Continuous evolutionary change in Plio-Pleistocene mammals of eastern Africa

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Much debate has revolved around the question of whether the mode of evolutionary and ecological turnover in the fossil record of African mammals was continuous or pulsed, and the degree to which faunal turnover tracked changes in global climate. Here, we assembled and analyzed large specimen databases of the fossil record of eastern African Bovidae (antelopes) and Turkana Basin large mammals. Our results indicate that speciation and extinction proceeded continuously throughout the Pliocene and Pleistocene, as did increases in the relative abundance of arid-adapted bovids, and in bovid body mass. Species durations were similar among clades with different ecological attributes. Occupancy patterns were unimodal, with long and nearly symmetrical origination and extinction phases. A single origination pulse may be present at 2.0–1.75 Ma, but besides this, there is no evidence that evolutionary or ecological changes in the eastern African record tracked rapid, 100,000-y-scale changes in global climate. Rather, eastern African large mammal evolution tracked global or regional climatic trends at long (million year) time scales, while local, basin-scale changes (e.g., tectonic or hydrographic) and biotic interactions ruled at shorter timescales.

turnover | Plio-Pleistocene | mammals | Bovidae | Africa

Modern faunal communities are the products of millions of years of evolutionary and ecological turnover, shaped by species origination, extinction, and migration. The primary driver of turnover at geological time scales is generally taken to be physical environmental change, but the importance of biotic interactions in modulating turnover is increasingly evident (1–5). Related to this has been a debate on whether faunal turnover is continuous or pulsed in mode. Building on Mayr's (6) allopatric speciation model, and Eldredge and Gould's (7) hypothesis of punctuated equilibrium, Vrba (8–11) proposed the turnover pulse hypothesis, which predicts that most faunal turnover is concentrated in pulses that are correlated with rapid environmental changes (see ref. 1 for a review of similar ideas). Outside of mass extinctions (these may be seen as extreme but uncommon turnover pulse events), several studies have found support for the turnover pulse hypothesis as a dominant mode of turnover (12–14). Other studies—including many of the African record—have concluded that the dominant mode of turnover was continuous, with limited or no evidence for turnover pulses (15–20). Some of these studies argued for an important role for biotic interactions (e.g., competition, predation) in shaping the often unpredictable responses of faunal communities to environmental change. More-direct evidence for the long-term influence of biotic interactions on turnover in the fossil record has been presented in the form of constant extinction likelihoods (21, 22) and symmetric wax−wane occupancy curves at several taxonomic levels (23–26). These findings suggest that biotic interactions can strongly determine the outcomes of the turnover process, even if physical environmental changes are important in initiating turnover under the allopatric speciation model (8, 10).

We here revisit the tempo and mode of evolutionary and ecological change in the eastern African Plio-Pleistocene large-mammal fossil record using updated data and approaches.

Eastern Africa (here including Eritrea, Ethiopia, Kenya, Tanzania, and Uganda) today encompasses primarily a single vegetational zone [Somalia-Masai (27)], and constitutes a reasonable subcontinental scale at which to examine turnover (1). We examine the fossil record for the occurrence of pulsed evolutionary events (here large-scale and rapid changes in turnover rates, relative abundances, or body size) based on expectations from changes in global climate. In particular, there are two temporal intervals during which elevated mammalian speciation rates have been reported in close timing with major global climatic changes, at 3–2.5 Ma (28, 29) and 2–1.5 Ma (reviewed in ref. 30). The first putative peak coincides with rapid global cooling and African aridification, and the second coincides with the inception of Walker Circulation above the Pacific (28–32). Further attention is drawn to these temporal windows given major developments in the hominid clade, including the appearance of *Homo*, *Paranthropus*, and Oldowan stone tools during the first, and the development of Achulean technology and the dispersal of *Homo erectus* from Africa in the second (30, 33).

We compiled and analyzed updated fossil specimen datasets of eastern African bovids (antelopes and relatives) and of Turkana Basin large mammals (see *SI Text* for full details). Older datasets have been used to investigate modes of turnover in African mammals, with often contradictory results (17, 29).

Turnover in Eastern African Plio-Pleistocene Mammals

Although we included sites from late Miocene to Holocene age in our data compilation, we focus our turnover analyses on the period between 3.75 Ma and 1.25 Ma (late Pliocene−early Pleistocene) because sample sizes and sampling completeness are too poor outside this interval and edge effects become prevalent when including older and younger bins (see *SI Text* and Figs. S1 and S2). In both the bovid and Turkana datasets, we find that speciation

Significance

Many have argued that major developments in mammalian (including human) evolution were timed with large and sudden changes to Earth's climate. Our new analyses of the eastern African Plio-Pleistocene mammalian fossil record indicate that most species originations and extinctions took place continuously and gradually. This means that evolution was not clustered in short intervals, nor were sudden global climatic changes the main cause of species extinction in the past. Global climate may have influenced longer-term (million year) evolutionary trends, but local environmental changes and species interactions were more important at shorter (100,000 y) time scales.

and extinction rates were highly variable through time (Fig. 1). We used 250-ka time bins, but results for 100-, 300-, and 500-ka bins are similar (Fig. S3). Elevated turnover rates are recorded at 3.25–2.75 Ma in the bovid data, and at 2.0–1.75 Ma in both the bovid and Turkana data. Only the origination peak in the Turkana data at 2.0–1.75 Ma is of statistically significant magnitude (more than 1.5 times outside the interquartile range). Two-timer counts (34) provide similar results, and subsampled species richness also indicates increases at 2.0–1.75 Ma in both datasets (Figs. S1 and S2).

Vrba (29) found evidence for statistically significant origination (and possibly extinction) pulses at 3.6 Ma, 2.7–2.5 Ma, and 1.8 Ma. A highly discontinuous fossil record before 3.75 Ma means we are unable to properly assess the record older than 3.5 Ma. However, we find no evidence for origination or extinction pulses anytime between 3.0 Ma and 2.5 Ma. Two main differences between our study and Vrba's are the exclusion of the North and South African records and the exclusion of single-interval species in our study. The North and South African records are sparse but include a large number of sites dated between 3 Ma and 2.5 Ma (29), potentially inflating turnover counts at this time. Additionally, Vrba's (29) original first appearance datum (FAD) pulse at 2.7–2.5 Ma included a large number of single-interval species (also found here; Fig. S1). Vrba (35) argued that single-interval taxa are important because environmental perturbations are expected to produce a large number of rare and short-lived species. However, simulations show that single-interval taxa are especially sensitive to preservational biases and lead to spurious correlations between origination and extinction rates (16, 36). No similar peak in single-interval taxa is seen in the Turkana Basin large-mammal record (Fig. S2; see also refs. 17, 37), nor in range compilations that retain singletons such as for suids (15, 38), carnivores (19, 39), or cercopithecids (20). This suggests that the single-interval taxon peak at 2.75–2.5 Ma, if real, is restricted to the bovid fossil record.

Subsampled species richness is also more or less stable at 3.25–2.0 Ma in both the bovid and Turkana datasets (Figs. S1 and S2). Global cooling and drying between 3 Ma and 2.5 Ma may have promoted the development of more open habitats and associated faunal communities (28, 33, 37, 40, 41), but our results indicate that such evolutionary and ecological changes took place gradually and without significant increases in turnover rates (42). This would fit with paleoclimate reconstructions indicating that global cooling and the end of the Pliocene warm period were not confined to between 3 Ma and 2.5 Ma but rather occurred gradually over a protracted time between about 4 Ma and 1.5 Ma (31).

The origination peak recovered here at 2.0–1.75 Ma does match Vrba's 1.8 Ma pulse. Elevated origination rates and associated increases in sampling-standardized species richness shortly after 2 Ma (cf. refs. 43 and 44) coincide with the expansion of C_4 grasslands as recorded in Turkana paleosol isotopes (45), Gulf of Aden pollen and plant biomarker records (40, 46), greater regional aridity through increased wind-borne dust in the Arabian Sea (32), and increases in open habitat faunal communities in both eastern and southern Africa around this time (47). These environmental and faunal changes may be related to the development of Walker Circulation above the Pacific Ocean around 1.9 Ma and resulting precipitation decreases over eastern Africa (31, 46, 48). Alternately, the origination pulse at 2.0–1.75 Ma may be an artifact of the record, because very few sites are known from the preceding interval, and the eastern African 2.5–2.0 Ma record is almost entirely dominated by the Shungura Formation. Removal of the Shungura Formation sharply reduces the origination pulse in the eastern African bovid data, but not the Turkana large mammals, suggesting the pulse may be even less prominent outside the Turkana Basin (Figs. S1 and S2). Further testing will require the improvement of the 2.5–1.5 Ma fossil record from outside the Turkana Basin (e.g., in the Afar).

Besides a possible origination pulse at 2.0–1.75 Ma, we find that most faunal change in the late Pliocene and early Pleistocene took place under variable turnover without unequivocal pulses. Although differing in taxonomic scope and geographic scale, the bovid and Turkana large-mammal datasets provide very similar results, and these furthermore match those of numerous studies cited above. All these studies, however, are heavily dependent on the Turkana Basin record, and further fossil data outside this basin is needed to be more certain that the pattern seen reflects a regional (if not continental) scale.

Species Duration and Occupancy Patterns

We examined whether the probability of extinction, measured through mean species durations (or residence times), varied among clades of varying ecological attributes. In particular, mammalian resource-use specialists, i.e., species dependent on a narrow range of environments (8, 49, 50), and herbivores (51) have been shown to have higher diversification rates than resource-use generalists and carnivores, respectively. Specialists and herbivores might therefore be expected to have shorter species durations if their ecological requirements left them more susceptible to abrupt environmental changes.

We find mean species duration of 1.4 ± 0.9 my (median = 1.2 My) for both eastern African bovids and Turkana Basin large mammals (Fig. 2). This is similar to the 1.3-My mean species duration of Neogene African large mammals (52) and the 1.5-My median species duration for North American Cenozoic mammals (16). Pairwise comparisons indicate that species durations are statistically indistinguishable among aepycerotin, alcelaphin, bovin, reduncin, and tragelaphin bovids (pairwise Wilcoxon, $P > 0.1$). Among Turkana large mammal families, species durations are statistically indistinguishable among bovids, cercopithecids, equids, felids, hyaenids, suids, and hippopotamids ($P > 0.09$). This
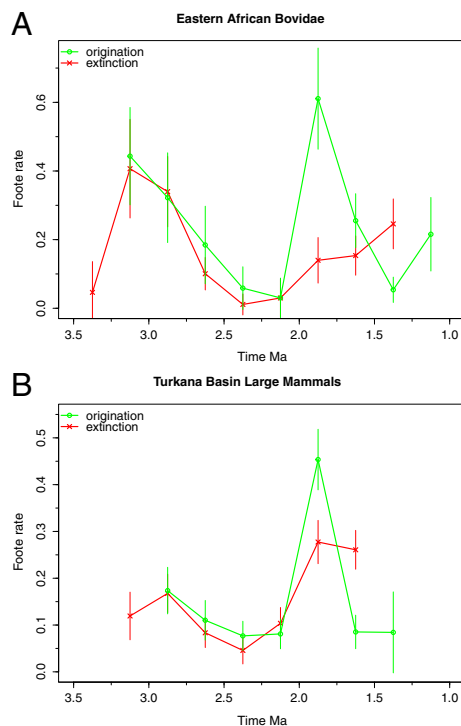
Fig. 1. Sampling-standardized origination and extinction rates in (A) eastern African Bovidae and (B) Turkana Basin large mammals. Older origination and younger extinction rates are increased by edge effects, and the oldest and youngest points, respectively, are omitted. Elevated turnover is recorded at 3.25–3.0 Ma (bovids) and 2.0–1.75 Ma (both). Turnover is low between 3 Ma and 2 Ma. (Error bars, 1 SD of 100 subsampling trials in each direction.)
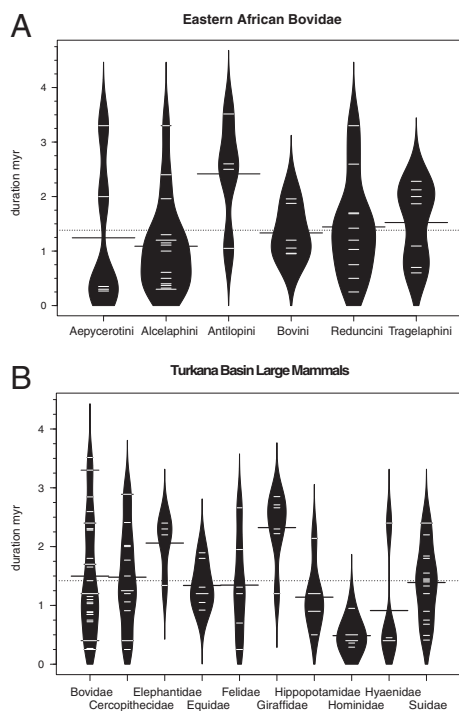
Fig. 2. Beanplots of species durations, arranged by tribe for eastern African bovid species (*A*) and by family for Turkana Basin large mammals (*B*). Durations among most bovid tribes and most Turkana families are statistically indistinguishable. Black lines indicate means for each clade, and dotted lines indicate the mean for the whole plot.

implies that similar probabilities of species persistence and extinction apply across large mammal communities, regardless of habitat (woodland vs. grassland) or dietary (herbivory vs. carnivory) preferences, and fits expectations for continuous turnover in interconnected biotic networks (e.g., food webs).

Significantly ($P < 0.05$) longer species durations were found for antilopins, elephantids, and giraffids and shorter durations in hominids, but these signals are likely to be artifacts of taxonomic practices rather than true biological differences. In particular, hominid species are highly susceptible to taxonomic splitting (53), especially in the current dataset. The inverse is probably true of antilopins, giraffids, and elephantids, which are rare and/or not well studied in the current datasets.

Additionally, we examined species occupancy, the number of sites at which a fossil species is recorded over its duration (e.g., Hadar, Omo, Kanapoi, Laetoli; see *SI Text*). Under continuous origination and extinction, species occupancy should show roughly symmetrical increase and decline phases (24–26, 54, 55). Pulsed extinction dynamics would be expected to produce asymmetrical patterns, with rapid truncations of species increase, equilibrial, or decline phases (25).

The occupancy trajectories we calculated (Fig. 3) show that, on average, species display a unimodal wax-and-wane pattern with long growth and decline phases, and no signs of long-term equilibrium or stasis (bovids do not differ from normal, Shapiro−Wilk test $P = 0.23$, but Turkana data do, $P = 0.046$). The decline phase is slightly longer than the growth phase, as also found for marine microfossils (55). Vrba and DeGusta (56) showed that newly originating African mammal species gradually increased their occupancy (over about 1 Ma), but they did not examine the mode of species decline. Our findings establish the presence of unimodal occupancy curves with long and gradual origination and extinction phases. Even a model in which the initiating causes of origination and extinction require physical environmental change (8, 10, 28)

would then have to allow for turnover under conditions of incremental and continuous (background-level) landscape change. Most turnover in the eastern African Plio-Pleistocene would have occurred at these background rates. Such wax–wane patterns also implicate biotic interactions in generating diversity-dependent turnover (23–25). Combining biotic interactions with continuous landscape change provides a powerful mechanism for species turnover, because even small environmental changes could have profound ecological consequences when amplified through food webs (57).

Relative Abundance of Arid-Adapted Bovids

In modern African ecosystems, the relative abundances of monophyletic bovid tribes vary according to habitat (58), reflecting primary climatic variables such as temperature and precipitation (59). In particular, the relative abundance of specimens of Alcelaphini plus Antilopini (AA) among all bovids serves as a relative measure of aridity or open habitats at African fossil sites (58, 60). Vrba found that the proportions of AA bovids in the African record increased significantly after ~2.5 Ma, signaling a shift to more arid and open conditions (28, 58, 61). Later studies indicated that this trend extended to between 3.5 Ma and 1 Ma, with changes at different times in different areas (44, 47, 62).

An expanded compilation of AA data (Fig. 4) indicates a significant long-term increase across eastern Africa since at least the late Miocene ($P < 0.001$). When broken down by site, the trend is significant in the Omo ($P = 0.01$), West Turkana ($P = 0.002$), and southern Kenya and northern Tanzania ($P = 0.02$). Except perhaps for the Afar, there is no evidence for a pulsed increase in AA associated with rapid global cooling between 3 Ma and 2.5 Ma. Rather, increases in AA bovids are part of a long-term trend that may be correlated with global or regional climatic changes such as
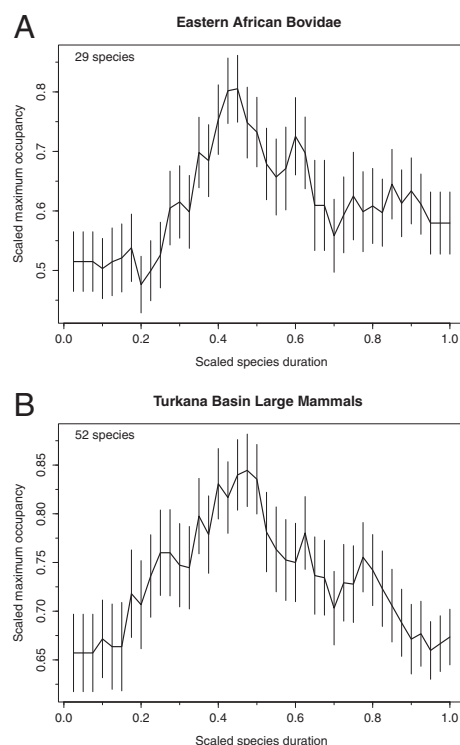
Fig. 3. Geographic occupancy curves of extinct species scaled from origination (0) to extinction (1) for (*A*) bovids and (*B*) Turkana Basin large mammals. Occupancy was measured as the proportion of sites where a species has been encountered and is scaled to the maximum occupancy for each species. (Error bars, 1 SD in each direction for 1,000 bootstrap replicates.)
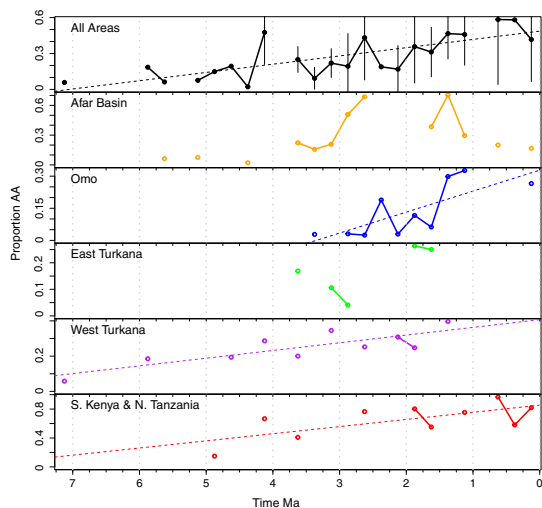
Fig. 4. Relative abundance of AA among eastern African areas and for time bins with at least 40 specimens identified to bovid tribe. Significant ($P < 0.05$) long-term increasing trends are shown by regression lines.

decreasing mean global temperatures (63) or regional drying through continental uplift/rifting (64) since the late Miocene. Differences in the rate and directionality of change in AA from one area to another, however, implicate local environmental factors (e.g., tectonic–hydrological) in modulating the timing and rate of local landscape change at any point in time (65, 66). Additionally, a consistently higher proportion of AA in southern Kenyan and northern Tanzanian sites reflects a long-term lack of perennial water sources there (e.g., ref. 67), as opposed to the more stable Omo and Awash rivers to the north. The same might be said of the predominantly karstic South African record as well, where greater than 50% of the bovid assemblages at sites like Langebaanweg (~5 Ma) and Sterkfontein (2.5 Ma) are made up of alcelaphins and antilopins (60, 68, 69). The most interesting AA record comes from the Afar Basin. In contrast to all other areas, there is a rapid increase between 3 Ma and 2.5 Ma that is followed by a reversal to lower values (better watered habitats) in the early and mid Pleistocene. In the Afar Basin at least, local hydrological changes appear to have been more important than global climate in modulating the timing and rate of local landscape change (65).

Changes in Bovid Body Mass

Citing Bergmann's Rule, Vrba (29, 70, 71) proposed that a significant number of large-bodied bovid species appeared in Africa between 3 Ma and 2.5 Ma in response to pronounced global cooling. We find that the mean body mass of eastern African Plio-Pleistocene bovid species increased gradually through time ($P = 0.048$) but with large scatter (Fig. 5). Comparisons of median body size across a moving breakpoint indicates that species originating earlier than 3.75 Ma, 3.5 Ma, 3.25 Ma, or 3.0 Ma are significantly ($P < 0.05$) smaller than those appearing later, but the comparison is no longer significant at or after 2.75 Ma (up to 1.25 Ma, $P > 0.05$). Therefore, whereas our methods differ from those of Vrba (71) and do not consider within-species increases, we do not see a disproportionate number of first appearances of large-bodied bovid species between 3 Ma and 2.5 Ma.

Furthermore, when broken down by tribe, only Reduncini show an increasing trend ($P < 0.01$, $R = 0.15$). Removal of Reduncini removes the trend for all bovids as well. Large body size confers dietary, not to mention defensive, advantages to open grassland ungulates (72), so one might have expected Plio-Pleistocene increases in body size to have been greatest among inhabitants of open grasslands (e.g., Alcelaphini, Antilopini).

Observed increases were therefore lineage specific, were not determined by the expansion of open habitats or rapid global temperature changes, and are probably indistinguishable from broader phenomena grouped under Cope's Rule, which has many possible explanations (e.g., ref. 73).

Conclusions

We originally set out to test whether faunal change in eastern Africa was pulsed and timed with major global climate change events. Instead, our results show that species turnover was mainly continuous. The only exception may be an origination pulse shortly after 2.0 Ma (29), which might be associated with the inception of Walker Circulation above the southern Pacific (30, 31). This should be further tested through the recovery of more fossil assemblages in the 2.5–1.5 Ma interval, particularly from outside the Turkana Basin.

In the paleontological record, continuous turnover, consistent species durations, and nearly symmetrical wax–wane patterns of geographic occupancy most likely reflect a continuum of physical and biotic processes acting at multiple scales (1, 5, 55). The initiation of turnover might always require changes in the physical environment (10), but it seems that continuous (background-level) environmental changes may have been sufficient for this. Physical changes probably acted through biotic networks, and even small changes to a taxon's physical environment may have been amplified or attenuated through the responses of the other species around it (4, 5). The Rift Valley is a tectonically dynamic environment, and this serves to produce a diverse patchwork of habitats within close proximity. From the point of view of the Red Queen's hypothesis, which predicts the constant deterioration of an organism's effective environment (21), environmental dynamics within the African Rift should promote constant taxonomic shifts, and increase the potential for population fragmentation leading to allopatric or peripatric speciation.

We conclude that global climate drove large mammal evolution at the million-year timescale, whereas local environmental changes and biotic interactions ruled at 100-ka and smaller scales. Much work during the last decades has (rightly) focused on the initiating role of physical drivers on the evolution of African mammals. As the fossil record continues to improve in both taxonomic and chronological resolution, the modulating role of biotic drivers should be increasingly investigated and integrated into the broader picture of community turnover.
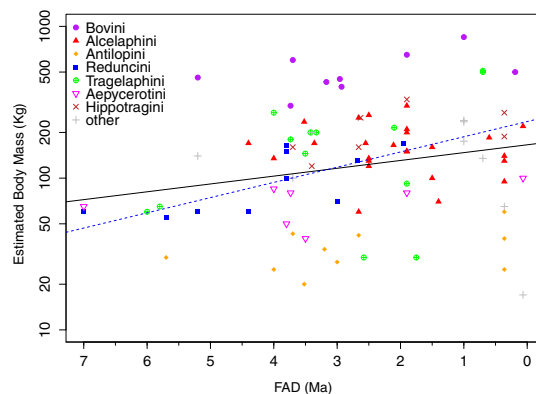
Fig. 5. Estimated body mass of extinct eastern African bovid species, plotted by FAD. There is a significant trend to body size increase when all bovids are considered together (black solid line). By tribe, only Reduncini (blue dashed line) show a significant (increasing) trend. Note log scale of y axis.

Materials and Methods

The eastern African bovid and Turkana Basin large-mammal specimen databases were assembled from numerous sources, with the largest contributions from the Turkana Public Database (74), the International Omo Research Expedition and Omo Group Research Expedition databases (both courtesy of J.-R. Boisserie), and Middle Awash (courtesy of T. White), and data from the literature (e.g., Hadar, Laetoli, Olduvai; see *SI Text*), with many updates based on specimen study by F.B. In total, these comprise 134 bovid species (77 non-single-interval taxa) (Dataset S1) and 172 Turkana large mammal species (130 nonsingletons) (Dataset S2). Turnover analyses used repeated specimen-based subsampling (rarefaction) and equal-coverage shareholder quorum methods (76) to standardize sample sizes among time bins. Calculations of turnover rates followed Foote (36), and those of two-timer and shareholder quorum counts followed Alroy (34, 75, 76). Calculation of species occupancy followed Foote (54). Each species

duration was rescaled to 0 (origin) and 1 (extinction) and binned into 40 intervals of equal duration. Occupancy was measured as the proportion of fossiliferous sites in which the species was encountered and also scaled between 0 (minimum occupancy) and 1 (maximum). Species durations and AA counts were calculated on raw data. Body mass estimates were made using molar tooth length regressions of Damuth (77) and Janis (78) with measurement data from the literature or taken by F.B. Full methods are provided in *SI Text*.

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