Early Cenozoic increases in mammal diversity cannot be explained solely by expansion into larger body sizes

Benevento, Gemma; Benson, Roger B J; Close, Roger; Butler, Richard

DOI:
10.1111/pala.12653

Palaeontology The Palaeontological Association www.palass.org

[Palaeontology, 2023, e12653]

Early Cenozoic increases in mammal diversity cannot be explained solely by expansion into larger body sizes

by GEMMA LOUISE BENEVENTO[1,2]*, ROGER B. J. BENSON[3,4], ROGER A. CLOSE[1,3] *and* RICHARD J. BUTLER[1]*

[1]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK; gemma.benevento@gmail.com; r.butler.1@bham.ac.uk
[2]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), 60325 Frankfurt am Main, Germany
[3]Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK
[4]American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA
*Corresponding author

Typescript received 7 November 2022; accepted in revised form 22 March 2023

Abstract: A prominent hypothesis in the diversification of placental mammals after the Cretaceous–Palaeogene (K/Pg) boundary suggests that the extinction of non-avian dinosaurs resulted in the ecological release of mammals, which were previously constrained to small body sizes and limited species richness. This 'dinosaur incumbency hypothesis' may therefore explain increases in mammalian diversity via expansion into larger body size niches, that were previously occupied by dinosaurs, but does not directly predict increases in other body size classes. To evaluate this, we estimate sampling-standardized diversity patterns of terrestrial North American fossil mammals within body size classes, during the Cretaceous and Palaeogene. We find strong evidence for post-extinction diversity increases in all size classes. Increases in the diversity of small-bodied species (less than 100 g, the common body size class of Cretaceous mammals, and much smaller than the smallest non-avialan dinosaurs (*c.* 400 g)) were similar to those of larger species. We propose that small-bodied mammals had access to greater energetic resources or were able to partition resources more finely after the K/Pg mass extinction. This is likely to be the result of a combination of widespread niche clearing due to the K/Pg mass extinctions, alongside a suite of biotic and abiotic changes that occurred during the Late Cretaceous and across the K/Pg boundary, such as shifting floral composition, and novel key innovations among eutherian mammals.

Key words: mammal, diversity, body size, Cretaceous–Palaeogene mass extinction, adaptive radiation.

MAMMALS underwent a major evolutionary radiation after the Cretaceous–Palaeogene (K/Pg) mass extinction event that played the key role in structuring their modern diversity (e.g. Grossnickle *et al.* 2019). This event, one of the 'Big Five' mass extinctions (Raup & Sepkoski 1982; Alvarez 1983), resulted in the extinction of an estimated *c.* 50% of genera and *c.* 70% of species on land and in the oceans (Jablonski 1994), including all non-avian dinosaurs (Brusatte *et al.* 2015a) and many groups of non-therian and stem-therian mammals. Palaeogene fossils document the post-extinction diversification of mammals, including the first fossil appearances of the placental crown-group (O'Leary *et al.* 2013; Grossnickle *et al.* 2019; Lyson *et al.* 2019), alongside expansion into considerably larger maximum body sizes (Alroy 1998, 1999; Smith *et al.* 2010) and large increases in species richness (e.g. Alroy 1999; Benson *et al.* 2016; Grossnickle & Newham 2016; Close *et al.* 2017, 2019). This has been recognized for over a century and formed the basis of the central macroevolutionary theory of adaptive radiation (Osborn 1902; Simpson 1937; Schluter 2000).

Although mammals attained considerable ecological diversity in the Mesozoic, this was almost exclusively at small body sizes (Luo 2007; Wilson *et al.* 2012; Close *et al.* 2015; Chen *et al.* 2019). Mesozoic mammals most frequently weighed less than 100 g and rarely exceeded 5 kg, whereas terrestrial Cenozoic mammals included large-bodied species up to 10 000 kg by the Oligocene (Alroy 1998; Smith *et al.* 2010; Slater 2013; Saarinen *et al.* 2014; Chen *et al.* 2019). Furthermore, mammalian species richness was lower throughout the Mesozoic, but increased abruptly after the K/Pg, reaching levels up to four times higher than pre-K/Pg levels by the mid-Paleocene (Benson *et al.* 2016; Grossnickle & Newham 2016; Close *et al.* 2017, 2019). Paleocene mammals also show increased rates of morphological evolution (Halliday *et al.* 2019). The disparity of mammalian jaws and teeth shows a slower pattern of increase, remaining

doi: 10.1111/pala.12653

within Mesozoic levels during the early Paleocene (Grossnickle & Polly 2013; Grossnickle & Newham 2016; Benevento *et al.* 2019) but exceeding them by the Eocene (Jernvall *et al.* 1996; Benevento *et al.* 2019).

One way in which these observations of increasing diversity and disparity have typically been explained is by the evolutionary expansion of mammals into novel niches following the extinction of dinosaurs; an ecological release hypothesis that we refer to as the 'dinosaur incumbency hypothesis' (equivalent to the 'suppression hypothesis' of Osborn 1910; see also Grossnickle & Newham 2016). According to this hypothesis, Mesozoic mammal evolution was constrained either by competition with dinosaurs, or by predation pressure from dinosaurs, and the extinction of dinosaurs caused a release from this constraint (Slater 2013; Grossnickle *et al.* 2019). The dinosaur incumbency hypothesis provides a particularly convincing explanation for the diversification of medium-sized mammals and the evolutionary expansion into larger body sizes during the early Cenozoic, and for increases in species richness resulting from diversification at these larger sizes (Alroy 1998; Slater 2013) that were previously occupied by dinosaurs. However, it does not explain all details of mammalian diversification, such as the origins of somewhat larger maximum body sizes and specialized diets among Late Cretaceous mammals, prior to the extinction of dinosaurs (Wilson *et al.* 2012, 2016; Wilson 2013; Grossnickle *et al.* 2019; Brannick & Wilson 2020; Krausse *et al.* 2020), which are most likely to be associated with the ecological expansion of flowering plants and increased endozoochory (e.g. Grossnickle & Newham 2016; Chen *et al.* 2019), or differences between fossil record occurrences of placental mammals and molecular clock estimates of their divergence times (e.g. Meredith *et al.* 2011; dos Reis *et al.* 2014; Grossnickle *et al.* 2019). It nevertheless provides a first-order explanation of a major transition in the ecological roles, abundance and species richness of mammals in terrestrial ecosystems immediately after the K/Pg.

Although the dinosaur incumbency hypothesis gives a clear explanation for diversification of larger-sized mammals, smaller-sized mammals within the common range of Mesozoic mammal body sizes are considerably more speciose even today. Present-day and Cenozoic mammal species body mass distributions exhibit a substantial right-skew (e.g. Stanley 1973; Brown 1995; Lyons *et al.* 2019), and counts of fossil species, uncorrected for variation in sampling intensity, suggest increases in the diversity of both small and large-bodied mammals after the K/Pg boundary (Alroy 1998, fig. 1). These observations may be consistent with a broader view of the end-Cretaceous mass extinction event as a wholescale remodelling and reorganization of biodiversity (Close *et al.* 2019), accentuating evolutionary changes and trajectories of flora and fauna that were probably already occurring during the Cretaceous as part of the Angiosperm Terrestrial Revolution (also known as the Cretaceous Terrestrial Revolution (KTR); Lloyd *et al.* 2008; Benton *et al.* 2021). The evolution and diversification of larger-bodied mammals is the most obvious and widely accepted evolutionary event catalysed by the end-Cretaceous mass extinction. However, a number of other factors may explain aspects of the early Cenozoic mammal radiation, and potentially allowed mammals of all body sizes to diversify in the early Paleocene and beyond. These factors include the evolution of particular key innovations in mammals (e.g. Luo 2007), the origin of crown eutherian mammals (Placentalia; e.g. Meredith *et al.* 2011; Liu *et al.* 2017), the diversification of flowering plants (e.g. Meredith *et al.* 2011; Wilson *et al.* 2012; Grossnickle & Newham 2016), and increases in the abundance and size of fruits (Eriksson *et al.* 2000), which would have increased the rate of energy transfer from plants to animals.

Here, we analyse changes in species richness within distinct body size classes of terrestrial North American fossil mammals, at regional and local spatial scales, in order to investigate how patterns of diversity differed across different body size classes. We use data from North America because it has yielded an exceptional and near-continuous record of mammals from the Late Cretaceous and Cenozoic. Our analyses use three size classes: (1) 'small' species, with body sizes that are common among Mesozoic mammals; (2) 'medium' species, with body sizes achieved only rarely during the Mesozoic and strongly overlapping with the body size distribution of dinosaurs; and (3) 'large' species, with body sizes exceeding the largest Mesozoic mammals in our dataset (see Body mass estimates, below). Our analysis of these patterns asks whether early Cenozoic increases in mammalian diversity occurred predominantly among medium and large-bodied species, best explained by a strict conception of ecological release as predicted by the dinosaur incumbency hypothesis, or whether increases in diversity were also prominent among small-bodied mammals; a finding that would suggest that other aspects of the transformation of terrestrial ecosystems over the K/Pg transition may be equally important as explanations of the increase in mammal diversity after the end-Cretaceous mass extinction.

METHOD

Data

Species occurrence records and first lower molar (m1) mesiodistal lengths and labiolingual widths for

Cretaceous–Oligocene North American terrestrial mammals were downloaded from the Paleobiology Database (PBDB; https://paleobiodb.org/) on 19 July 2022. Additional m1 measurements for 216 species were obtained from the literature, including measurements from images of m1s using GIMP (https://www.gimp.org). Points were placed to characterize maximum length and width, and the distances between these points (in mm) were obtained using R (v4.2.2; R Core Team 2013). After discarding occurrences with extremely uncertain ages (see Binning occurrence data, below), the resulting dataset contained 14 886 occurrences (comprising 1495 unique species) with m1 measurements (Benevento *et al.* 2023). Mean values were used when multiple individual specimens of the same species were measured.

Body mass estimates. Species body masses were estimated using published regressions of body mass against m1 measurements derived from extant species (Legendre 1986; Damuth 1990; Wilson *et al.* 2012). Three separate regressions were used to account for the differences in these relationships in artiodactyls and perissodactyls (Damuth 1990; Alroy 1998), multituberculates (Wilson *et al.* 2012) and all other mammals (Legendre 1986). This follows the approach used by other studies of mammalian body size evolution in the fossil record (Alroy 1998).

Only m1 length was used to estimate body mass in artiodactyls and perissodactyls based on previous studies that showed this measurement correlates best with body mass in extant species (Damuth 1990; Alroy 1998), according to Equation 1:

$$\ln(\text{mass}_{\text{m1}}) = 1.24 + (3.11 \times (\ln(\text{length}_{\text{m1}}))) \quad (1)$$

Multituberculates have a uniquely large m1 resulting in over-estimates of body mass when using 'standard' mammalian equations (Wilson *et al.* 2012). Skull length is thought to provide better estimates of body mass in multituberculates (Wilson *et al.* 2012) but complete skulls are rare in the fossil record. As a result, we used a formula (Eqn 2) that modifies inferred body mass (based on m1 size; Legendre 1986; Eqn 3) using the relationship of skull length to body mass in more complete specimens (Millien & Bovy 2010) as developed by Wilson *et al.* (2012):

$$\ln\left(\text{mass}_{\text{skull length}}\right) = 0.87 + (0.79 \times (\ln(\text{mass}_{\text{m1}}))) \quad (2)$$

The final regression used here (Eqn 3) is a generic body mass regression for all mammals (Legendre 1986), and is applied to all species in the dataset except artiodactyls, perissodactyls and multituberculates:

$$\ln(\text{mass}_{\text{m1}}) = 1.81 + (1.827 \times (\ln(\text{length}_{\text{m1}} \times \text{width}_{\text{m1}}))) \quad (3)$$

Body mass estimates were used to categorize species in our dataset as 'small', 'medium', or 'large'. The cut off size for each size class was based on the distribution of mammal body sizes globally throughout the Mesozoic (Fig. S1; see also Fig. S2). This global Mesozoic dataset includes 195 species with m1 measurements allowing us to calculate an estimate of body size. 131 of these m1 measurements were collected from the literature, and the remaining 64 were taken from the PBDB. 'Small' mammals are equivalent in mass to the most common Mesozoic mammals (body masses below 100 g; below red line A on Figs S1, S2). 'Medium' mammals have body masses that are rare but present among Mesozoic mammals, from 100 g to an upper bound defined by the estimated body mass of the largest Mesozoic mammal in our dataset (between red lines A and B on Figs S1, S2). 'Large' mammals are larger than the largest Mesozoic mammal in our dataset, and by definition include only Cenozoic species (above red line B on Figs S1, S2; see also Data S1 for a list of species assigned to each size class).

Binning occurrence data

Occurrences were binned into discrete Mesozoic stages and Cenozoic North American land mammal ages (NALMA). PBDB boundary ages were updated to reflect the most up-to-date stage ages reported in the International Chronostratigraphic Chart (v2022/02; Cohen *et al.* 2013) for the Mesozoic, and NALMA ages taken from Gradstein *et al.* (2020, fig. 28.12) for the Cenozoic. Where bins were particularly short, they were merged with adjacent ones (e.g. the Clarkforkian NALMA was combined with the preceding Tiffanian NALMA). Occurrences with stratigraphic ages spanning three or more time bins were deleted from our dataset (50 occurrences). For our sampling-standardized diversity estimates (see Sampling-standardized diversity estimates, below) occurrences which have stratigraphic ages with uncertainties that span two of our time bins (571 of the remaining occurrences) were assigned to a bin by drawing from a uniform distribution within their possible age range. Randomization was conducted across 1000 iterations, each of which was subsequently analysed separately for diversity estimates.

Raw species richness

Raw species richness was obtained by assigning occurrences to bins using the occurrence age range midpoint. Unique species occurrences per bin were then calculated and plotted in Figure 1.

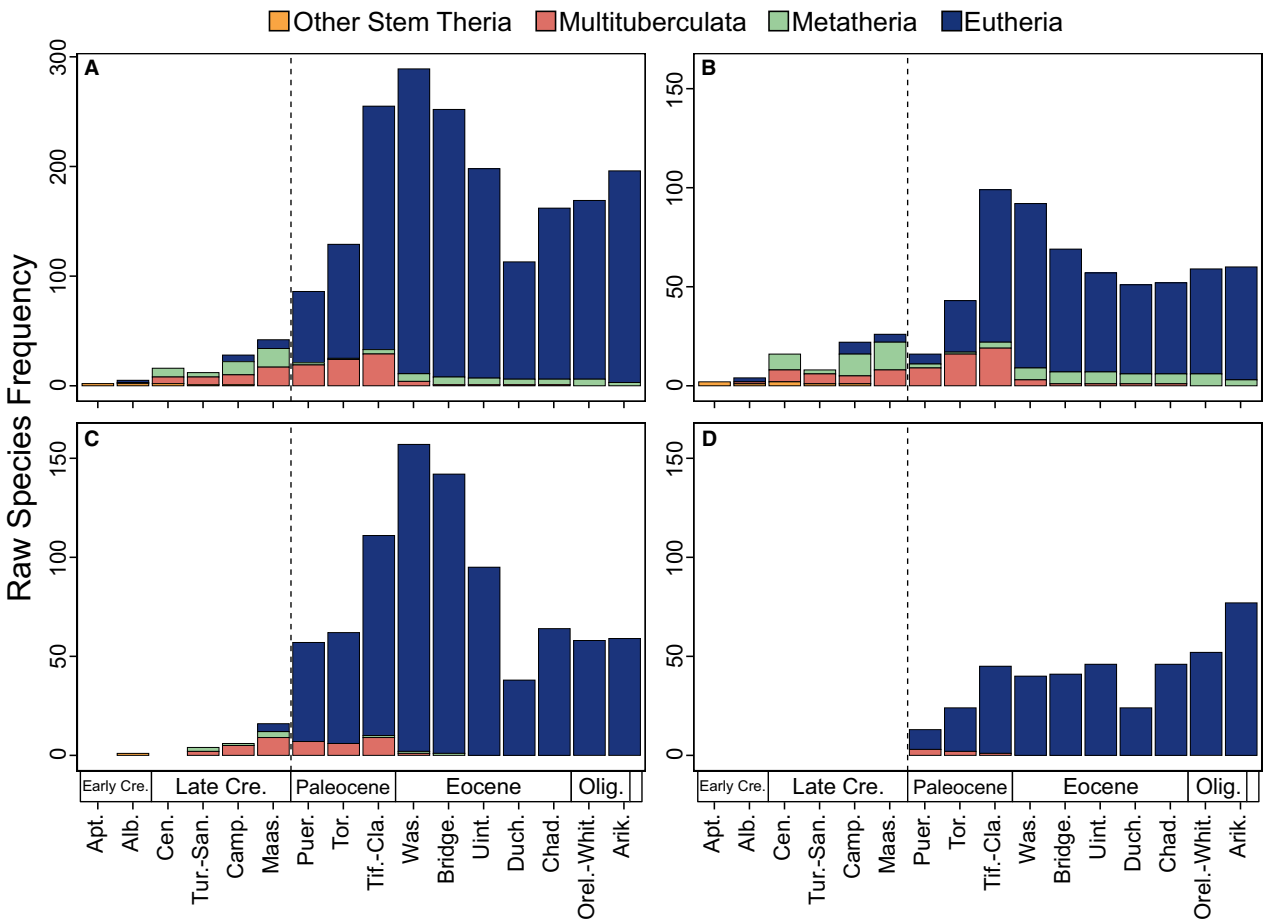

FIG. 1. Raw species frequencies per time interval for North American mammals, representing: A, species of all body sizes; B, small species; C, medium species; D, large species. Colours within the bar plots indicate the frequencies of different mammal clades; other stem Theria (orange), Multituberculata (pink), Metatheria (green) and Eutheria (blue). Figure S5 shows a version of this figure, but with eutherian clade frequencies plotted in different shades of blue. Panel A has different *y*-axis values to panels B–D. Vertical dashed black line indicates the K/Pg boundary. Interval names are provided in Figure S5.

Sampling-standardized diversity estimates

We estimated sampling-standardized species richness from the terrestrial North American mammal occurrence data using shareholder quorum subsampling (SQS, also known as coverage-based rarefaction; Alroy 2010; Chao & Jost 2012; Close *et al.* 2018), implemented via the *estimateD*() function in the package iNEXT (v3.0.0; Hsieh *et al.* 2016, 2022) in R (v4.2.2; R Core Team 2013). Occurrence data were observed, subsampled or extrapolated to target coverage levels, but estimates were considered unreliable and discarded if extrapolated sample sizes were more than twice the reference sample size (Hsieh *et al.* 2016, 2022). SQS was performed for each of the 1000 iterations described above. Mean values and 95% confidence intervals were obtained from these 1000 iterations (Figs 2, S3, S4). SQS diversity was calculated for all body sizes, small mammals, medium mammals, and large mammals, for the following clades: Total Mammalia; Multituberculata; Eutheria; Metatheria; Condylarthra; Pantodonta; Primates and Plesiadapiformes; Carnivora and Creodonta; Artiodactyla and Perissodactyla; and Rodentia (see Data S1 for a list of species assigned to each clade). Five quorum levels were analysed: 0.7, 0.8, 0.85, 0.9 and 0.95. Results for all clades, size classes and quorums are presented in Data S2, and Data S3 contains data on which results were observed, subsampled or extrapolated.

Individual diversity curves can be compared through time to establish relative patterns of diversity change, and the overall patterns of the total data and subset data are comparable, but the absolute values of diversity through time obtained for subsets of the data should not be directly compared to one another (see Appendix S1).

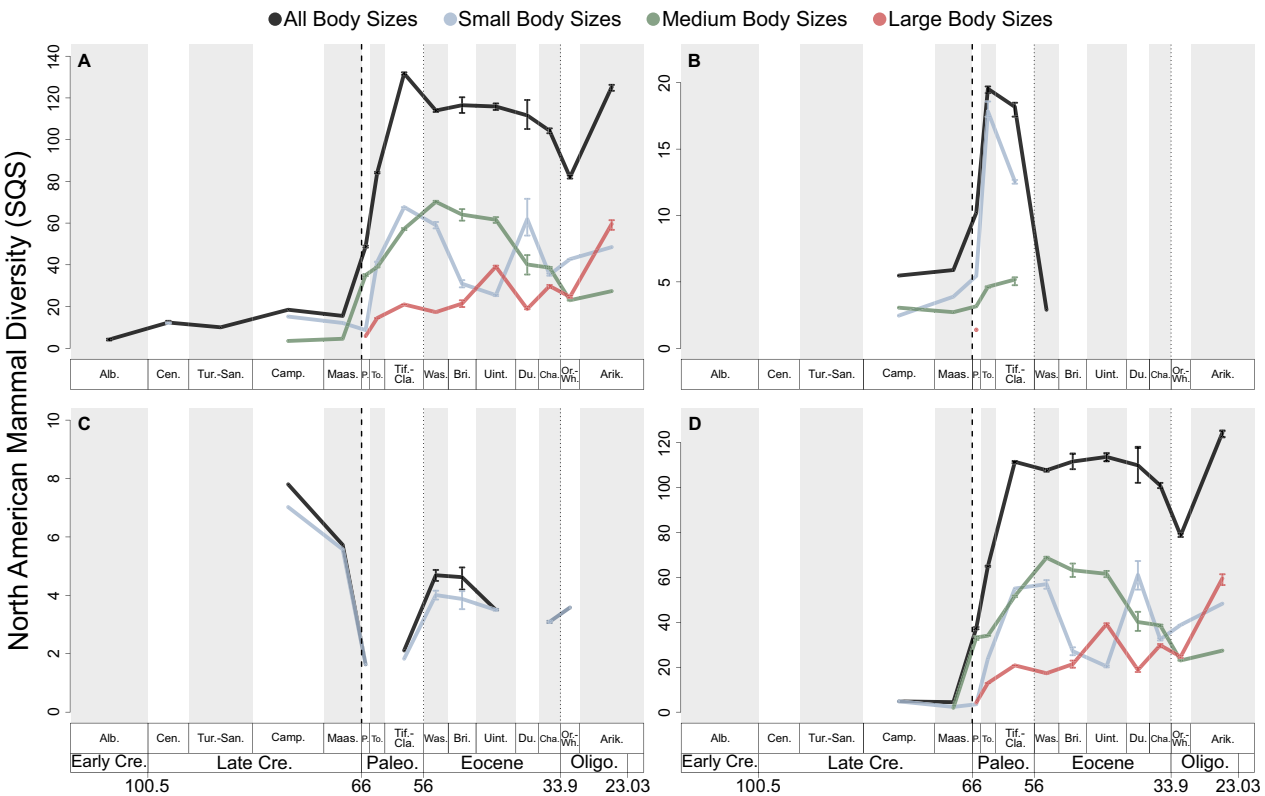

FIG. 2. Sampling-standardized diversity through time for North American species of: A, total Mammalia; B, Multituberculata; C, Metatheria; D, Eutheria. For each clade, all mammal (black line), small mammal (blue line), medium mammal (green line) and large mammal (red line) diversity was calculated using coverage-based rarefaction at a quorum of 0.8 (SQS; Fig. S3 shows sampling corrected diversity for species of all body sizes, small species, medium species and large species for total Mammalia, at quorums 0.7, 0.8, 0.85, 0.9 and 0.95. Fig. S4 shows additional subclade SQS diversity curves at quorum 0.8). All panels are plotted against different *y*-axes. Vertical dashed black line indicates the K/Pg boundary. Vertical dotted black lines indicate the Paleocene–Eocene and Eocene–Oligocene boundaries, respectively. Interval names are provided in Figure S3. Data on which bins are observed, subsampled, or extrapolated can be found in Data S3.

Local richness

Counts of species within individual PBDB collections (broadly equivalent to fossil sites or localities), were plotted through time for each mammalian size class to assess changes in local richness (alpha diversity; Close *et al.* 2019). In contrast to Close *et al.* (2019), who also counted indeterminate but distinct species, only valid named species were included here, as body size data has only been collected at the species level.

Local richness rarefaction curves

Face-value local richness estimates (simple counts of species per collection) and per-bin richness quantiles are both sensitive to sampling intensity biases (Close *et al.* 2019), such that sampling greater numbers of fossil collections tends to result in higher local richness estimates. Within-collection abundance data is needed to standardize estimates of species per collection, but this data is not systematically available in the literature. Instead, we follow Close *et al.* (2019) in generating local richness rarefaction curves, for each body size category, at a range of informative local richness quantile levels: 0.9, 0.95, 0.99 and 1 (the last value being maximum local richness per bin). Rarefaction curves of local richness quantiles were generated as per Close *et al.* (2019), and entailed 1000 replicates of drawing fixed numbers of per-collection richness values per bin (with replacement; i.e. bootstrapping) for sample quotas ranging from one collection up to the maximum number of collections in each bin (sample quotas spaced logarithmically). Subsampled levels of local richness quantiles were also used to generate diversity curves using standardized per-bin estimates. A minimum quota of 35 collections was used to maximize coverage among bins while omitting poorly sampled Mesozoic bins. Results for standardized and unstandardized local richness curves are presented in Data S4.

Sample coverage

Good's *u*, an estimate of sample coverage (Good 1953), was calculated for each size class per time bin per bootstrap replicate (Data S5). Although the original formula for calculating Good's *u* only uses information about singletons, we used a modified version of the formula (Chao 1984), which estimates coverage using both singletons (species represented by only one specimen) and doubletons (species represented by two specimens).

RESULTS

Face-value species counts

Face-value (uncorrected or 'raw') counts of terrestrial North American fossil mammal species, pooling all body sizes, remain low throughout the Cretaceous, albeit with a small increase during the final two stages, the Campanian and Maastrichtian (Figs 1, S5). Species counts show overall increases after the K/Pg boundary in all size classes, with the exception of a small decline during the Puercan for small mammals, before increasing in the Torrejonian (note that by definition there are no Mesozoic representatives of the large-bodied size class; see Body mass estimates). Counts of small and medium-sized mammals continue to increase up to a maximum in the well-sampled early Eocene time bins, before declining through the remainder of the Cenozoic. Large mammals show their highest fossil species counts later in time, during the Arikareean North American Land Mammal Age (NALMA; Oligocene/earliest Miocene, the final time bin included in our study). Eutherian mammals make up an increasing percentage of overall fossil species counts through time in all size classes (Figs 1, S5), with the greatest increase in the relative abundance of eutherians across the K/Pg boundary. Non-eutherian groups show extremely low species counts by the end of the study interval (Oligocene/earliest Miocene). Face-value species counts of individual clades, coloured by body size class, can be seen in Figure S6. In our dataset, only multituberculates, cimolestans, condylarths and rodents span all three body size classes. The remaining clades comprise either mostly small-sized mammals and fewer medium-sized mammals, or mostly medium-sized mammals and fewer large-bodied mammals (Fig. S6).

Sampling-standardized diversity

Sampling-standardized diversity across all terrestrial North American mammal species (Fig. 2A, black line; Fig. S3A) appears low throughout the Cretaceous. Sampling-standardized diversity increases abruptly across the K/Pg boundary, and substantial further increases continue throughout the Paleocene, such that late Paleocene diversity is approximately six times higher than that of the Late Cretaceous (we present results at a quorum of 0.8 in Fig. 2, but other quora show consistent patterns: Fig. S3). Diversity shows an essentially stationary pattern during the Eocene and Oligocene, with a dip in diversity after the Eocene–Oligocene boundary. Despite these fluctuations, mammalian diversity shows overall long-term stability at levels which are at least five times greater than those of the Late Cretaceous.

Sampling-standardized diversity of small mammals (Fig. 2A, blue line; Fig. S3B) shows a small decline in the immediate aftermath of the K/Pg extinction event (the Puercan NALMA). It then increases to substantially higher levels by the late Paleocene. Small mammal diversity fluctuates throughout the Eocene and Oligocene, in particular declining during the Bridgerian, Uintan and Chadronian, but never drops as low as Campanian–Paleocene levels.

Sampling-standardized diversity of medium-sized mammals (Fig. 2A, green line; Fig. S3C) shows an immediate increase across the K/Pg boundary, and continues to increase throughout the Paleocene and across the Paleocene/Eocene boundary to an acme in the early Eocene. Medium-sized mammals then show a general pattern of diversity decline from the early Eocene to the late Oligocene/earliest Miocene.

Sampling-standardized diversity of large-bodied mammals (Fig. 2A, red line; Fig. S3D), which by definition are not present in the Mesozoic, show a long-term pattern of overall increase from the earliest Paleocene to the late Oligocene and earliest Miocene. Large mammals show a pronounced increase in the Uintan NALMA, followed by a decrease across the Uintan–Dutchesnean boundary.

Eutherian diversity patterns (Fig. 2D) are similar to those of 'total' mammals (Fig. 2A), but with relatively lower diversity during the Cretaceous among all mammals and small-bodied mammals, as would be expected. In contrast, patterns in multituberculates (Fig. 2B) and metatherians (Fig. 2C) deviate more substantially from those of 'total' mammals (we also note that there are insufficient large-bodied multituberculates and medium-sized metatherians to provide consistent sampling-standardized diversity estimates, and that large-bodied metatherians are absent from our North American dataset). Multituberculates show increases across the K/Pg boundary (Fig. 2B, black line), followed by an even more substantial increase in the mid-Paleocene, and then an abrupt decline to below Cretaceous levels across the Paleocene–Eocene boundary. Metatherian diversity shows a substantial decline across the K/Pg boundary (Fig. 2C; for both all and small-bodied Metatheria), with their

highest diversity levels attained during the Cretaceous. Metatherian diversity increases across the Paleocene–Eocene boundary, but does not reach pre-K/Pg values, before declining slightly on average throughout the Eocene and Oligocene.

Local species richness

Face-value counts of mammal species per collection (local richness, or alpha diversity) were low during the Mesozoic (Fig. 3). Curves for unstandardized (Fig. 4A) and standardized (Fig. 4B) local richness quantiles are similar, but rarefying down to a fixed quota of 35 collections excludes all Mesozoic bins apart from the Campanian and Maastrichtian. Prior to the Campanian, rarefaction curves of local richness quantiles for Mesozoic intervals are based on low counts of collections and show no signs of levelling off (Fig. 4C–F), suggesting that the data are insufficient to draw reliable inferences. Local standardized richness (quantile = 0.99) drops slightly across the boundary, and then increases abruptly in the Torrejonian, reaching a high point for our study interval. Local total mammal richness then exhibits an overall decline, albeit with short term fluctuations, through to the end of the Oligocene.

Standardized local richness of small mammals shows a short-term decline in the immediate aftermath of the K/Pg mass extinction event. By the late early Paleocene, however, local richness levels are considerably higher than those of the latest Cretaceous. The unstandardized curve of local richness quantiles for small mammals (Fig. 4A) is flatter throughout the remainder of the Cenozoic, while the standardized curve exhibits more variation and discontinuities due to bins that do not meet the collection quota (Fig. 4B).

Medium-sized mammal local richness quantiles show an immediate increase across the K/Pg boundary. Local richness for this size class peaks in the Torrejonian and then again in the Wasatchian, which is then followed by a general decline through to the end of the study interval, punctuated by a smaller peak in the Chadronian. Local richness quantiles for large mammals begin in the Puercan, and remain relatively stable through time, with a very slight overall increase towards the end of the time series, punctuated by a small decline in the Bridgerian.

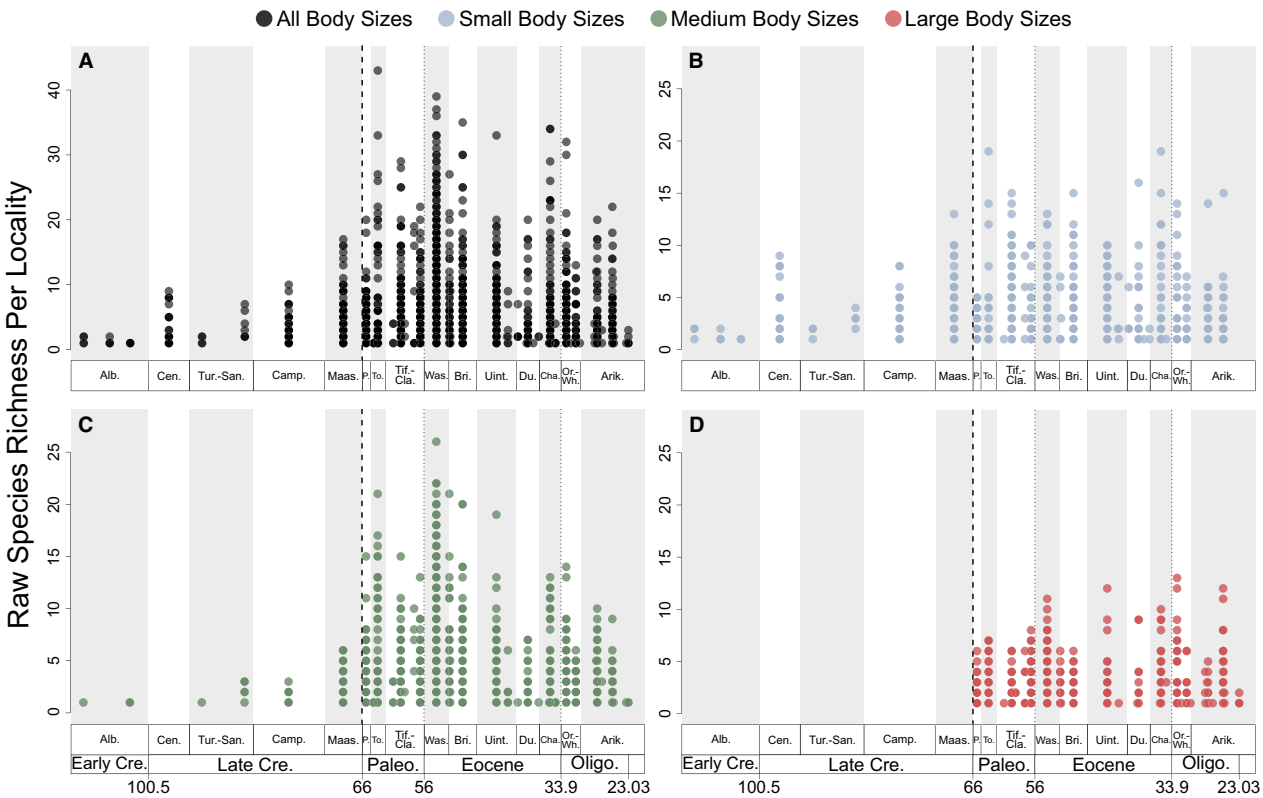

FIG. 3. Face-value counts of species per collection in North America for: A, all mammals; B, small mammals; C, medium mammals; D, large mammals. Panel A has a different *y*-axis to panels B–D. Vertical dashed black line indicates the K/Pg boundary. Vertical dotted black lines indicate the Paleocene–Eocene and Eocene–Oligocene boundaries, respectively. Interval names are provided in Figure S3.

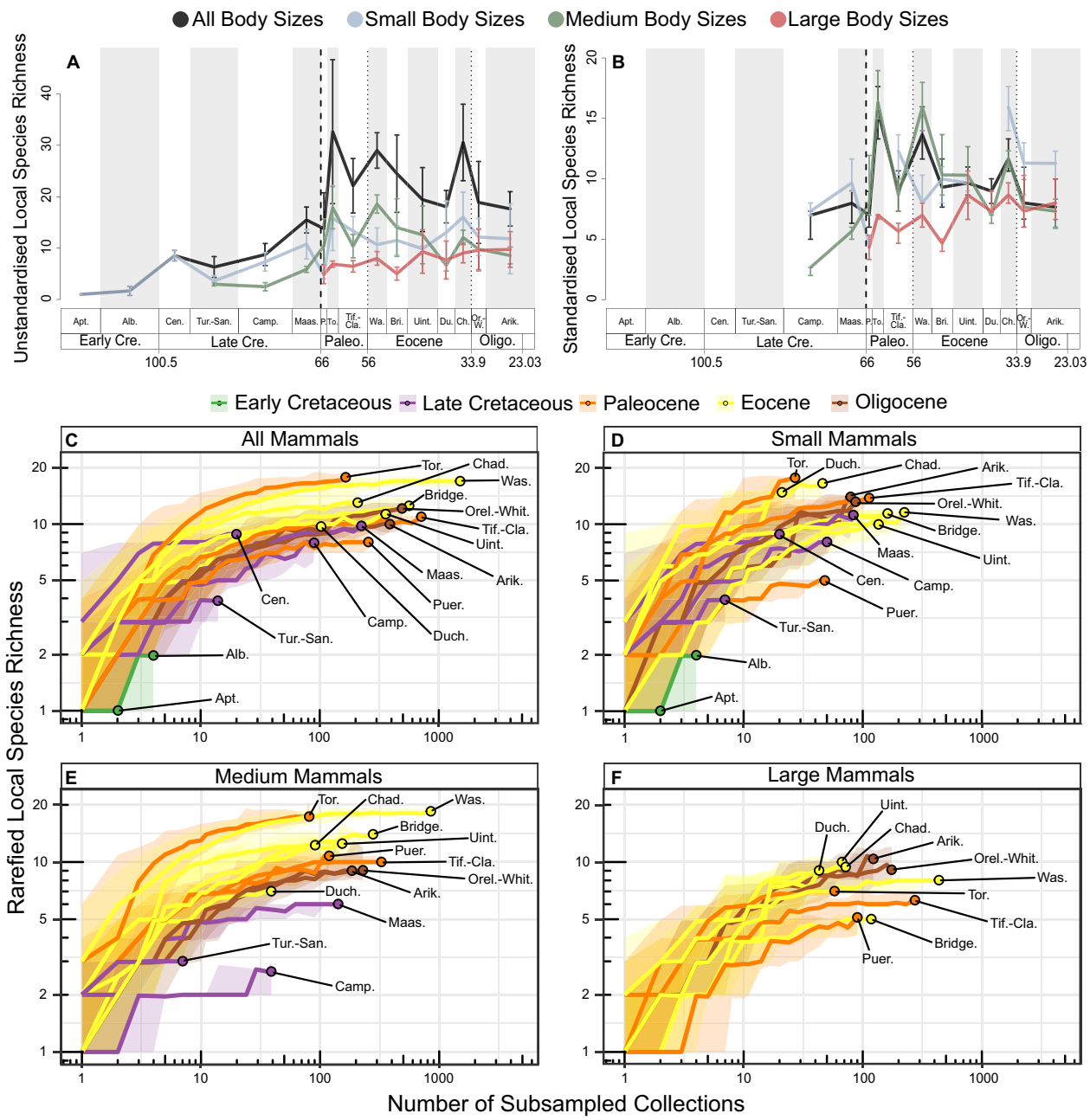

FIG. 4. Local richness for North American mammals from the Mesozoic–Palaeogene, shown for all mammals, along with small, medium and large mammals. A, unstandardized curves of local richness quantiles (quantile = 0.99). B, standardized curves of local richness quantiles (quantile 0.99), using a rarefaction quota of 35 collections. C–F, rarefaction curves of local richness quantiles. Interval names are provided in Figure S3.

Body mass frequency distributions

Species body mass frequency distributions for Mesozoic and early Cenozoic (Palaeogene) mammals, plotted by diet, is shown in Figure S7. In the Palaeogene, all mammals, faunivorous mammals, and herbivorous mammals exhibit a prominent right-skew to their size-frequency distribution. However, omnivorous mammals do not.

DISCUSSION

Our analyses confirm previous findings of a substantial (at least four-fold) increase in mammal diversity in the aftermath of the K/Pg extinction event (e.g. Benson *et al.* 2016; Grossnickle & Newham 2016; Close *et al.* 2017, 2019). Increases occurred in North America at both local and regional scales, and took place throughout

the first 10 myr of the Cenozoic (Figs 2, 4). Crucially, diversity increases occur in all body size classes, including among small-bodied mammals, after a short time lag (diversity of small-bodied mammals is low in the Puercan, earliest Paleocene; Figs 2–4). Indeed, early Cenozoic increases in small-bodied mammal diversity were similar to those seen in medium and large-bodied mammals (Figs 2A, 3B–D). Large-bodied mammals, by our definition, were absent before the Palaeogene, and the maximal local richness of large mammals during the early Cenozoic is comparable to that of non-avian dinosaur species in the Mesozoic (Fig. 4; cf. Close *et al.* 2019). This observation is consistent with a long-term incumbent/replacement dynamic between dinosaurs and large-bodied mammals. However, when also including smaller-bodied species, Cenozoic increases in total mammalian diversity were considerably greater than extinctions of non-avian dinosaur species (see also Benson *et al.* 2016; Close *et al.* 2017, 2019).

Our findings for large-bodied mammals are consistent with previous studies which showed that the dinosaur incumbency hypothesis and replacement of large-bodied dinosaurs by large-bodied mammals explains some aspects of the early Cenozoic mammal radiation (e.g. Alroy 1999; Slater 2013; Chen *et al.* 2019). Nevertheless, this hypothesis alone does not explain the scale of Cenozoic mammalian diversification across all body size classes, or the observation of large increases in small-bodied mammal diversity (and see Chen *et al.* 2019 for ecological diversification of small mammals). The smallest non-avian dinosaurs known from definite adult specimens weighed *c.* 400 g, and dinosaur species body masses less than 750 g were extremely rare (Benson *et al.* 2014, 2018; Benson 2018). It is therefore unlikely that adult non-avian dinosaurs were frequent ecological competitors of small-bodied mammals (<100 g as defined here).

When discussing the ecological release of mammals, predation by the dinosaurs is often also cited alongside competition as a constraining factor for mammal evolution during the Mesozoic (e.g. it is central to the 'suppression hypothesis'; Osborn 1902; Grossnickle *et al.* 2019 and references therein). While some smaller-bodied dinosaurs probably did prey on small mammals (e.g. Simpson *et al.* 2010; Varricchio *et al.* 2021), predator–prey relationships are extremely complex, and these complexities remain poorly understood. Furthermore, the effects of predation pressure on species richness are also poorly understood at a macroevolutionary scale. On macroevolutionary time scales, predator–prey relationships may potentially result in evolutionary arms races (Dawkins & Krebs 1979) and do not necessarily reduce species diversity (Paine 1966; Stroud & Losos 2016; but see also Schoener *et al.* 2001; Ryberg *et al.* 2012). Although some studies suggest that the removal of predators can promote the radiation of prey species (Yoder *et al.* 2010 and references therein), there is no reason to expect that predation pressure from non-avian dinosaurs was substantively more intensive on small-bodied mammals in the Mesozoic than the effects of mammalian predators of the Cenozoic. It is likely that by the Late Cretaceous, interactions among small-bodied mammals, birds and squamates were also similar to those of today (Chen *et al.* 2019). Relaxation of predation pressure was probably substantial, but also transient due to the replacement of dinosaurian predators with mammalian predators in the early Cenozoic. This transient effect therefore cannot readily explain the long-term persistence of high standing diversity among small-bodied mammals following the K/Pg.

We also identified noteworthy diversity dynamics among medium and large-bodied mammals within the Cenozoic. The body masses of the smallest adult dinosaurs overlap with the medium-sized mammals in our study. Therefore, the extinction of non-avian dinosaurs potentially does explain increases in this size class and expansion into still larger body sizes, as has been previously hypothesized. Although total mammal diversity reached a plateau during the Eocene, mammal diversity within individual body size classes is more variable. Medium-sized mammals exhibit their highest diversity during the late Paleocene and early/middle Eocene, followed by declining diversity from the middle Eocene onward (Figs 2A; S3C). In contrast, large-bodied mammals show a long-term increase in diversity through time from the Paleocene to Oligocene and Early Miocene. By the late Eocene, declines in medium-sized mammals correspond with more substantial increases in large-bodied mammals. These observations are consistent with previously-documented patterns of mammalian body size evolution, in which groups of medium-sized mammals were abundant during the early Cenozoic, but mostly evolved towards larger body sizes by the end of the Eocene (Alroy 1999; Smith *et al.* 2010).

Changes in sampling-standardized diversity within body size classes during the Eocene also coincide with a pattern of turnover among groups of eutherian mammals, as well as with the final extinctions of stem-therian mammals. Long term declines in medium-sized mammals from the early Eocene onward (Fig. 2A, D) can be attributed to the decline and subsequent loss during the Eocene of multituberculates (Figs 2B, S6A), condylarths (Figs S4B, S6D), cimolestans (Figs S4A, S6C), and primates and plesiadapiforms (Figs S4C, S6E). Long term increases in large mammal diversity are driven primarily by increases in the diversity of artiodactyls and perissodactyls (Figs S4G, S6I), and an expansion of large bodied carnivores (Figs S4E, S6G).

Hypotheses for the diversification of small-bodied mammals after the K/Pg mass extinction

Explaining the increases in small-bodied mammal diversity that we document requires deeper exploration of the dinosaur incumbency hypothesis, as well as the investigation of complementary biotic and abiotic factors. Together, hypotheses must explain an abrupt and long-lasting state-shift in mammalian species richness in all body size classes during the K/Pg transition, and not just the attainment of large body sizes for the first time during the early Cenozoic, which has classically been the focus of this faunal transition. It is likely that such hypotheses will invoke fundamental ecological differences between Mesozoic and Cenozoic ecosystems. We suggest the need for new hypotheses that explain how Cenozoic mammals were able to better partition or pack body-size niche space, allowing them to achieve greater diversity even within small-body-sized macroevolutionary adaptive zones (*sensu* Simpson 1953; Stanley 1973) that were already established in the Mesozoic. Successful explanations must invoke persistent state-shifts in terrestrial ecosystems rather than transient factors associated with catastrophic events over the boundary itself, particularly as Cenozoic mammals continued to diversify substantially throughout the Paleocene.

We discuss five potential explanations for this long-term pattern: (1) 'life history differences between dinosaurs and mammals', differences in ontogeny and parental care may have allowed mammals to achieve higher species richness than dinosaurs in similar environments; (2) 'extinctions among other mammaliaforms', small-bodied non- and stem-therian mammals probably competed with Mesozoic therian mammals for resources, and could have been incumbent in small-bodied niches; (3) 'extinctions among other small-bodied tetrapods', niches available to small-bodied mammals may have been cleared by extinctions among other small-bodied tetrapods; (4) 'environmental change', environmental changes that created novel niches, such as floral changes that produced new opportunities for herbivores; and (5) 'key innovations', a novel ability to evolve key traits which increases speciation rates or the upper limits to species richness of ecosystems.

Life history differences between mammals and dinosaurs. Differences between the ontogenetic shifts seen in dinosaurs compared to mammals may provide one possible or partial explanation for an increase in mammal diversity in all body size classes across the K/Pg boundary (Close *et al.* 2019). Dinosaur species range from 400 g to 70 tonnes as adults (Benson *et al.* 2018), but emerged from eggs, as hatchlings, at smaller sizes. Dinosaur species therefore occupied a large range of different body sizes as they grew, and had little parental care (although data on this are missing for many groups). Therefore, individuals from the same species of dinosaur may have filled multiple ecological niches throughout their lifecycle, commonly referred to as 'ontogenetic niche partitioning' (Varricchio 2011; O'Gorman & Hone 2012; Codron *et al.* 2013). This differs from the situation in mammals (e.g. Janis & Carrano 1991), which produce many fewer offspring, with a high degree of parental investment per individual, providing parental care until the offspring are able to fend for themselves. Therefore, mammals do not undergo ontogenetic niche shifts to the same extent as dinosaurs, if at all.

Schroeder *et al.* (2021) recently suggested that the widespread occurrence of ontogenetic niche shifts in dinosaurs may explain the perceived low species richness of dinosaurs. However, we find no evidence that dinosaurs had low species richness, beyond what would be explained already by their large body sizes; dinosaurs had approximately the same species richness that dinosaur-sized mammals do today (>750 g; Le Loeuff 2012; Benson 2018, e.g. by comparison of Maastrichtian dinosaur species richness to the count of mammal species within the common body size range of dinosaurs). Our findings corroborate this, by showing that large-sized mammals of the early Cenozoic had similar species richness to Late Cretaceous dinosaurs (Figs 2A and S3D in combination with Close *et al.* 2019). Nevertheless, juvenile individuals of smaller-bodied dinosaur species may potentially explain the low diversity of small-bodied mammals (weighing <100 g) during the Mesozoic, and removal of dinosaurs at the K/Pg boundary may therefore explain increases in species richness of small and medium-sized mammals, allowing for higher taxonomic diversity of mammals compared to dinosaurs (Codron *et al.* 2013). We note that this is not our favoured hypothesis because strong evidence that differences in the life history of dinosaurs compared to mammals resulted in different body size distributions or species richness patterns remains elusive due to size-related sampling biases (e.g. Brown *et al.* 2013; Benson *et al.* 2018, 2022). Nevertheless, it remains a live and important hypothesis.

Extinctions among other mammaliaforms. Dinosaurs were not the only clade to undergo major extinctions at the K/Pg boundary. During the Mesozoic, non-therian and stem-therian mammals were much larger components of mammal diversity. Like the therian mammals that survived the K/Pg extinction and subsequently radiated, non-therians and stem-therians were confined to small body sizes during the Mesozoic. During this time period, these groups seem to have been more readily able to evolve novel phenotypic traits and therefore exploit a larger range of ecological niches (Brocklehurst

et al. 2021). The removal of many of these mammaliaform clades at the K/Pg boundary, and the decline of the late-surviving multituberculates throughout the late Paleocene and Eocene, probably contributed to relaxing competition on the surviving therian mammals (Brocklehurst *et al.* 2021). We note that this hypothesis may have contributed to diversification in placental and marsupial mammals, but does not provide a clear explanation for the magnitude of the increase seen in the total species richness of all mammaliaforms in the early Cenozoic compared to those in the Late Cretaceous.

Extinctions among other small-bodied tetrapods. Higher competition between other small-bodied tetrapods and small mammals during the Mesozoic when compared to the Cenozoic could also potentially explain the diversification of small mammals after the K/Pg boundary. Other small-bodied tetrapods include small-bodied members of the amphibian, bird and lepidosaur clades, and we consider each in turn.

Amphibians were well-established by the beginning of the Mesozoic, having evolved *c.* 370 million years ago during the Late Devonian (Romer 1956). Roelants *et al.* (2007) presented a molecular time tree of amphibian species, representing a small but phylogenetically diverse sample of their living diversity. They found that net diversification of higher clades was high at the start of the Mesozoic, levelled during the mid-Mesozoic, and peaked in the Late Cretaceous. This peak in net diversification is broadly concurrent with radiations among some mammaliaform clades (Grossnickle *et al.* 2019) in the aftermath of faunal turnover during the KTR (Lloyd *et al.* 2008; Grossnickle *et al.* 2019; Benton *et al.* 2021). Evidence for amphibian extinctions across the K/Pg boundary is limited (Feijó *et al.* 2023). Moreover, many modern amphibian clades probably originated in the Palaeogene, and taxonomic diversity increased when amphibians radiated across the K/Pg boundary (Roelants *et al.* 2007; Feng *et al.* 2017). As amphibian diversity increased alongside small mammal diversity, and almost all amphibians are small-bodied (e.g. extant amphibians; O'Gorman & Hone 2012, fig. 2d), there is no evidence that amphibians competed with Mesozoic small mammals more than they did with Cenozoic small mammals. Furthermore, we currently find it difficult to envision a mechanism by which Mesozoic amphibians could have suppressed the diversity of small-bodied mammals, with each clade exhibiting distinct ecologies and life histories.

The first birds (Aves) evolved *c.* 150 million years ago in the mid-Jurassic (Brusatte *et al.* 2015b), at least 50 million years after the first mammaliaforms (Grossnickle *et al.* 2019). While we know of no previous studies that have tested the diversification of exclusively small-bodied birds across the K/Pg boundary, modern and fossil birds are overwhelmingly small-bodied (e.g. extant birds; O'Gorman & Hone 2012, fig. 2b), with larger and often flightless birds less common. Therefore, diversity dynamics for all birds are likely to be driven by small-bodied birds. The fossil record of Mesozoic birds is extremely incomplete (Brocklehurst *et al.* 2012). Nevertheless, exceptional fossil sites provide evidence for diverse bird faunas by the Cretaceous (Brusatte *et al.* 2015b). Enantiornithes were the most taxonomically diverse Mesozoic bird clade, but were likely to have been exclusively arboreal and ecomorphologically constrained (Wang *et al.* 2021). Birds underwent major extinctions at the K/Pg boundary (Longrich *et al.* 2011; Field *et al.* 2018), and Neornithes (crown-group birds) replaced the more dominant Mesozoic groups including the Enantiornithes (Brusatte *et al.* 2015b; Field *et al.* 2018). Neornithes exhibited a radiation that paralleled that seen in mammals in the aftermath of the K/Pg extinction event and today are almost twice as diverse as mammals, with over 10 000 species (Brusatte *et al.* 2015b). It is possible that some Mesozoic mammals and birds did compete for limited resources within an already reduced range of niches, and that both clades were constrained to fewer niches and smaller body sizes by a common cause (e.g. environmental constraints and the presence of the non-avian dinosaurs). This could have reduced diversity among both clades to some extent during the Cretaceous. Nevertheless, as extant birds are even more diverse at small body sizes than both their Mesozoic counterparts and extant mammals, it is implausible that competition from Mesozoic birds would have constrained Mesozoic small-bodied mammals to a greater extent than extant birds constrain extant small-bodied mammals.

Lepidosaurs comprise squamates (lizards and snakes) and rhynchocephalians. As with birds, we are not aware of any analyses that have sought to investigate lepidosaur diversity dynamics exclusively at small body sizes. Nevertheless, many species of lepidosaur are small (e.g. extant reptiles; O'Gorman & Hone 2012, fig. 2c) and so here we consider patterns reported for the total group. During the period from the Triassic to the Oligocene, total lepidosaur species richness peaked in the Late Cretaceous (Cleary *et al.* 2018), once again congruent with Late Cretaceous increases in mammal diversity (Fig. 3; see also Grossnickle *et al.* 2019). Many lepidosaur clades underwent extinctions across the K/Pg boundary (e.g. lizards and snakes; Longrich *et al.* 2012), but subsequent taxonomic radiations (snakes; Klein *et al.* 2021) and niche expansion (snakes; Grundler & Rabosky 2021) in the wake of the K/Pg mass extinction replaced diversity losses, resulting in consistently high lepidosaur diversity throughout the Palaeogene (Cleary *et al.* 2018). With *c.* 10 000 species of lepidosaur alive today (Cleary *et al.* 2018), and a

significant right-skew to extant lepidosaur body size distributions (e.g. extant reptiles; O'Gorman & Hone 2012, fig. 2c), it is likely that competition between lepidosaurs and small mammals is higher today than it was during the Mesozoic.

Overall, previous works provide evidence that the main groups of small-bodied land vertebrates that were abundant in Cretaceous ecosystems, in fact share patterns of higher taxon appearance and turnover with those seen in mammals, and may have undergone species-radiations in the earliest Cenozoic, co-occurring with the patterns documented here for small-bodied mammals (e.g. Roelants *et al.* 2007; Brusatte *et al.* 2015b; Cleary *et al.* 2018; Field *et al.* 2018; Klein *et al.* 2021). This makes it unlikely that small-bodied mammal diversity was suppressed by the occurrence of other small-bodied groups prior to the K/Pg boundary, rejecting a hypothesis of ecological release of small-bodied mammal diversity. Instead, the occurrence of potentially shared patterns across multiple groups may be taken as evidence for an environmental driver, which deserves further investigation.

Environmental change. Of potential environmental explanations, floral composition is the most prominent and we focus on that here. Floral composition and structure has a strong influence on the structure of small mammal communities today and has been proposed as a strong influence on mammalian evolutionary history (Chen *et al.* 2019; Grossnickle *et al.* 2019; Benton *et al.* 2021). Much of the ecological diversity of Mesozoic mammals resulted from a Jurassic diversification of the mammalian crown-group and their proximate stem-lineage (Luo 2007; Close *et al.* 2015). This resulted in substantial locomotor diversity, but more limited dietary diversity compared to extant small-bodied mammals (Chen *et al.* 2019). The evolution of dietary specialization among Late Cretaceous multituberculates, therians and other groups has been attributed to the ecological diversification of flowering plants (e.g. Wilson *et al.* 2012; Chen *et al.* 2019; Grossnickle *et al.* 2019). Nevertheless, Eocene mammal communities show dramatically more varied dietary adaptations than those of the Late Cretaceous (Benevento *et al.* 2019). This has been linked to events in angiosperm evolution, which continued from the mid-Cretaceous up to the Paleocene (Chen *et al.* 2019). Angiosperms are thought to provide a greater output of nutrient-rich organs, including leaves, fruits and seeds, than other plant groups, and to have promoted diversification of insect groups that also provide prey items for small-bodied mammals (reviewed by Chen *et al.* 2019).

Understanding of the timing of shifts in floral communities and their relationship to events in the ecological diversification of mammals is limited by a lack of detailed study of floral community structure during the K/Pg transition (Chen *et al.* 2019). Nevertheless, floral assemblages are known to have undergone substantial change through this interval. Although angiosperms comprised a high proportion of plant species by the early Late Cretaceous, tree-like forms were initially rare, and angiosperms constituted a low proportion of biomass and cover in many environments until the latest Cretaceous or early Cenozoic (Wings & Boucher 1998). Maximum fruit and seed sizes also underwent continual increases through the Late Cretaceous and Paleocene to reach a peak during the Eocene, with hypothesized links to mammalian diversification (Eriksson 2016). Angiosperm leaf-vein density, and implied capacity for photosynthetic production, underwent a large, stepwise increase during the Maastrichtian (latest Cretaceous; Feild *et al.* 2011), coincident with the timing of increases in local richness of small-bodied mammals found here (Fig. 3B). Plant diversity was reduced in the immediate aftermath of the extinction, with spikes in fern and palm abundance representing the expansion of disaster taxa (Lyson *et al.* 2019). The post-extinction aftermath saw diversification of numerous angiosperm clades (Lyson *et al.* 2019; Magallón *et al.* 2019). Legumes, one of the largest families of flowering plants and prominent nitrogen-fixers, diversified in the immediate aftermath of the K/Pg extinction, and may have provided a rich new food source for mammals to exploit (Lyson *et al.* 2019), alongside increases in angiosperm fruit size distributions and diversity (Eriksson *et al.* 2000). In the context of these observations, the apparently increased capacity of Palaeogene biomes to host greater small-bodied mammal richness might well be explained by changes in the nature of plant communities, where increases in resources may have expanded the number of niches in Cenozoic ecosystems. Better quantification of floral change and patterns of plant diversity across the K/Pg boundary in the future will allow a test of this hypothesis.

Key innovations. Another non-mutually-exclusive alternative for the diversification of small mammals following the K/Pg relates to the intrinsic evolution of new biological traits, or 'key innovations'. Key innovations are defined as the evolution of a novel phenotype that promotes evolutionary 'success' in a clade (Hunter 1998). These traits can change the ability of an evolutionary lineage to diversify, increase competitiveness, or enable the exploitation of novel environments or resources (Hunter 1998). The composition of mammal faunas changes substantially after the K/Pg extinction event (Figs 1, S5), with eutherian mammals making up much larger proportions of overall diversity (Fig. 2A, D;

Cenozoic eutherian mammal diversity is extremely similar to Cenozoic total mammal diversity). Thus, the post-K/Pg diversification of small mammals could be linked to one or more key innovations present in eutherians. Several potential key innovations of eutherians have been proposed. For example, the effects of the placental reproductive mode on the evolutionary success of the clade has long been discussed (Lillegraven *et al.* 1987; Rose & Archibald 2005). Placental reproduction is key for eutherian evolutionary success, and is particularly advantageous for mammals of small body sizes (Lillegraven *et al.* 1987). Placental mammal reproduction has positive effects on metabolic rate, brain size, social evolution and longevity (Lillegraven *et al.* 1987). Furthermore, the hypocone, a small modification to tribosphenic molars which adds a fourth cone and increases the occlusal surface area, has also been hypothesized as a key innovation among eutherian mammals that facilitates grinding, and is proposed to have underpinned the evolution of numerous herbivorous strategies (Hunter & Jernvall 1995).

CONCLUSION

We show that mammals of all body sizes diversified substantially during the K/Pg transition, at both local and regional scales. This occurred abruptly, resulting in large increases in mammalian richness that persisted throughout the Cenozoic and more than made up for the loss of dinosaur species richness. These findings necessitate a reframing of the dinosaur incumbency hypothesis within the wider context of early Cenozoic mammal evolution, and alternative hypotheses should be further explored as significant contributing factors in the Cenozoic mammal radiation. While the extinction of non-avian dinosaurs and the removal of competition from large-bodied dinosaurs could have driven the diversification of large-bodied mammals following the K/Pg event, additional hypotheses are needed to fully explain large increases in the diversity of small-bodied mammal species with similar body sizes to those in the Mesozoic, as well as to explain more subtle increases in mammal diversity and body sizes that occurred during the later stages of the Cenozoic. Despite mammals having been present at small body sizes for at least 100 million years, since the late Early Jurassic, by the K/Pg boundary, Cenozoic mammals in this size class appear to have either had access to a greater total amount of resources or been able to better pack or partition niche space after the K/Pg mass extinction event. We are unable to conclusively demonstrate the drivers of diversification among small-bodied mammals after the K/Pg mass extinction. However, it is likely that various extrinsic and intrinsic factors were collectively important. In particular, factors such as extinctions among non- and stem-therian mammals, a state-change in floral composition, or key innovations of placental mammals, which became important components of terrestrial assemblages after the K/Pg boundary, were probably important in the resulting adaptive radiation. Future work should focus on better understanding the complex drivers of mammal diversification during the early Palaeogene.

Acknowledgements. We thank all contributors to the Paleobiology Database, and in particular J. Alroy, W. Clyde, P. Holroyd and L. Gannon who contributed substantially to the datasets used herein. This is Paleobiology Database official publication number 451. This research was funded by the European Union's Horizon 2020 research and innovation program under grant numbers 637483 (ERC Starting Grant TERRA to R.J.B.) and 677774 (ERC Starting Grant TEMPO to RBJB). We thank Thomas Halliday, Emma Dunne, John Clarke, and Shan Huang for helpful discussion, and four anonymous reviewers of an earlier version of this manuscript, whose comments added much to our discussion. We thank Susanne Fritz for considerable academic encouragement and support during the finalization of this project, particularly in the form of a current postdoctoral position given to GLB, funded by the Leibniz Competition (Grant P52/20017) awarded to Susanne Fritz by the Leibniz Association.

Author contributions. **Conceptualization** GL Benevento (GLB), RJ Butler (RJB), RBJ Benson (RBJB), and RA Close (RAC); **Data Curation** GLB; **Formal Analysis** GLB, RAC; **Funding Acquisition** RJB; **Investigation** GLB, RAC; **Methodology** GLB, RAC; **Project Administration** GLB, RJB, RBJB, RAC; **Resources** RJB; **Software** GLB, RAC; **Supervision** RJB, RBJB, RAC; **Validation** GLB; **Visualization** GLB; **Writing – Original Draft Preparation** GLB, RJB, RBJB, RAC; **Writing – Review & Editing** GLB, RJB, RBJB, RAC.

DATA ARCHIVING STATEMENT

Data and code for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.ht76hdrm5.

Editor. Mary Silcox

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12653):

Appendix S1. Includes details of all supporting information and data available for this study. Also, Figures S1–S7, supplementary methods, results and discussion.
Data S1. List of species with taxonomic and size groupings.
Data S2. Sampling corrected diversity results.
Data S3. Sampling corrected diversity method.
Data S4. Local diversity results.
Data S5. Good's *u* results.

REFERENCES

ALROY, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, **280**, 731–734.

ALROY, J. 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Systematic Biology*, **48**, 107–118.

ALROY, J. 2010. The shifting balance of diversity among major marine animal groups. *Science*, **329**, 1191–1194.

ALVAREZ, L. W. 1983. Experimental evidence that an asteroid impact led to the extinction of many species 65 million years ago. *Proceedings of the National Academy of Sciences*, **80**, 627–642.

BENEVENTO, G. L., BENSON, R. B. J. and FRIEDMAN, M. 2019. Patterns of mammalian jaw ecomorphological disparity during the Mesozoic/Cenozoic transition. *Proceedings of the Royal Society B*, **286**, 20190347.

BENEVENTO, G. L., BENSON, R. B. J., CLOSE, R. A. and BUTLER, R. J. 2023. Data from: Early Cenozoic increases in mammal diversity cannot be explained solely by expansion into larger body sizes. Dryad Digital Repository. https://doi.org/10.5061/dryad.ht76hdrm5

BENSON, R. B. J. 2018. Dinosaur macroevolution and macroecology. *Annual Review of Ecology, Evolution, & Systematics*, **49**, 379–408.

BENSON, R. B. J., CAMPIONE, N. E., CARRANO, M. T., MANNION, P. D., SULLIVAN, C., UPCHURCH, P. and EVANS, D. C. 2014. Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biology*, **12**, e1001853.

BENSON, R. B. J., BUTLER, R. J., ALROY, J., MANNION, P. D., CARRANO, M. T. and LLOYD, G. T. 2016. Near-stasis in the long-term diversification of Mesozoic tetrapods. *PLoS Biology*, **14**, e1002359.

BENSON, R. B. J., HUNT, G., CARRANO, M. T. and CAMPIONE, N. 2018. Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology*, **61**, 13–48.

BENSON, R. B. J., BROWN, C. M., CAMPIONE, N. E., CULLEN, T. M., EVANS, D. C. and ZANNO, L. E. 2022. Comment on "The influence of juvenile dinosaurs on community structure and diversity". *Science*, **375**, eabj5976.

BENTON, M. J., WILF, P. and SAUQUET, H. 2021. The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytologist*, **233**, 2017–2035.

BRANNICK, A. L. and WILSON, G. P. 2020. New specimens of the Late Cretaceous metatherian *Eodelphis* and the evolution of hard-object feeding in the Stagodontidae. *Journal of Mammalian Evolution*, **27**, 1–16.

BROCKLEHURST, N., UPCHURCH, P., MANNION, P. D. and O'CONNOR, J. 2012. The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. *PLoS One*, **7**, e39056.

BROCKLEHURST, N., PANCIROLI, E., BENEVENTO, G. L. and BENSON, R. B. J. 2021. Mammaliaform extinctions as a driver of the morphological radiation of Cenozoic mammals. *Current Biology*, **31**, 2955–2963.

BROWN, J. H. 1995. *Macroecology*. University of Chicago Press.

BROWN, C. M., CAMPIONE, N. E., GIACOMINI, H. C., O'BRIEN, L. J., VAVREK, M. J. and EVANS, D. C. 2013. Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: a comment on Codron *et al.* (2012). *Biology Letters*, **9**, 20120582.

BRUSATTE, S. L., BUTLER, R. J., BARRETT, P. M., CARRANO, M. T., EVANS, D. C., LLOYD, G. T., MANNION, P. D., NORELL, M. A., PEPPE, D. J., UPCHURCH, P. and WILLIAMSON, T. E. 2015*a*. The extinction of the dinosaurs. *Biological Reviews*, **90**, 628–642.

BRUSATTE, S. L., O'CONNOR, J. K. and JARVIS, E. D. 2015*b*. The origin and diversification of birds. *Current Biology*, **25**, R888–R898.

CHAO, A. 1984. Non-parametric estimation of the classes in a population. *Scandinavian Journal of Statistics*, **11**, 265–270.

CHAO, A. and JOST, L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533–2547.

CHEN, M., STRÖMBERG, C. A. E. and WILSON, G. P. 2019. Assembly of modern mammal community structure driven by Late Cretaceous dental evolution, rise of flowering plants, and dinosaur demise. *Proceedings of the National Academy of Sciences*, **116**, 9931–9940.

CLEARY, T. J., BENSON, R. B. J., EVANS, S. E. and BARRETT, P. M. 2018. Lepidosaurian diversity in the Mesozoic–Palaeogene: the potential roles of sampling biases and environmental drivers. *Royal Society Open Science*, **5**, 171830.

CLOSE, R. A., FRIEDMAN, M., LLOYD, G. T. and BENSON, R. B. J. 2015. Evidence for a Mid-Jurassic adaptive radiation in mammals. *Current Biology*, **25**, 2137–2142.

CLOSE, R. A., BENSON, R. B. J., UPCHURCH, P. and BUTLER, R. J. 2017. Controlling for the species-area effect supports constrained long-term Mesozoic terrestrial vertebrate diversification. *Nature Communications*, **8**, 15381.

CLOSE, R. A., EVERS, S. W., ALROY, J. and BUTLER, R. J. 2018. How should we estimate diversity in the fossil record? Testing richness estimators using sampling-standardised discovery curves. *Methods in Ecology & Evolution*, **9**, 1386–1400.

CLOSE, R. A., BENSON, R. B. J., ALROY, J., BEHRENSMEYER, A. K., BENITO, J., CARRANO, M. T., CLEARY, T. J., DUNNE, E. M., MANNION, P. D., UHEN, M. D. and BUTLER, R. J. 2019. Diversity dynamics of Phanerozoic terrestrial tetrapods at the local community scale. *Nature Ecology & Evolution*, **3**, 590–597.

CODRON, D., CARBONE, C. and CLAUSS, M. 2013. Ecological interactions in dinosaur communities: influences of small offspring and complex ontogenetic life histories. *PLoS One*, **8**, e77110.

COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013 (updated). The ICS international chronostratigraphic chart. *Episodes*, **36**, 199–204.

DAMUTH, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. 229–253. *In* DAMUTH, J. and MacFADDEN, B. J. (eds) *Body size in*

mammalian paleobiology: Estimation and biological implications. Cambridge University Press.

DAWKINS, R. and KREBS, J. R. 1979. Arms races between and within species. *Proceedings of the Royal Society B*, **205**, 489–511.

DOS REIS, M., DONOGHUE, P. C. J. and YANG, Z. 2014. Neither phylogenomic nor palaeontological data support a Palaeogene origin of placental mammals. *Biology Letters*, **10**, 20131003.

ERIKSSON, O. 2016. Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. *Biological Reviews*, **91**, 168–186.

ERIKSSON, O., FRIIS, E. M. and LÖFGREN, P. 2000. Seed size, fruit size, and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. *The American Naturalist*, **156**, 47–58.

FEILD, T. S., BRODRIBB, T. J., IGLESIAS, A., CHATELET, D. S., BARESCH, A., UPCHURCH, G. R. Jr, GOMEZ, B., MOHR, B. A. R., COIFFARD, C., KVACEK, J. and JARAMILLO, C. 2011. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proceedings of the National Academy of Sciences*, **108**, 8363–8366.

FEIJÓ, A., KARLSSON, K. M., GRAY, R., YANG, Q. and HUGHES, A. C. 2023. Extreme-sized anurans are more prone to climate-driven extinctions. *Climate Change Ecology*, **4**, 100062.

FENG, Y.-J., BLACKBURN, D. C., LIANG, D., HILLIS, D. M., WAKE, D. B., CANNATELLA, D. C. and ZHANG, P. 2017. Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *Proceedings of the National Academy of Sciences*, **114**, E5864–E5870.

FIELD, D. J., BERCOVICI, A., BERV, J. S., DUNN, R., FASTOVSKY, D. E., LYSON, T. R., VAJDA, V. and GAUTHIER, J. A. 2018. Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Current Biology*, **28**, 1825–1831.

GOOD, I. J. 1953. The population frequencies of species and the estimation of population parameters. *Biometrika*, **40**, 237–264.

GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. and OGG, G. M. 2020. *Geologic time scale 2020*. Elsevier.

GROSSNICKLE, D. M. and NEWHAM, E. 2016. Therian mammals experience an ecomorphological radiation during the Late Cretaceous and selective extinction at the K–Pg boundary. *Proceedings of the Royal Society B*, **283**, 20160256.

GROSSNICKLE, D. M. and POLLY, P. D. 2013. Mammal disparity decreases during the Cretaceous angiosperm radiation. *Proceedings of the Royal Society B*, **280**, 20132110.

GROSSNICKLE, D. M., SMITH, S. M. and WILSON, G. P. 2019. Untangling the multiple ecological radiations of early mammals. *Trends in Ecology & Evolution*, **34**, 936–949.

GRUNDLER, M. C. and RABOSKY, D. L. 2021. Rapid increase in snake dietary diversity and complexity following the end-Cretaceous mass extinction. *PLoS Biology*, **19**, e3001414.

HALLIDAY, T. J. D., DOS REIS, M., TAMURI, A. U., FERGUSON-GOW, H., YANG, Z. and GOSWAMI, A. 2019. Rapid morphological evolution in placental mammals post-dates the origin of the crown group. *Proceedings of the Royal Society B*, **286**, 20182418.

HSIEH, T. C., MA, K. H. and CHAO, A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology & Evolution*, **7**, 1451–1456.

HSIEH, T. C., MA, K. H. and CHAO, A. 2022. iNEXT: interpolation and extrapolation for species diversity. R package. https://cran.r-project.org/web/packages/iNEXT/index.html

HUNTER, J. P. 1998. Key innovations and the ecology of macroevolution. *Trends in Ecology & Evolution*, **13**, 31–36.

HUNTER, J. P. and JERNVALL, J. 1995. The hypocone as a key innovation in mammalian evolution. *Proceedings of the National Academy of Sciences*, **92**, 10718–10722.

JABLONSKI, D. 1994. Extinctions in the fossil record. *Philosophical Transactions of the Royal Society B*, **344**, 11–17.

JANIS, C. M. and CARRANO, M. 1991. Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? *Annales Zoologici Fennici*, **28**, 201–216.

JERNVALL, J., HUNTER, J. P. and FORTELIUS, M. 1996. Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. *Science*, **274**, 1489–1492.

KLEIN, C. G., PISANI, D., FIELD, D. J., LAKIN, R., WILLS, M. A. and LONGRICH, N. R. 2021. Evolution and dispersal of snakes across the Cretaceous-Paleogene mass extinction. *Nature Communications*, **12**, 5335.

KRAUSSE, D. W., HOFFMANN, S., HU, Y., WIBLE, J. R., ROUGIER, G. W., KIRK, E. C., GROENKE, J. R., ROGERS, R. R., ROSSIE, J. B., SCHULTZ, J. A., EVANS, A. R., VON KOENIGSWALD, W. and RAHANTARISOA, L. J. 2020. Skeleton of a Cretaceous mammal from Madagascar reflects long-term insularity. *Nature*, **581**, 421–427.

LE LOEUFF, J. 2012. Paleobiogeography and biodiversity of Late Maastrichtian dinosaurs: how many dinosaur species went extinction at the Cretaceous-Tertiary boundary? *Bulletin de la Société Géologique de France*, **183**, 547–559.

LEGENDRE, S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of Southern France. *Palaeovertebrata*, **16**, 191–212.

LILLEGRAVEN, J. A., THOMPSON, S. D., McNAB, B. K. and PATTON, J. L. 1987. The origin of eutherian mammals. *Biological Journal of the Linnean Society*, **32**, 281–336.

LIU, L., ZHANG, J., RHEINDT, F. E., LEI, F., QU, Y., WANG, Y., ZHANG, Y., SULLIVAN, C., NIE, W., WANG, J., YANG, F., CHEN, J., EDWARDS, S. V., MENG, J. and WU, S. 2017. Genomic evidence reveals a radiation of placental mammals uninterrupted by the KPg boundary. *Proceedings of the National Academy of Sciences*, **114**, E7282–E7290.

LLOYD, G. T., DAVIS, K. E., PISANI, D., TARVER, J. E., RUTA, M., SAKAMOTO, M., HONE, D. W. E., JENNINGS, R. and BENTON, M. J. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. *Proceedings of the Royal Society B*, **275**, 2483–2490.

LONGRICH, N. R., TOKARYK, T. and FIELD, D. J. 2011. Mass extinction of birds at the Cretaceous–Paleogene (K–Pg)

boundary. *Proceedings of the National Academy of Sciences*, **108**, 15253–15257.

LONGRICH, N. R., BHULLAR, B.-A. S. and GAUTHIER, J. A. 2012. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *Proceedings of the National Academy of Sciences*, **109**, 21396–21401.

LUO, Z.-X. 2007. Transformation and diversification in early mammal evolution. *Nature*, **450**, 1011–1019.

LYONS, S. K., SMITH, F. A. and ERNEST, S. K. M. 2019. Macroecological patterns of mammals across taxonomic, spatial, and temporal scales. *Journal of Mammalogy*, **100**, 1087–1104.

LYSON, T. R., MILLER, I. M., BERCOVICI, A. D., WEISSENBURGER, K., FUENTES, A. J., CLYDE, W. C., HAGADORN, J. W., BUTRIM, M. J., JOHNSON, K. R., FLEMING, R. F., BARCLAY, R. S., MACCRACKEN, S. A., LLOYD, B., WILSON, G. P., KRAUSE, D. W. and CHESTER, S. G. B. 2019. Exceptional continental record of biotic recovery after the Cretaceous–Paleogene mass extinction. *Science*, **366**, 977–983.

MAGALLÓN, S., SÁNCHEZ-REYES, L. L. and GÓMEZ-ACEVEDO, S. L. 2019. Thirty clues to the exceptional diversification of flowering plants. *Annals of Botany*, **123**, 491–503.

MEREDITH, R. W., JANEČKA, J. E., GATESY, J., RYDER, O. A., FISHER, C. A., TEELING, E. C., GOODBLA, A., EIZIRIK, E., SIMÃO, T. L. L., STADLER, T., RABOSKY, D. L., HONEYCUTT, R. L., FLYNN, J. J., INGRAM, C. M., STEINER, C., WILLIAMS, T. L., ROBINSON, T. J., BURK-HERRICK, A., WESTERMAN, M., AYOUB, N. A., SPRINGER, M. S. and MURPHY, W. J. 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science*, **334**, 521–524.

MILLIEN, V. and BOVY, H. 2010. When teeth and bones disagree: body mass estimation of a giant extinct rodent. *Journal of Mammalogy*, **91**, 11–18.

O'GORMAN, E. J. and HONE, D. W. E. 2012. Body size distribution of the dinosaurs. *PLoS One*, **7**, e51925.

O'LEARY, M. A., BLOCH, J. I., FLYNN, J. J., GAUDIN, T. J., GIALLOMBARDO, A., GIANNINI, N. P., GOLDBERG, S. L., KRAATZ, B. P., LUO, Z.-X., MENG, J., NI, X., NOVACEK, M. J., PERINI, F. A., RANDALL, Z. S., ROUGIER, G. W., SARGIS, E. J., SILCOX, M. T., SIMMONS, N. B., SPAULDING, M., VELAZCO, P. M., WEKSLER, M., WIBLE, J. R. and CIRRANELLO, A. L. 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science*, **339**, 662–667.

OSBORN, H. F. 1902. The law of adaptive radiation. *American Naturalist*, **36**, 353–363.

OSBORN, H. F. 1910. *The age of mammals in Europe, Asia and North America*. Macmillan.

PAINE, R. T. 1966. Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org

RAUP, D. M. and SEPKOSKI, J. J. 1982. Mass extinctions in the marine fossil record. *Science*, **215**, 1501–1503.

ROELANTS, K., GOWER, D. J., WILKINSON, M., LOADER, S. P., BIJU, S. D., GUILLAUME, K., MORIAU, L. and BOSSUYT, F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences*, **104**, 887–892.

ROMER, A. S. 1956. The early evolution of land vertebrates. *Proceedings of the American Philosophical Society*, **100**, 157–167.

ROSE, K. D. and ARCHIBALD, J. D. (eds) 2005. *The rise of placental mammals*. Johns Hopkins University Press.

RYBERG, W. A., SMITH, K. G. and CHASE, J. M. 2012. Predators alter the scaling of diversity in prey metacommunities. *Oikos*, **121**, 1995–2000.

SAARINEN, J. J., BOYER, A. G., BROWN, J. H., COSTA, D. P., ERNEST, S. K. M., EVANS, A. R., FORTELIUS, M., GITTLEMAN, J. L., HAMILTON, M. J., HARDING, L. E., LINTULAAKSO, K., LYONS, S. K., OKIE, J. G., SIBLY, R. M., STEPHENS, P. R., THEODOR, J., UHEN, M. D. and SMITH, F. A. 2014. Patterns of maximum body size evolution in Cenozoic land mammals: ecoevolutionary processes and abiotic forcing. *Proceedings of the Royal Society B*, **281**, 20132049.

SCHLUTER, D. 2000. *The ecology of adaptive radiation*. Oxford University Press.

SCHOENER, T. W., SPILLER, D. A. and LOSOS, J. B. 2001. Predators increase the risk of catastrophic extinction of prey populations. *Nature*, **412**, 183–186.

SCHROEDER, K., LYONS, S. K. and SMITH, F. A. 2021. The influence of juvenile dinosaurs on community structure and diversity. *Science*, **371**, 941–944.

SIMPSON, G. G. 1937. The beginning of the age of mammals. *Biological Reviews*, **12**, 1–46.

SIMPSON, G. G. 1953. *The major features of evolution*. Columbia University Press.

SIMPSON, E. L., HILBERT-WOLF, H. L., WIZEVICH, M. C., TINDALL, S. E., FASINSKI, B. R., STORM, L. P. and NEEDLE, M. D. 2010. Predatory digging behavior by dinosaurs. *Geology*, **38**, 699–702.

SLATER, G. J. 2013. Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary. *Methods in Ecology & Evolution*, **4**, 734–744.

SMITH, F. A., BOYER, A. G., BROWN, J. H., COSTA, D. P., DAYAN, T., ERNEST, S. K. M., EVANS, A. R., FORTELIUS, M., GITTLEMAN, J. L., HAMILTON, M. J., HARDING, L. E., LINTULAAKSO, K., LYONS, S. K., McCAIN, C., OKIE, J. G., SAARINEN, J. J., SIBLY, R. M., STEPHENS, P. R., THEODOR, J. and UHEN, M. D. 2010. The evolution of maximum body size of terrestrial mammals. *Science*, **330**, 1216–1219.

STANLEY, S. M. 1973. An explanation for Cope's Rule. *Evolution*, **27**, 1–26.

STROUD, J. T. and LOSOS, J. B. 2016. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, & Systematics*, **47**, 507–532.

VARRICCHIO, D. J. 2011. A distinct dinosaur life history? *Historical Biology*, **23**, 91–107.

VARRICCHIO, D. J., HOGAN, J. D. and FREIMUTH, W. J. 2021. Revisiting Russell's troodontid: autecology, physiology, and speculative tool use. *Canadian Journal of Earth Sciences*, **58**, 1–16.

WANG, M., LLOYD, G. T., ZHANG, C. and ZHOU, Z. 2021. The patterns and modes of the evolution of disparity in Mesozoic birds. *Proceedings of the Royal Society B*, **288**, 20203105.

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

WILSON, G. P., EVANS, A. R., CORFE, I. J., SMITS, P. D., FORTELIUS, M. and JERNVALL, J. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. *Nature*, **483**, 457–460.

WILSON, G. P., EKDALE, E. G., HOGANSON, J. W., CALEDE, J. J. and LINDON, A. V. 2016. A large carnivorous mammal from the Late Cretaceous and the North American origin of marsupials. *Nature Communications*, **7**, 13734.

WINGS, S. L. and BOUCHER, L. D. 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth & Planetary Sciences*, **26**, 379–421.

YODER, J. B., CLANCEY, E., DES ROCHES, S., EASTMAN, J. M., GENTRY, L., GODSOE, W., HAGEY, T. J., JOCHIMSEN, D., OSWALD, B. P., ROBERTSON, J., SARVER, B. A. J., SCHENK, J. J., SPEAR, S. F. and HARMON, L. J. 2010. Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology*, **2**, 1581–1596.