generalized linear models to analyse the effect of biotic and abiotic factors (i.e. global climate, estimated species richness per million years, the proportion of archaic mammals) against continental and local FD metrics (see electronic supplementary material, table S10). The FD metrics on continental and local spatial scales were the response variables and species richness, $\delta^{18}O$ and proportion of archaic orders as the predictor variables. Continental-scale FD metrics were calculated in 1 Myr time bins, whereas the local-scale FD metrics were calculated for each palaeocommunity. To run the generalized linear models, we standardized all data by analysing the relationship between the abiotic and biotic variables and FD metrics in 1 Myr time bins. This allowed us to compare the influence of biotic and abiotic factors on local and continental-scale FD metrics. For the local scale, we averaged palaeocommunity FD in 1 Myr time bins. All analyses of potential predictors were run for the entire Cenozoic (electronic supplementary material, datafile 3). For each FD metric, we ran seven generalized linear models with each model containing a unique combination of predictor variables for a total of 42 generalized linear models. The generalized linear models were run using the 'glm' function in the R package 'lme4'. The best models for explaining variance in each FD metric were determined by the lowest AIC value (electronic supplementary material, table S9).

(i) Species richness

We estimated extinction and origination rates in 1 Myr time bins using sampling + survivorship (sampling + reverse − survivorship or nascence for origination) analyses [38–40], which accommodates sampling heterogeneity among contemporaneous taxa [41]. The procedure was the same for both origination and extinction rates, save that we estimated extinction based on taxa sampled in younger intervals and origination based on taxa sampled in older ones. We estimated the distribution of sampling rates for each 1 Myr bin following the approach set out by Wagner & Marcot [42]. As in prior studies, lognormal distributions typically do much better than either exponential distributions or the null invariant model. We therefore used lognormal distributions for each 1 Myr bin. Origination and extinction rate likelihoods for each bin reflect the probability of all possible survivors from the prior bin (origination) or to the next subsequent bin (extinction) multiplied by the probability of sampling the observed number of species given the possible richness and the best lognormal distribution of sampling rates (electronic supplementary material, figure S8). Owing to origination and extinction rates being used for estimating species richness, they were not included in the generalized linear models. Instead, origination and extinction rates were analysed independently against local- and continental-scale FD metrics using generalized linear regression.

(ii) Climate

To evaluate the potential relationship between global climate and local mammalian FD, $\delta^{18}O$ values were taken from the most recent compilation of mean global temperature through the Cenozoic [25]. The $\delta^{18}O$ values represent the proportion of the heavier to lighter oxygen isotope ($^{18}O/^{16}O$) from deep-sea benthic foraminifera [25,43]. Higher ratios suggest colder global temperatures and more glaciation, and vice versa [25,43]. The $\delta^{18}O$ values were averaged for each palaeocommunity based on the age range of that locality. For example, if a locality has an estimated age between 50 and 48 Myr, all $\delta^{18}O$ values within those 2 Myr were averaged and assigned to that palaeocommunity. For continental FD, we averaged the $\delta^{18}O$ in 1 Myr time bin.

(iii) Proportion of archaic orders

We evaluated the proportion of archaic (extinct) orders in palaeocommunities to determine if assembly rules were different in the past. We averaged the proportion of archaic orders found in all palaeocommunities for each 1 Myr time bin. For the continental scale, we used the overall proportion of archaic to extant orders within each 1 Myr time bin. If they did assemble differently than modern orders, we expected to see a shift in mammal palaeocommunity structure co-occurring with the gradual extinction of archaic orders. We used ordinary least square regressions to characterize the individual relationships of abiotic and biotic factors and the continental and local FD of North American mammal palaeocommunities.

3. Results

(a) Functional metrics

(i) Functional richness—volume of trait space

Local scale

For the first 10 Myr of the early Cenozoic, the volume of functional space of North American mammal palaeocommunities continuously rose (figure 2). The first breakpoint occurred during the latest Palaeocene to earliest Eocene (58.3 ± 1.7 Ma) when functional richness peaked. We ensured that the rise in functional richness from the early Palaeocene to the early Eocene was not driven by an increasing number of palaeocommunities using a sub-sampling routine (see electronic supplementary material, figure S9). Following this peak was a long period of decline until the second and final breakpoint (20.6 ± 2.6 Ma) during the early Miocene. Functional richness rose again and continued to increase through the Pleistocene epoch (figure 2). Although there was a relationship between functional richness and the species richness of palaeocommunities, this relationship did not drive our results (see electronic supplementary material, figure S4).

Continental scale

The functional richness of the North American mammalian fauna had four breakpoints (figure 2). Three of the breakpoints occurred in the middle of the Cenozoic in a relatively short period of time. The first breakpoint (64 ± 0.4 Ma) was in the early Palaeocene as functional richness began an initial rise. It gradually rose until the second breakpoint in the middle Eocene (45.3 ± 0.7 Ma). There was a brief decline of ~5 Ma before the third breakpoint (41.7 ± 0.6 Ma; figure 2) and then increased briefly until the last breakpoint (35 ± 1 Ma). After the shift in the latest Eocene/earliest Oligocene until the Pleistocene, functional richness remained relatively consistent.

(ii) Functional divergence—variation of species traits relative to the centroid of trait space

Local scale

Of all three metrics, functional divergence showed the largest increase during the Palaeocene epoch (figure 2). We determined that the rise in functional divergence from the early Palaeocene to the early Eocene was not driven by an increasing number of palaeocommunities (see electronic supplementary material, figure S11). Functional divergence began in the Cenozoic at its lowest point and rapidly increased until the first of three breakpoints (57.3 ± 0.7 Ma) at the Palaeocene–Eocene transition. A sharp decline followed that ended in the middle Eocene at the second breakpoint (48.3 ± 1.8 Ma). Throughout the middle of the Cenozoic until the late Miocene, there were no significant shifts as functional divergence remained relatively consistent. The last breakpoint occurred during the late Miocene when functional divergence dropped (7.4 ± 5.8 Ma). However, this breakpoint had a large confidence interval, making the timing of the shift unreliable (figure 2).

Continental scale

Functional divergence began in the Cenozoic with an initial increase beginning at the first breakpoint (62 ± 1.2 Ma; figure 2). It increased until the second breakpoint in the late Eocene (44.7 ± 2.7 Ma) and then began declining. The period of decline ended with the third and final breakpoint in the middle Oligocene (28 ± 2.8 Ma). Functional divergence remained relatively constant for the rest of the Cenozoic (figure 2).

(iii) Functional evenness—the distribution of species across trait space

Local scale

Functional evenness varied more than the other metrics with four significant shifts over the last 66 Myr (figure 2). Similar to functional richness and functional evenness, it started low in the earliest Palaeocene but increased until reaching the first breakpoint at the Palaeocene–Eocene boundary (56.3 ± 1.2 Ma). We determined that the rise in functional evenness from the early Palaeocene to the early Eocene was not driven by an increasing number of palaeocommunities (see electronic supplementary material, figure S12). As with other metrics, it declined to the second breakpoint in the middle Eocene (49.9 ± 1.6 Ma). There was a slight increase until the third breakpoint (28.1 ± 3.1 Ma). It then entered a period of decline into the middle Miocene (16.5 ± 1.7 Ma). After which, it rose into the Pleistocene (figure 2).

Continental scale

Functional evenness had two significant shifts. Similar to regional functional richness, the shifts occurred over a relatively short period of time during the middle Cenozoic (figure 2). Functional evenness increased starting in the early Palaeocene until the middle Eocene (39.7 ± 1.7). There was a brief period of decline to the second breakpoint in the latest Eocene/earliest Oligocene (35 ± 2.1). Regional functional evenness changed little for the rest of the Cenozoic (figure 2).

(b) Addressing potential biases affecting broad-scale patterns in FD

We found that FD metrics fluctuated frequently across the Cenozoic on both the continental and the local scale. Owing to the geographic and temporal extent of our study, components of our data were potentially variable. To confirm the solidity of our results and the integrity of our study, we performed extensive sensitivity analyses to assess that the FD variability we identified through time was not a result of data biases (see methods in electronic supplementary material, Sensitivity Analyses). All sensitivity analyses addressing individual FD metrics or time periods are mentioned above.

First, we determined that averaging species body mass at higher taxonomic levels for species with missing body mass data did not alter the overall pattern in our findings (electronic supplementary material, figure S5; see methods in electronic supplementary material, Sensitivity Analyses). Second, we used a combination of continuous and categorical variables to calculate FD. Previous studies have demonstrated possible complications with this approach owing to variations in the magnitude of traits [33]. However, the exclusion of body mass from our FD analysis and the conversion of body mass to categories did not alter the overall trends in FD indices through time (electronic supplementary material, figures S7). Therefore, it was unlikely that our combination of numerical and categorical traits led to inaccurate conclusions. In fact, this analysis demonstrated the strong influence of body size on the variation of ecological roles in mammals. Because ecological traits in mammals are highly correlated with body size, the imprint of body size is still reflected in the three other traits we use. Third, we addressed the possible bias against small-bodied mammals, in that they are less likely to preserve and tend to be more common in more recent fossil localities. Many studies exclude mammals under 1 kg to remove this issue. However, including small-bodied mammals is essential for gaining an accurate understanding of palaeocommunity FD. We found no relationship between time and the number of small-bodied mammals (electronic supplementary material, figure S10).

(c) Biotic and abiotic variables

(i) Continental

Functional richness (FRic)

The best generalized linear model indicated a significant relationship between functional richness and the proportion of archaic orders within the 1 Myr time bins (figure 3; electronic supplementary material, table S9; $R^2 = 0.11$, $p = 0.0095$). There was a weak, positive relationship between functional richness and the proportion of archaic orders. Furthermore, we found that functional richness was significantly associated with origination rates, showing a positive relationship. However, the relationship was only driven by two-time bins in the early Palaeocene (electronic supplementary material, figure S24).

Functional divergence (FDiv)

The best generalized linear model indicated a positive, significant relationship between functional divergence and $\delta^{18}O$ averaged values for the 1 Myr time bins across the Cenozoic (figure 3; electronic supplementary material, table S9; $R^2 = 0.32$, $p =$ 78e−07).

Functional evenness (FEve)

Based on the generalized linear models, no single biotic or abiotic variable or combination of variables had a significant relationship with continental functional evenness in this study (electronic supplementary material, table S9 and figure S21).

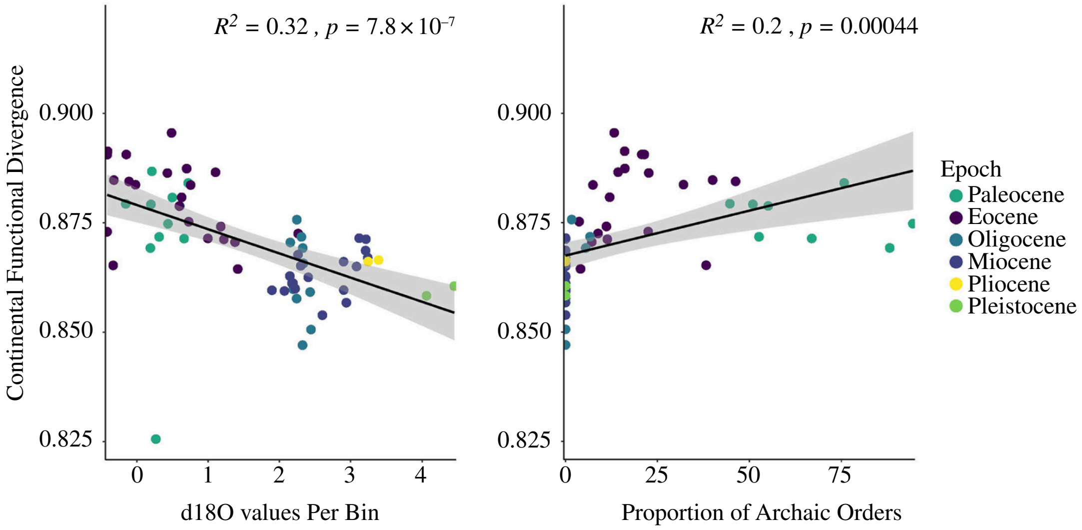

Figure 3. Regressions of the biotic and abiotic variables that have a significant relationship with a continental FD index. $\delta^{18}O$ values were averaged for each 1 Myr time bin and run against the functional divergence of the continental fauna for each 1 Myr time bin ($R^2 = 0.32$, $p = 78e{-}07$). The continental proportion of archaic orders had a significant relationship with functional richness. The continental proportion of archaic orders represents the proportion of archaic versus extant orders within each 1 Myr time bin ($R^2 = 0.11$, $p = 0.0095$).

(ii) Local

Functional richness (FRic)

There was no significant relationship between local functional richness and the biotic and abiotic variables tested in this study (electronic supplementary material, table S9).

Functional divergence (FDiv)

The best generalized linear model indicated a positive, significant relationship between functional divergence and the proportion of archaic orders in 1 Myr time bins (figure 4; electronic supplementary material, table S9; $R^2 = 0.15$, $p = 0.0048$). Although the relationship between functional divergence and the averaged proportion of archaic orders were weakly associated.

Functional evenness (FEve)

The generalized linear models did not show a significant relationship between local functional evenness and the biotic and abiotic variables tested in this study (electronic supplementary material, table S9).

4. Discussion

We found that North American mammalian FD changed over evolutionary timescales. Moreover, this fluctuation in FD over time was independent of potential data bias caused by averaging species body mass at higher taxonomic levels (electronic supplementary material, figure S5), combining continuous and categorical traits (electronic supplementary material, figures S7) or body size selectivity (electronic supplementary material, figure S10). Individual metrics of FD differed in the timing and direction of change suggesting that the influence of driving mechanisms differs among components of FD. The decoupling of FD metrics was found locally and regionally for most of the Cenozoic. While the decoupling of FD patterns through time was evident at both continental and local scales, the two spatial scales differed in the timing and direction of change in each FD metric. Our results are consistent with modern studies that have shown significant change across habitats that vary in topography and vegetative cover across much smaller geographic regions, such as Costa Rica [44]. Our study not only highlights the pronounced variation in FD over time and space but also identifies a distinct period in the earliest Cenozoic when all FD metrics at both spatial scales aligned.

(a) Synchrony in the Palaeocene

The Palaeocene epoch (~66–56 Ma) was a period of ecological change with mammals rapidly diversifying in response to newly available resources following the K-Pg mass extinction (~66 Ma) [10,19,22]. This led to ~10 Myr of unique mammalian dynamics in local and regional faunas. Mammals expanded their niche occupancy, exhibited greater variation in ecological roles and became more functionally distinct, while at the same time, the distribution of ecological roles became more even (figures 2; electronic supplementary material, figure S13). These changes occurred at both local and continental scales. Mammalian diversity had a fourfold increase across this 10 Myr period [45,46], with increasing body size and body size variation within

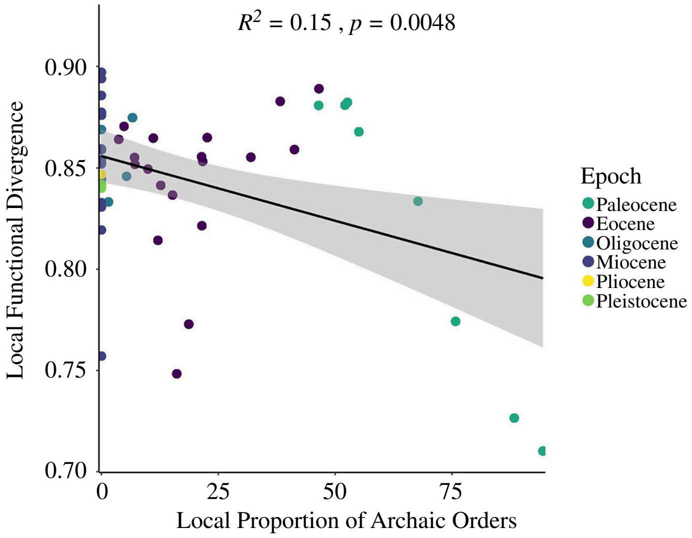

Figure 4. Regressions of the biotic and abiotic variables that have a significant relationship with a local FD index. The local proportion of archaic orders is the mean of all palaeocommunities within 1 Myr time bin against the average functional divergence of all palaeocommunities in each 1 Myr time bin. It is the only abiotic or biotic variable that had a significant relationship with a FD index ($R^2 = 0.15$, $p = 0.0048$).

~300 000 ka following the mass extinction [47]. Increasing body size was likely a major contributor to the expansion in ecological roles [11] as body size strongly influences mammal ecology [23,47–50]. We determined that this rapid rise in FD metrics during the Palaeocene is not attributed to rise in richness or the number of palaeocommunities between the Palaeocene to the Eocene (electronic supplementary material, figures S11). The magnitude of the ecological recovery resulted in a unified change among community components that spanned all FD metrics and spatial scales. The pronounced concurrence likely reflected the degree of filling of ecological niche space by mammals in the ecosystem. However, this was a short-lived event. By the early Eocene, these metrics were largely decoupled.

(b) Synchrony ends: the next 56 Ma

Between the latest Palaeocene and the earliest Eocene, there was a major immigration event into the Americas of cursorial and arboreal mammals from Asia and Europe (~56 Ma). This included the arrival of Primates, Perissodactyls and Artiodactyls [51]. This coincided with the first disassociation in FD patterns between local and continental scales. Meanwhile, metrics within spatial scales remained synchronous. The new mammal orders probably contributed to a brief rise in local FD; however, all local metrics declined soon after (figure 2). The abrupt shift into a synchronous decline was unexpected, as mammals did not reach their maximum body size for another 15 Ma (~41 Ma) [23]. In contrast, continental FD continued to increase through the immigration event, only to decline approximately when maximum body size was reached (~41 Ma) (figure 2) [23]. This may suggest that the rate of niche saturation during the ecological recovery was dependent on spatial scale. For instance, local communities saturated faster than regional or continental faunas. These results stress the importance of diverse spatial perspectives in understanding ecological recovery following a mass extinction.

The decline in local FD metrics following the immigration event (~56 Ma) overlapped with a period of reorganization for the North American fauna, called the Bridgerian Crash (50–47 Ma; figures 1 and 2) [52,53]. This event was marked by a cooling climate with increased seasonality and aridity, leading to the reduction of forests [53]. The reduced forest cover caused the gradual loss of arboreal, archaic and medium-sized mammals (figures 2 and 4) [53,54]. Interestingly, FD metrics of the continental fauna continued to increase. The rise in continental FD may have been partially owing to increasing body size as landscapes opened. Specifically, we saw higher concentrations of large-bodied browsers in trait space after the Bridgerian Crash (figure 5; Bridgerian Crash).

Shortly after the Bridgerian Crash, there was a major change in mammalian dynamics when all three FD metrics became decoupled within the local and continental scales (figure 2). Local niche differentiation and evenness of ecological roles increased after the Bridgerian Crash [53], while occupied trait space continued to shrink. The gradual reduction in trait space may have been partially owing to the continued loss of medium-sized and arboreal species with the opening of the landscape and expansion of grasslands into the Miocene (figure 2). Meanwhile, niche differentiation entered a period of extensive consistency, lasting ~40 Myr (figure 2). The long period of consistency suggests that the amount of variation among species traits did not change despite mammal taxonomic and functional turnover within North America during this time, even with the loss of archaic mammals and the development of grasslands (figure 5; electronic supplementary material, figure S13) [55]. However, open-landscape species began to increase in richness during the late Eocene to early Oligocene, and this created greater evenness in the dispersal of species throughout functional space (figure 2).

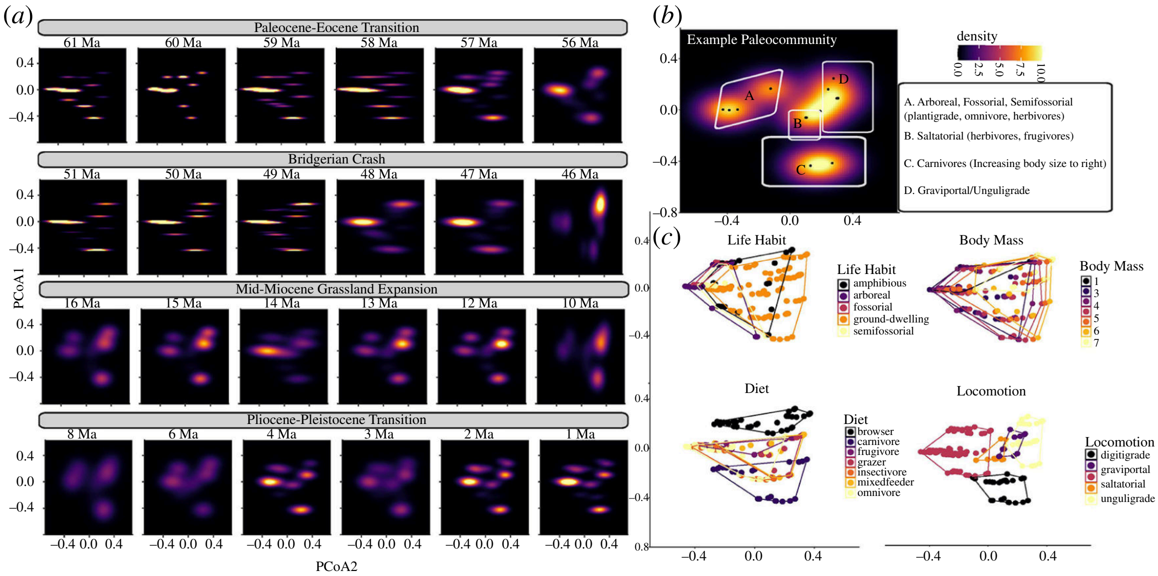

Figure 5. The trait space density of North American mammals. (*a*) Species were divided into 1 Myr time bins and species PCoA axes used to ordinate in multidimensional space. Each time bin included all palaeocommunities that fell within the date range. Titles indicate major events within the included time. (*b*) an example palaeocommunity made from a combination of palaeocommunities in the dataset to display the full range of niches occupied by mammals across the Cenozoic. Boxes are used to identify the location of key niches discussed in our study (e.g. large carnivores, medium-sized mammals, etc.). This example palaeocommunity can be used as a general reference to better understand what structural components of mammal palaeocommunities are changing in section A. (*c*) The location of each trait category and the range of multidimensional space occupied by each trait enclosed by convex hulls. Each point represents a unique combination of traits occupied by a species in the database (see electronic supplementary material).

(c) The rise and spread of North American grasslands

During the middle Oligocene to middle Miocene, the widespread expansion of grasslands across the North American landscape led to a large degree of ecological change. Ungulates and carnivores diversified, such as horses and canids [56,57]. For example, by the middle Oligocene there were over 25 species of canids present on the landscape [58,59]. The diversification of these two groups created greater redundancy in functional space, causing a decline in local functional evenness (figure 2). Ungulates experienced rapid diversification until reaching their highest diversity around 16–14 Ma, at which, diversity declined and functional evenness began to rise again [56]. In addition to decreasing ungulate diversity during the middle-to-late Miocene, the richness of medium-sized mammals increased. This included more lagomorphs and burrowing rodents, as well as medium-sized carnivores like procyonids and mustelids [56,59]. During the latest Cenozoic, the richness of large-bodied mammals occupying niche space in the colder climate also increased (figure 5; electronic supplementary material, figure S13) [22,56,59,60]. These factors probably contributed to the shift in local functional richness during the early to middle Miocene when functional trait space began increasing for the first time since the Eocene (figures 2 and 4). The expansion of functional space also coincided with the arrival of true felids [61] and proboscideans [62] into North America, resulting in unique large-bodied carnivores and herbivores. Interestingly, continental functional richness not only did not increase, but instead slightly declined during the Pliocene and Pleistocene (figure 2). We suggest that the cooling climate probably caused a decline in habitat heterogeneity and may have impacted the faunal FD.

However, the level of local niche differentiation evinced a different response to the climatic and ecological changes and was the last of the local metrics to shift. Functional divergence transitioned into a decline in the later Miocene. With a colder climate, species within palaeocommunities became more similar in overall functional traits. Specifically, medium-sized mammals and carnivores became more concentrated in trait space (figure 5, Plio-Pleistocene transition). However, the transition period of functional divergence had a large confidence interval, making it difficult to infer influential abiotic and biotic factors (figure 2). Nonetheless, the confidence interval encompassed several major environmental changes, such as the C3/C4 photosynthesis transition in grasslands [55] and the expansion of glaciers in North America [27].

Continental functional divergence was also the last of the spatial scale metrics to transition. However, the shift occurred much earlier in the Oligocene to early Miocene. It stopped declining and like continental functional evenness and richness, it remained relatively stable for the rest of the Cenozoic. The ~25 Myr of consistency within continental FD metrics may suggest that FD on larger spatial scales was more resistant to ecological and environmental events than local-scale FD. These results further highlight the differentiation in mammalian dynamics among spatial scales.

(d) Biotic and abiotic factors—local FD

In our evaluation of abiotic and biotic factors on local-scale FD, we demonstrated that only functional divergence and the proportion of archaic orders in 1 Myr time bins had a significant, yet weak relationship (figure 4; electronic supplementary material, figures S14–S18). As the average local proportion of archaic orders increased within 1 Myr time bins, the average functional divergence of palaeocommunities decreased. The weak, negative relationship was likely caused by the increasing diversity of ecological roles and body size following the Palaeocene epoch. In fact, the four points driving the relationship between local functional divergence and local proportion of archaic orders were all Palaeocene time bins. This would explain why functional divergence was lower and the local proportion of archaic orders was higher. To ensure this relationship was not being driven by the period of the Cenozoic when all archaic orders were extinct (<30 Ma), we also ran local functional divergence against the average local proportion of archaic orders from 66 to 30 Ma (electronic supplementary material, figure S19). We find that the relationship became only slightly stronger but remained weak (electronic supplementary material, figure S11). In contrast, there was no relationship between species richness or origination/extinction rates over time and local FD (electronic supplementary material, figures S14–S18 and table S10). Nor did we find a relationship between local FD and global temperature using $\delta^{18}O$ values as a global climate proxy (figure 4; electronic supplementary material, figures S16–S18) [25]. Studies have found local climate to influence FD [63] but owing to a lack of available data, we could not analyse the local climate for each palaeocommunity. Estimated origination and extinction rates did not exhibit any significant associations with local-scale FD (electronic supplementary material, figures S14 and S15).

(e) Biotic and abiotic factors—continental FD

We analysed the relationship between continental FD metrics and abiotic and biotic factors ($\delta^{18}O$, the proportion of archaic orders, species richness, origination and extinction rates; electronic supplementary material, figures S20–S24). We only identified three significant relationships. Averaged $\delta^{18}O$ values for 1 Myr time bins had a significant relationship with continental functional divergence (figure 5). There was a trend of decreasing functional divergence across the Cenozoic, with lower $\delta^{18}O$ values during the Pleistocene (figure 5). This suggests that with a cooling climate, a fewer number of species had extreme traits and there were greater similarities among species within a palaeocommunity [17]. Similarly, we see a slight decline in functional divergence on the local scale (figure 2) during the Pleistocene. The Pleistocene decline could have been explained by environmental filtering and increased abiotic stresses [64]. However, we would have expected higher continental functional divergence during the middle Cenozoic with greater habitat heterogeneity. It was important to note that the variation in continental functional divergence across the Cenozoic was small and the breakpoint analysis did not identify any significant shifts following the late Oligocene and functional divergence remained relatively consistent. The response in continental-scale patterns in functional divergence would benefit from further investigation to illuminate the possible biotic and abiotic drivers leading to the small decline. In our study, we also found that the continental proportion of archaic orders had a relationship with continental functional richness (figure 5; electronic supplementary material, figure S19). However, when we subsetted the data to only include the period before archaic orders went extinct (66–30 Ma), there was no longer a significant relationship (electronic supplementary material, figure S22). This suggested that the relationship was only owing to the stability in continental functional richness in the later Cenozoic and the continued lack of archaic orders following 30 Ma. Owing to this, we did not consider this a true relationship. Extinction and origination rates had little to no effect on the variation we found in continental FD metrics on evolutionary timescales. Functional richness was positively associated with origination rates; however, the association was solely driven by the two earliest time bins in the Palaeocene with low functional richness (electronic supplementary material, figures S23 and S24). Higher origination rates were a reflection of the rapid radiation of mammals during this period [11].

The lack of a straightforward relationship between these individual large-scale abiotic and biotic factors despite the apparent changes in FD around major ecological and evolutionary transitions, suggested that long-term variation in local FD was more likely a reflection of a complicated interplay between ecological and evolutionary processes. It is possible that processes had varying influences on FD metrics over time. It may be that a single process (or combination of processes) was not consistently driving FD metrics or the same metric. The variability in driving processes would explain the lack of a relationship we found. Although investigating this concept is outside the scope of this paper, we suggest it would be beneficial to further explore if the effects of ecological processes changed through time. Understanding the mechanistic drivers of FD continues to prove difficult and complex but remains an important aim of ecology.

5. Conclusion

Our results demonstrated that mammal community structure was highly variable temporally and across spatial scales. Moreover, spatial scales and FD metrics were disassociated in the direction and timing of shifts. FD metrics of mammal palaeocommunities did not synchronously change without an extreme degree of ecological disturbance. Our analysis found regular variation in components of the palaeocommunity and the continental faunal structure. FD metrics were decoupled across evolutionary timescales and between spatial scales. Moreover, the Palaeocene was unique in the 66 Myr of North American mammal history, with extraordinary synchronicity across metrics and spatial scales. The differences in the trajectories of FD metrics during the Palaeocene and other intervals of significant environmental change suggest that Palaeocene community dynamics were distinct from the rest of the Cenozoic. The magnitude of the radiation event was strong enough to link FD metrics across the spatial scale. Modern mammal communities are again experiencing extreme disturbance from multiple sources, including human impacts and climate change, which are causing shifts in FD [18]. However, ignoring the variation in how these metrics change through time probably hides key information about the effects of these disturbances on a community's structure. By evaluating synchronous responses across metrics, we can identify communities that have been significantly disrupted and are at the highest risk for FD loss.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data are available in the main text or the supplementary materials and the code and also deposited on GitHub [65] and Dryad [66].

Supplementary material is available online [67].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.B.S.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; P.J.W.: formal analysis, funding acquisition, methodology, writing—review and editing; F.A.S.: investigation, writing—review and editing; S.K.L.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Cornell HV, Lawton JH. 1992 Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* **61**, 1–12. (doi:10.2307/5503)
2. Lessard JP, Borregaard MK, Fordyce JA, Rahbek C, Weiser MD, Dunn RR, Sanders NJ. 2012 Strong influence of regional species pools on continent-wide structuring of local communities. *Proc. R. Soc. B* **279**, 266–274. (doi:10.1098/rspb.2011.0552)
3. Gotelli NJ, Ellison AM. 2002 Assembly rules for New England ant assemblages. *Oikos* **99**, 591–599. (doi:10.1034/j.1600-0706.2002.11734.x)
4. Hurlbert AH, Jetz W. 2007 Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl Acad. Sci. USA* **104**, 13384–13389. (doi:10.1073/pnas.0704469104)
5. Liu Y, Bi J, Lv J, Ma Z, Wang C. 2017 Spatial multi-scale relationships of ecosystem services: a case study using a geostatistical methodology. *Sci. Rep*. **7**, 9486. (doi:10.1038/s41598-017-09863-1)
6. Sepkoski JJ. 1988 Alpha, beta, or gamma: where does all the diversity go? *Paleobiology* **14**, 221–234. (doi:10.1017/s0094837300011969)
7. Arellano G, Tello JS, Jørgensen PM, Fuentes AF, Loza MI, Torrez V, Macía MJ. 2016 Disentangling environmental and spatial processes of community assembly in tropical forests from local to regional scales. *Oikos* **125**, 326–335. (doi:10.1111/oik.02426)
8. Siefert A *et al*. 2012 Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data. *J. Veg. Sci*. **23**, 942–951. (doi:10.1111/j.1654-1103.2012.01401.x)
9. Bannar-Martin KH. 2014 Primate and nonprimate mammal community assembly: the influence of biogeographic barriers and spatial scale. *Int. J. Primatol*. **35**, 1122–1142. (doi:10.1007/s10764-014-9792-2)
10. Cadotte MW, Carscadden K, Mirotchnick N. 2011 Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol*. **48**, 1079–1087. (doi:10.1111/j.1365-2664.2011.02048.x)
11. Alroy J. 1999 The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Syst. Biol*. **48**, 107–118. (doi:10.1080/106351599260472)
12. Halliday TJD, Goswami A. 2016 Eutherian morphological disparity across the end-Cretaceous mass extinction. *Biol. J. Linn. Soc* **118**, 152–168. (doi:10.1111/bij.12731)
13. Tucker CM, Davies TJ, Cadotte MW, Pearse WD. 2018 On the relationship between phylogenetic diversity and trait diversity. *Ecology* **99**, 1473–1479. (doi:10.1002/ecy.2349)
14. Oliveira BF, Machac A, Costa GC, Brooks TM, Davidson AD, Rondinini C, Graham CH. 2016 Species and functional diversity accumulate differently in mammals. *Global Ecol. Biogeogr* **25**, 1119–1130. (doi:10.1111/geb.12471)
15. Jarzyna MA, Jetz W. 2018 Taxonomic and functional diversity change is scale dependent. *Nat. Commun*. **9**, 2565. (doi:10.1038/s41467-018-04889-z)
16. Zhou S, Edie SM, Collins KS, Crouch NMA, Jablonski D. 2023 Cambrian origin but no early burst in functional disparity for Class Bivalvia. *Biol. Lett*. **19**, 20230157. (doi:10.1098/rsbl.2023.0157)
17. Villéger S, Mason NWH, Mouillot D. 2008 New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301. (doi:10.1890/07-1206.1)
18. Laméris DW, Tagg N, Kuenbou JK, Sterck EHM, Willie J. 2020 Drivers affecting mammal community structure and functional diversity under varied conservation efforts in a tropical rainforest in Cameroon. *Anim. Conserv*. **23**, 182–191. (doi:10.1111/acv.12526)
19. Figueirido B, Janis CM, Pérez-Claros JA, De Renzi M, Palmqvist P. 2012 Cenozoic climate change influences mammalian evolutionary dynamics. *Proc. Natl Acad. Sci. USA* **109**, 722–727. (doi:10.1073/pnas.1110246108)
20. Blanco F, Calatayud J, Martín-Perea DM, Domingo MS, Menéndez I, Müller J, Fernández MH, Cantalapiedra JL. 2021 Punctuated ecological equilibrium in mammal communities over evolutionary time scales. *Science* **372**, 300–303. (doi:10.1126/science.abd5110)
21. Short RA, McGuire JL, Polly PD, Lawing AM. 2023 Trophically integrated ecometric models as tools for demonstrating spatial and temporal functional changes in mammal communities. *Proc. Natl Acad. Sci. USA* **120**, e2201947120. (doi:10.1073/pnas.2201947120)
22. Alroy J. 1998 Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**, 731–734. (doi:10.1126/science.280.5364.731)
23. Smith FA *et al*. 2010 The evolution of maximum body size of terrestrial mammals. *Science* **330**, 1216–1219. (doi:10.1126/science.1194830)
24. Zachos JC, Dickens GR, Zeebe RE. 2008 An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283. (doi:10.1038/nature06588)
25. Westerhold T *et al*. 2020 An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* **369**, 1383–1387. (doi:10.1126/science.aba6853)
26. Weijers JWH, Schouten S, Sluijs A, Brinkhuis H, Sinninghe Damsté JS. 2007 Warm arctic continents during the Palaeocene–Eocene thermal maximum. *Earth Planet. Sci. Lett*. **261**, 230–238. (doi:10.1016/j.epsl.2007.06.033)

27. Brierley CM, Fedorov AV. 2010 Relative importance of meridional and zonal sea surface temperature gradients for the onset of the ice ages and Pliocene-Pleistocene climate evolution. *Paleoceanography* **25**, PA2214. (doi:10.1029/2009PA001809)
28. Gagic V *et al*. 2015 Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B* **282**, 20142620. (doi:10.1098/rspb.2014.2620)
29. Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009 Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett*. **12**, 22–33. (doi:10.1111/j.1461-0248.2008.01255.x)
30. Weaver LN, Grossnickle DM. 2020 Functional diversity of small-mammal postcrania is linked to both substrate preference and body size. *Curr. Zool*. **66**, 539–553. (doi:10.1093/cz/zoaa057)
31. Laliberté E, Legendre P, Shipley B. 2014 FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. *R. Pack. Ver.* **1**, 0–12.
32. Laliberté E, Legendre P. 2010 A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305. (doi:10.1890/08-2244.1)
33. Voje KL *et al*. 2023 Measurement theory and paleobiology. *Trends Ecol. Evol.* **38**, 1165–1176. (doi:10.1016/j.tree.2023.08.005)
34. Gower JC. 1971 A general coefficient of similarity and some of its properties. *Biometrics* **27**, 857. (doi:10.2307/2528823)
35. Priyadarshana W, Sofronov G. 2016 Package 'Breakpoint. *Intell. CEC2012*. 1020–1027.
36. Muggeo VM, Muggeo MVM. 2017 Package 'Segmented. *Biometrika 58, 516*.
37. Wickham H, Chang W, Wickham MH. 2016 Package 'Ggplot2'.' *Create Elegant Data Vis. Using Gramm. Graph*.
38. Foote M. 2001 Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology* **27**, 602–630. (doi:10.1666/0094-8373(2001)027<0602:ITPOPO>2.0.CO;2)
39. Foote M. 2003 Origination and extinction through the phanerozoic: a new approach. *J. Geol*. **111**, 125–148. (doi:10.1086/345841)
40. Alroy J. 2008 Colloquium paper: dynamics of origination and extinction in the marine fossil record. *Proc. Natl Acad. Sci. USA* **105 Suppl 1**, 11536–11542. (doi:10.1073/pnas.0802597105)
41. Congreve CR, Patzkowsky ME, Wagner PJ. 2021 An early burst in brachiopod evolution corresponding with significant climatic shifts during the great ordovician biodiversification event. *Proc. R. Soc. B* **288**, 20211450. (doi:10.1098/rspb.2021.1450)
42. Wagner PJ, Marcot JD. 2013 Modelling distributions of fossil sampling rates over time, space and taxa: assessment and implications for macroevolutionary studies. *Methods Ecol. Evol*. **4**, 703–713. (doi:10.1111/2041-210X.12088)
43. Wright JD. 2013 Global climate change in marine stable Isotope records. In *AGU reference shelf* (eds JS Noller, JM Sowers, WR Lettis), pp. 427–433. Washington, DC: American Geophysical Union. (doi:10.1029/RF004p0427)
44. González-Maya JF, Víquez-R LR, Arias-Alzate A, Belant JL, Ceballos G. 2016 Spatial patterns of species richness and functional diversity in Costa Rican terrestrial mammals: implications for conservation. *Divers. Distrib*. **22**, 43–56. (doi:10.1111/ddi.12373)
45. Benevento GL, Benson RBJ, Close RA, Butler RJ. 2023 Early Cenozoic increases in mammal diversity cannot be explained solely by expansion into larger body sizes. *Palaeontology* **66**, e12653. (doi:10.1111/pala.12653)
46. Grossnickle DM, Newham E. 2016 Therian mammals experience an ecomorphological radiation during the late Cretaceous and selective extinction at the K–Pg boundary. *Proc. R. Soc. B* **283**, 20160256. (doi:10.1098/rspb.2016.0256)
47. Lyson TR *et al*. 2019 Exceptional continental record of biotic recovery after the Cretaceous-Paleogene mass extinction. *Science* **366**, 977–983. (doi:10.1126/science.aay2268)
48. Lyons S, Smith F. 2013 Macroecological patterns of body size in mammals across time and space. In *Animal body size: linking pattern and process across space, time, and Taxonomic group* (eds FA Smith, SK Lyons), pp. 114–142. (doi:10.7208/chicago/9780226012285.001.0001)
49. Brown JH, Marquet PA, Taper ML. 1993 Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat*. **142**, 573–584. (doi:10.1086/285558)
50. Pineda-Munoz S, Evans AR, Alroy J. 2016 The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42**, 659–669. (doi:10.1017/pab.2016.6)
51. Tiffney BH. 1994 An estimate of the early tertiary Paleoclimate of the Southern Arctic. In *Cenozoic plants and climates of the Arctic* (eds MC Boulter, HC Fisher), pp. 267–295. Berlin, Germany: Springer. (doi:10.1007/978-3-642-79378-3_19)
52. Gingerich P. 2003 Mammalian responses to climate change at the Paleocene-Eocene boundary: polecat bench record in the northern Bighorn Basin, Wyoming. *Geol. Soc. Am. Spec. Pap.* **369**, 463–478. (doi:10.1130/SPE369)
53. Woodburne MO, Gunnell GF, Stucky RK. 2009 Climate directly influences Eocene mammal faunal dynamics in North America. *Proc. Natl Acad. Sci. USA* **106**, 13399–13403. (doi:10.1073/pnas.0906802106)
54. Smits PD. 2015 Expected time-invariant effects of biological traits on mammal species duration. *Proc. Natl. Acad. Sci. U.S.A*. **112**, 13015–13020. (doi:10.1073/pnas.1510482112)
55. Strömberg CAE. 2011 Evolution of grasses and grassland ecosystems. *Annu. Rev. Earth Planet. Sci.* **39**, 517–544. (doi:10.1146/annurev-earth-040809-152402)
56. Janis CM, Damuth J, Theodor JM. 2002 The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **177**, 183. (doi:10.1016/S0031-0182(01)00359-5)
57. Wesley-Hunt GD. The morphological diversification of carnivores in North America. *Paleobiology* **31**, 35–55.
58. Wang X, Tedford RH, Taylor BE. *Phylogenetic systematics of the Borophaginae (Carnivora Canidae)*. New York, NY: American Museum of Natural History.
59. Van Valkenburgh B. 2007 Deja vu: the evolution of feeding morphologies in the Carnivora. *Integr. Comp. Biol*. **47**, 147–163. (doi:10.1093/icb/icm016)
60. Lucas SG, Yuan W, Min L. 2013 The palaeobiogeography of South American gomphotheres. *J. Palaeogeogr.* **2**, 19–40. (doi:10.3724/SP.J.1261.2013.00015)
61. Rothwell T. 2001 A partial skeleton of Pseudaelurus (Carnivora: Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. *Am. Mus. Nov.* **3342**, 1–31. (doi:10.1206/0003-0082(2001)342<0001:APSOPC>2.0.CO;2)
62. Schmitz OJ, Haynes G. 1991 *Mammoths, mastodants and elephants: biology, behavior and the fossil record*. vol. **6**. Cambridge, UK: Cambridge University Press. (doi:10.1046/j.1420-9101.1993.6010147.x)
63. Tsianou MA, Lazarina M, Michailidou DE, Andrikou-Charitidou A, Sgardelis SP, Kallimanis AS. 2021 The effect of climate and human pressures on functional diversity and species richness patterns of amphibians, reptiles and mammals in Europe. *Diversity* **13**, 275. (doi:10.3390/d13060275)
64. Spasojevic MJ, Suding KN. 2012 Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J. Ecol*. **100**, 652–661. (doi:10.1111/j.1365-2745.2011.01945.x)
65. Abshup22. 2024 UniqueFunctionalDiversity_Datafiles. See https://github.com/Abshup22.
66. Wagner P, Smith F, Lyons S, Shupinski A. 2024 . Data for: Unique functional diversity during early Cenozoic mammal radiation of North America. Dryad Digital Repository. (doi:10.5061/dryad.q573n5tp2)

67. Shupinski AB, Wagner PJ, Smith FA, Lyons SK. Supplementary material from: Unique functional diversity during early Cenozoic mammal radiation of North America. Figshare. (doi: 10.6084/m9.figshare.c.7304862)