

PALEONTOLOGY

The end-Cretaceous mass extinction restructured functional diversity but failed to configure the modern marine biota

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The end-Cretaceous (K-Pg) mass extinction shows how large-scale taxonomic loss affects functional diversity over short and long timeframes. In a macroevolutionary model system, we find that, despite losing ~60% of genera and ~20% of family-level diversity, marine bivalves lost only ~5% of their functional diversity, inconsistent with random extinction. Even with evolutionary opportunities presented by a disrupted ecosystem, low-diversity groups prior to the extinction or those originating in the Cenozoic rarely reach higher ranks today, implying long-term diversity ceilings to certain ecological roles. Clades that survived the extinction tend to dominate functions today, 66 million years post-extinction, but both relative richness and phylogenetic structure of those functional groups have been significantly shuffled. Thus, neither the composition of the pre-extinction biota nor the set of taxa that survived the extinction fully accounts for the functional and phylogenetic structure of today's biota. The extinction disrupted Mesozoic biodiversity but did not fully determine the present-day configuration.

INTRODUCTION

Biodiversity has been subject to severe global stresses throughout Earth's history. The numbers of taxa and their phylogenetic relationships, morphologies, and functional ecologies show complex and varied patterns of loss and rebound from these global perturbations (1–5). Here, we analyze the most recent mass extinction, the end-Cretaceous or Cretaceous-Paleogene (K-Pg) event ~66 Ma, as a natural experiment on how taxonomic loss affected the global configuration of functional diversity over short and long timeframes. Although many marine functional groups survived the K-Pg event despite severe taxonomic losses [as in other Big Five mass extinctions (6–10)], we find that the structure of bivalve functional diversity and its phylogenetic underpinnings were strongly altered. Nevertheless, although mass extinctions are generally viewed as key events resetting taxonomic and ecological composition, the structural shifts at the K-Pg are insufficient to account fully for the configuration of the Recent biota.

Bivalves are one of the most diverse animal groups in past and present oceans and have become a model system for macroevolutionary analyses. Many of the 7000+ species play key roles in ecosystem function across all depths and latitudes (11), occupying a wide range of trophic groups from suspension feeding through chemo- and photosymbiosis to parasitism and carnivory (12). These functional ecologies are largely well understood today and through the geologic past because shell morphology in its phylogenetic context is highly informative on modes of life (13–15). Bivalve family-level phylogeny is increasingly well supported by molecular data at the family level (16–18), and morphologically defined genera significantly capture the macroecological features of corresponding molecular clades (19). These attributes allow multidimensional analyses of their biodiversity throughout an exceptionally rich fossil record, which

provides robust estimates of origination, extinction, and standing diversity through time (20, 21). Furthermore, many major bivalve clades and ecological functions present in today's oceans evolved prior to the end-Cretaceous event, allowing us to analyze not only potential origins and losses but also the expansion and contraction of functional groups with respect to taxonomic and phylogenetic diversity.

Here, we analyze changes in taxonomic and phylogenetic structure within functional groups and shifts in genus richness among them, testing the extent to which the K-Pg event redirected the trajectory of functional evolution. We use a comprehensive database of 438 marine bivalve genera (82 families) occurring in the latest Cretaceous, 172 genera (64 families) that survived the end-Cretaceous event, and 1349 Recent genera (85 families), drawn from a compendium of first and last stratigraphic occurrences based on the primary literature; each genus was assigned to a functional group defined on four traits: feeding, position relative to substratum surface, attachment, and mobility [as in (9); developed following categorical approaches in refs. (22, 23)]. This framework captures approximate ecological equivalencies among distantly related taxa and can thus detect stability, shifts, and expansions in ecological attributes at macroevolutionary scales for disparate biological systems [e.g., bivalves and birds (9, 12)]. To assess the role of the end-Cretaceous mass extinction in shaping present day biodiversity, we compare the distribution of taxa among functional groups in three sets of taxa: (i) the “end-Cretaceous biota”—genera occurring within the Maastrichtian age of the Late Cretaceous epoch (72.2 to 66.0 Ma); (ii) the “survivor pool”—genera known to survive the Cretaceous-Paleogene mass extinction (K-Pg, or end-Cretaceous event) into the Cenozoic; and (iii) the “Recent biota”—genera occurring in today's oceans.

RESULTS AND DISCUSSION

Biodiversity loss across the K-Pg mass extinction

Despite losing 61% of their genera (266 of 438) and 22% of their families (18 of 82) through the end-Cretaceous extinction, marine bivalves lost only 5% of their functional groups (2 of 37; Fig. 1, A and B). Both of those functional groups involve photosymbiosis, a

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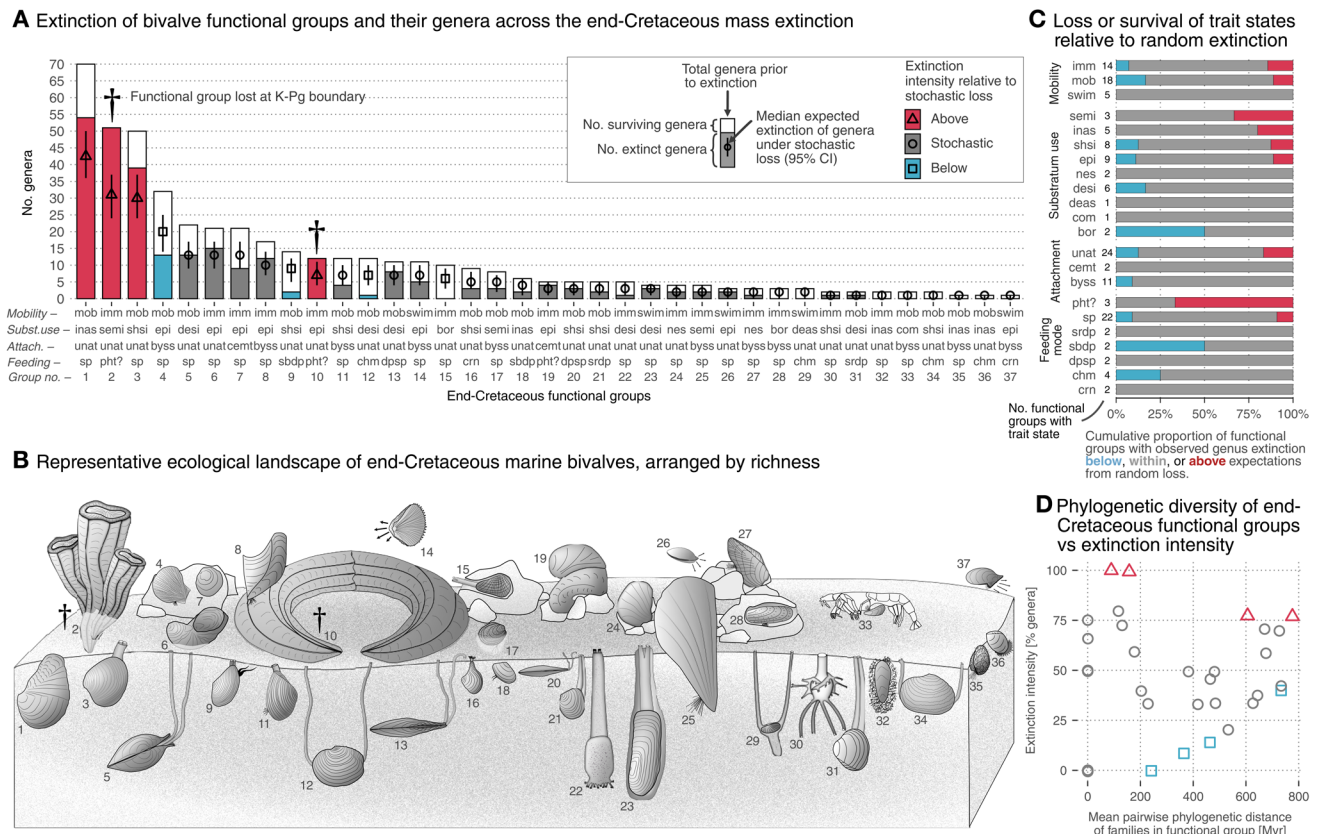


Fig. 1. Extinction dynamics of marine bivalve functional groups across the end-Cretaceous mass extinction (~66 Ma). (A) Observed extinction intensity of genera within functional groups compared to random loss. CI, confidence interval. (B) Representative members of end-Cretaceous functional groups in life position, arranged by rank of genus richness in (A). Illustrations are not to scale but do reflect general differences in the sizes of taxa. Abbreviations for functional states: Mobility—imm, immobile; mob, mobile; swim, swimming; Substratum use—bor, borer; com, commensal; deas, deep infaunal asiphonate; desi, deep infaunal siphonate; epi, epifaunal; inas, infaunal asiphonate; nes, nestler; semi, semi-infaunal; shsi, shallow infaunal siphonate; Attachment—byss, byssate; cemt, cemented; unat, unattached; Feeding mode—chm, chemosymbiotic; crn, carnivore; dsp, mixed deposit/suspension; pht, photosymbiotic; sbdep, subsurface deposit; srdep, surface deposit; sp, suspension. †, extinct functional group. “Group numbers” are unique to a functional group and shared across all figures. (C) Association of functional trait states with the extinction intensity of genera in functional groups. For example, three functional groups include the semi-infaunal state, and one of those groups (i.e., 33% of the total) had higher than expected genus extinction compared to random loss. (D) Phylogenetic diversity of functional groups prior to the K-Pg event compared to their extinction intensity of genera. Symbols and colors show the observed extinction intensity in a functional group relative to random loss as in (A).

debated view (24–28); if the clade occupying those functions (the rudists, order Hippuritida, and the related Megalodontida) is treated as suspension feeding (26, 28), then only one functional group was lost—strengthening the discordance between taxonomic and functional extinction. Our data allow us to exclude three obvious mechanisms for this discordance and the differential loss of genera among the functional groups.

Random genus loss?

Random genus extinction cannot account for the survival of all but two functional groups through the end-Cretaceous event. Ninety-six percent of random-extinction simulations removed three or more functional groups, almost always drawn from the tail of the richness-frequency distribution (Fig. 1A and fig. S1). Thus, the persistence of low-diversity functional groups and the apparent focus of extinction in the richer ones are strong evidence against a simple by-product of random loss among genera.

Functional buffering?

Relative to random loss, few trait states were evidently tied to the elevated or muted extinction of genera within functional groups

(Fig. 1C). Low-diversity groups (defined as ≤10 genera in the end-Cretaceous biota) all survived and were spread among different trophic, mobility, and substratum-use categories, as were the most heavily depleted groups (Fig. 1, A and C). The groups inferred to be photosymbiotic are the strongest exception, where all but one genus was lost and two of the three photosymbiotic groups were lost entirely (Fig. 1C). Excess loss among putatively photosymbiotic functional groups is a common syndrome among mass extinction events across the animal kingdom (5, 29–31), perhaps owing to the narrow range of environmental settings favoring this mode of life (5). Suspension feeding bivalve groups suffered some of the highest losses of genera, in absolute terms. This would be consistent with the diversity-dependent model in ref. (9), in which the extinction-driver intensified intraguild competition owing to diminished resources, thereby permitting the persistence of just a few taxa within each group. However, extinction intensities of genera within suspension feeding groups did not exceed the random expectation, and even the genus-poor suspension feeding groups survived. Furthermore, feeding modes not directly tied to solar radiation—chemosymbioses, carnivory,

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and deposit feeding, long held as buffers to the K-Pg extinction (32)—neither universally enhanced survivorship of genera with those functions nor acted as a liability (Fig. 1C) [ref. (33) revising ref. (34); see also refs. (35–38)]. This lack of clear selectivity patterns among feeding groups at the global scale argues against the collapse of primary production as the principal extinction mechanism. Some—but not all—local sites report substantial shifts in taxonomic and functional compositions of communities (and their habitats) across the extinction boundary (10, 39–41), so that the net persistence of functions likely emerges from a mixture of local pressures and the global disruption. The failure of ecological traits to robustly predict overall extinction patterns, as in many other biological systems across other extinction events, suggests that additional, as yet unidentified, factors were involved in survivorship patterns, e.g., geographic range sizes or physiologies of constituent taxa (9, 42, 43).

Persistence via phylogenetic diversity?

High phylogenetic diversity within functional groups might have promoted their persistence via disparity of morphology, physiology, and other attributes inherited along separate phylogenetic lines. However, when analyzed across the entire functional landscape, functional groups with the highest extinction intensities ranged from monophyletic to highly polyphyletic and thus nearly spanned the observed range of phylogenetic diversities (calculated by the mean pairwise phylogenetic distance of families in a functional group; Fig. 1D). Two of the four groups with extinction exceeding random expectations had among the highest phylogenetic diversities; the other two groups did have low phylogenetic diversity (falling within the clade formed by rudists and their relatives,

which were driven entirely extinct), but 13 functional groups with even lower phylogenetic diversity survived. The loss of the entire rudist clade and its unique functions may have entailed mutually reinforcing factors (44): low phylogenetic diversity plus narrow geographic and/or environmental ranges (9, 45). Thus, high phylogenetic diversity did not guarantee survival, and low values were not necessarily a liability (Fig. 1D).

Contrasting structures between survivors and Recent biota

Functional restructuring

The mass extinction flattened the distribution of genera among functional groups in the survivor pool, i.e., the genera known to cross the K-Pg boundary regardless of their presence in the earliest Paleogene time interval (Fig. 2). With at least 95% of functional groups surviving and all but one persisting to the present day, the null expectation is that the post-extinction biota should ultimately converge on an ecological structure similar to the latest Cretaceous, the “recovery” model of ref. (5). However, although genera are again distributed unevenly among today’s functional groups, the identities of the richest and poorest groups have changed (Fig. 2). This shift cannot be attributed simply to taphonomic distortion of the Maastrichtian record because the richness rankings of each group are unrelated to the preservation potential of their constituent genera (fig. S2). Analyses that exclude genera in the Recent biota that lack a known fossil record also do not qualitatively change the results (see Supplementary Text and fig. S3). Thus, the rank order of the high-diversity functional groups in the end-Cretaceous biota (richest 50%) has been scrambled, as in the “rebound” model of ref. (5), although the low-

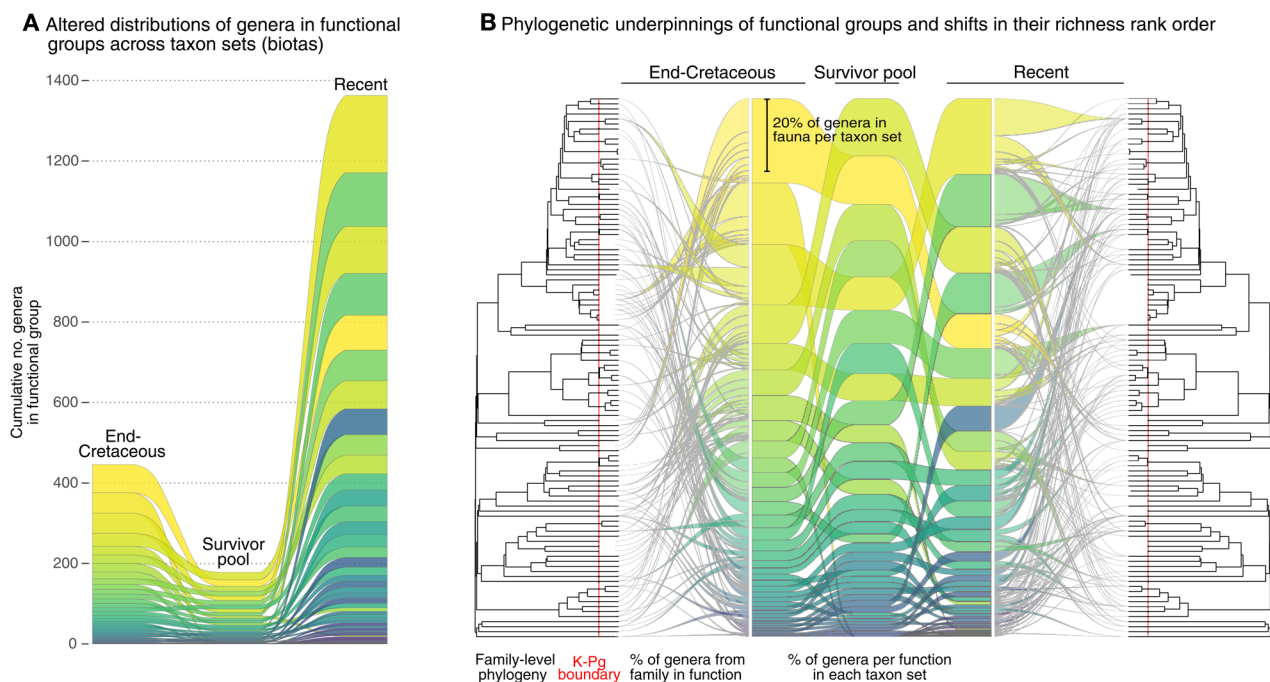


Fig. 2. Shifting distributions of genera within functional groups and their phylogenetic underpinnings among the end-Cretaceous, survival pool, and Recent biotas. (A) Changes in absolute richness of genera within functional groups between the end-Cretaceous biota, the survivor pool, and today. Warmer colors indicate higher genus richness. Mixing of the color gradient in the survivor pool and Recent biota indicates shifts in the richness rank order of functional groups. (B) Phylogenetic underpinnings of functional group composition for the end-Cretaceous and Recent biotas. The proportion of genera in a functional group per family is reflected by the widths of ribbons connecting the tips of the family-level phylogeny to functional groups. The middle panel shows the proportional changes in genus richness of functional groups among taxon sets. The connections between the taxon sets are to visualize shifts in the rank order of functional groups and do not imply smooth transitions between them.

diversity functional groups largely remain confined to the tail of the richness-frequency distribution, as are the 12 functional groups that evolved in the Cenozoic (Figs. 2 and 3A).

These shifts diverge significantly from simulations that randomly accumulate taxa in functional groups according to their richness at the start of the Cenozoic: 10 functional groups exceed, 23 fall short of, and 14 conform to the random expectation (Fig. 3A). Thus, a “head start” does not guarantee overaccumulation and starting at a low value is not necessarily a hindrance (Fig. 3C). Certain traits may be tied to under- or overaccumulation, e.g., mixed feeders have exceeded expectations of random accumulation (Fig. 3B) in association with the diversification of a particular clade, the superfamily Tellinoidea. If rudists were photosymbiotic, then this group shows a notable contrast between the pre-extinction biota and the present

day, with families capturing this function in the Cenozoic never achieving Mesozoic diversity levels (Fig. 3A). If rudists were not photosymbiotic, then this trophic mode may represent a novel Cenozoic functional group. Even in that scenario, one functional group was still lost at the end-Cretaceous and never regained. Thus, the present-day number and rank of functional groups neither resembles that of the end-Cretaceous biota nor does it match the structure of the survivor pool that seeded the Cenozoic biota (compare landscapes in Figs. 1B and 4B). The mismatch cannot be attributed to the strong resurgence of coral reefs in the early and mid-Cenozoic (46), because the functional groups that rise high in the rank order from the survival pool to the Recent biota are not closely associated with reefs today (e.g., ectosymbiotic, chemosymbiotic, and deep infaunal groups).

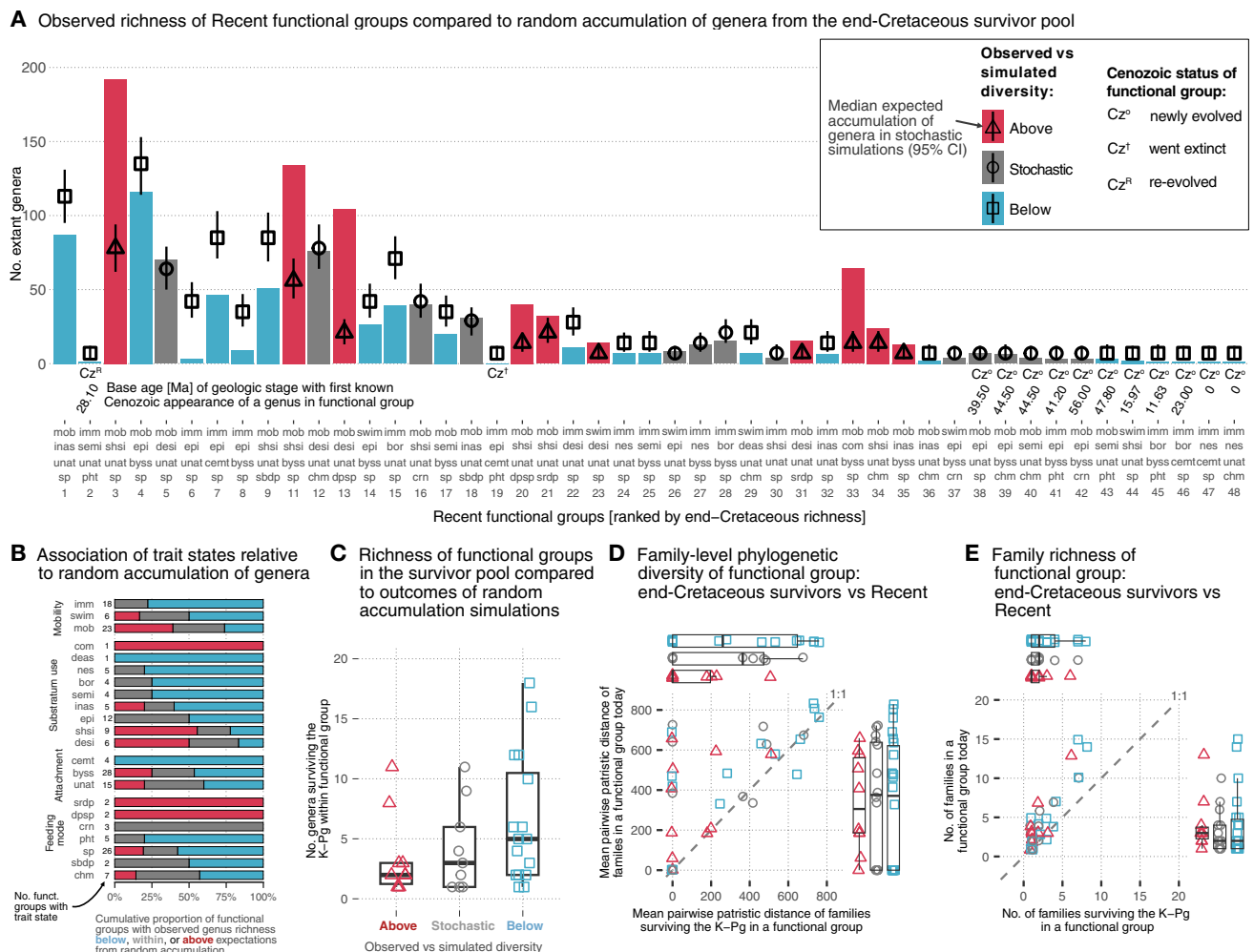


Fig. 3. Marine bivalve functional diversity in the Recent biota relative to random diversity accumulation from the end-Cretaceous survival pool. (A) Genus richness of Recent functional groups arrayed by their richness rank in the end-Cretaceous biota; observed richness is compared to the expectations from the random accumulation of genera starting from the distribution of genera in the survivor pool. Functional abbreviations as in Fig. 1B. (B) Richness of functional trait states in the Recent biota relative to the expectation of random accumulation of genera. For example, all three of the functional groups with cemented attachment accumulated fewer genera than expected. (C) Number of genera surviving within a functional group compared to its Recent richness relative to random accumulation. (D) Phylogenetic diversity of families surviving the K-Pg event within a functional group compared to the phylogenetic diversity of families within the group today. Boxplots along axes show the phylogenetic diversity of families surviving the K-Pg event within functional groups (top) and for the entire Recent biota (right). (E) Number of families surviving the K-Pg event within a functional group compared to the number of families within the group today. Boxplots along axes show the numbers of families surviving the K-Pg event within functional groups (top) and for the entire Recent biota (right).

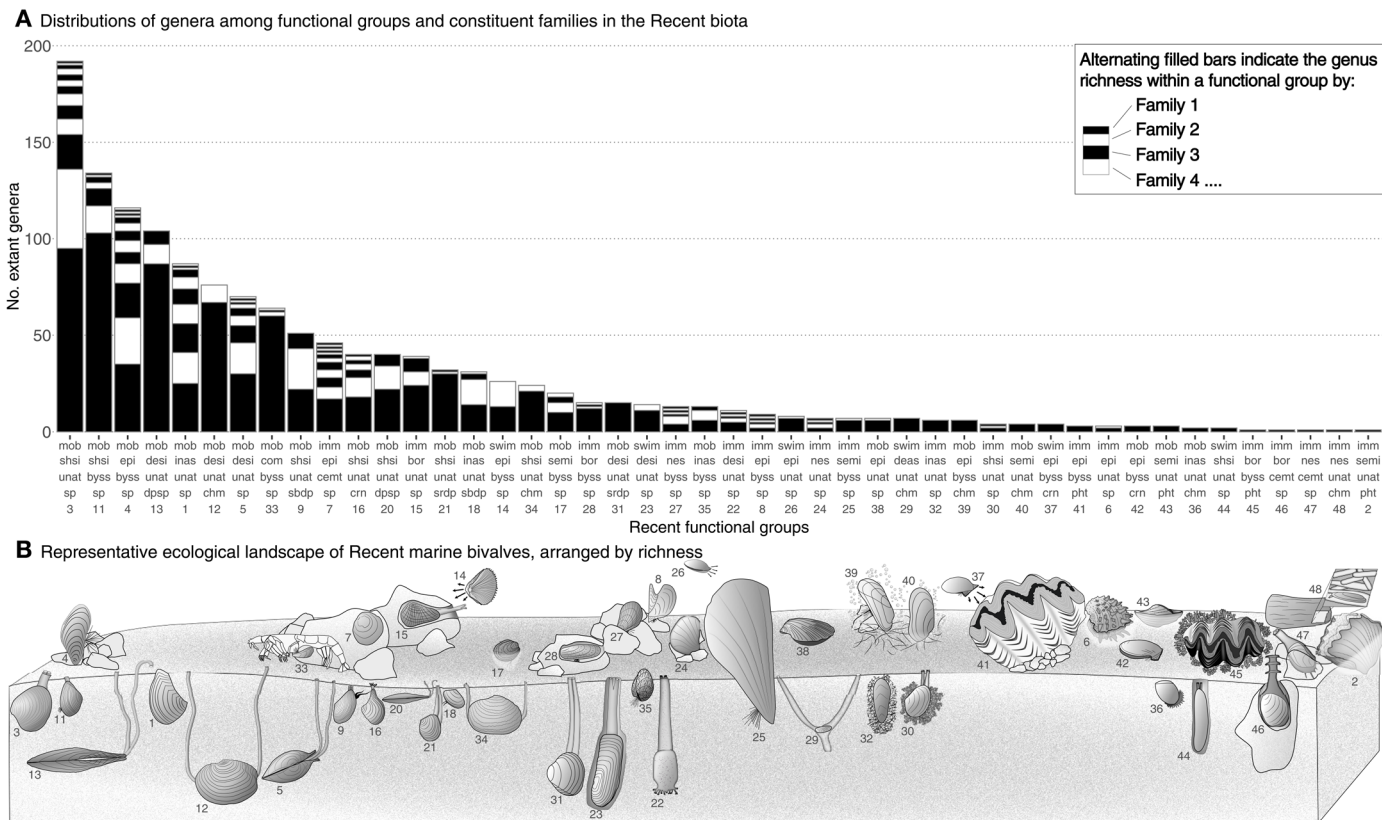


Fig. 4. Ecological landscape of marine bivalves in the Recent biota and its taxonomic underpinnings. (A) Genus richness of functional groups today, showing the distribution of genus richness per family within groups as alternating black and white bars. Functional abbreviations as in Fig. 1B. (B) Representative members of Recent functional groups in life position, arranged by rank of genus richness [see numbers along the x axis in (A)].

Evolutionary novelty in the wake of the mass extinction also has not conferred evolutionary success on functions today. All 12 of the functional groups that appeared after the K-Pg event have remained genus poor (no more than six genera apiece; Fig. 3A). Sixty-percent of these groups appeared in the Paleogene [i.e., prior to 28 Ma; Fig. 3A], so that their low, present-day richness cannot be attributed simply to recent origination. None of these functional groups are strictly high latitude today [$>35^{\circ}\text{N}$ or $>35^{\circ}\text{S}$, also seen in ref. (12)], implying that polar refrigeration and increased climate zonation through the Cenozoic was not key to their origin either. Escalating predation intensity and the resurgence of coral reefs might also have promoted the evolution of these new functional groups, but neither factor has allowed genus richness within those groups to reach high ranks (Fig. 3A), despite the apparently enormous diversity accommodation space in the Indo-West Pacific (47, 48). Thus, as for the functional groups that have remained in the tail of the richness-frequency distribution since the latest Cretaceous, many post-extinction functional groups appear to have a long-term limit to the production or accommodation of taxa, with the most prolific or least constrained functional groups originating before the end-Cretaceous event.

Taxonomic and phylogenetic restructuring

High phylogenetic diversity of families in a functional group, today or in the survivor pool, also did not guarantee exceptionally high present-day taxonomic richness (nor does the raw number of families; Fig. 3, D and E). Although almost every functional group has increased in phylogenetic diversity today owing to the entry

of additional families, the accumulation of genera within groups is not strictly related to the relative increase in phylogenetic diversity (Fig. 3D). Functional groups accumulating more genera than expected in our simulations actually tended to have lower family-level phylogenetic diversity in the survivor pool (Fig. 3D). These are unexpected results because higher phylogenetic diversity might be expected to promote the accumulation of taxa by allowing diversification across disparate morphologies and/or life histories. Instead, genus richness within functional groups tends to be underlain by strong diversification in one or a few prolific clades, rather than by even diversification among constituent taxa (Fig. 4A).

Families that survived the end-Cretaceous event within their functional groups tend to dominate them today, suggesting incumbency effects. In all but seven of the surviving functional groups, at least 50% of their genera belong to these “survivor” families (Fig. 5A), despite the origination of 26 families in the Cenozoic (Fig. 2). Even the 11 functional groups that first appeared in the Cenozoic, and the one that re-evolved, are composed mainly of survivor families (Fig. 5B). For the functional groups shared between the latest Cretaceous and today, the dominant family has shifted in 15 of 35 groups, but only three of those shifts were tied to a family originating in the Cenozoic (Fig. 2B). When such relays do occur, newly dominant families range from being closely to distantly related to their predecessors (fig. S4), implying a more contingent process rather than strong deterministic effects of shared ecological functions among close relatives. Replacement of dominant families within functional

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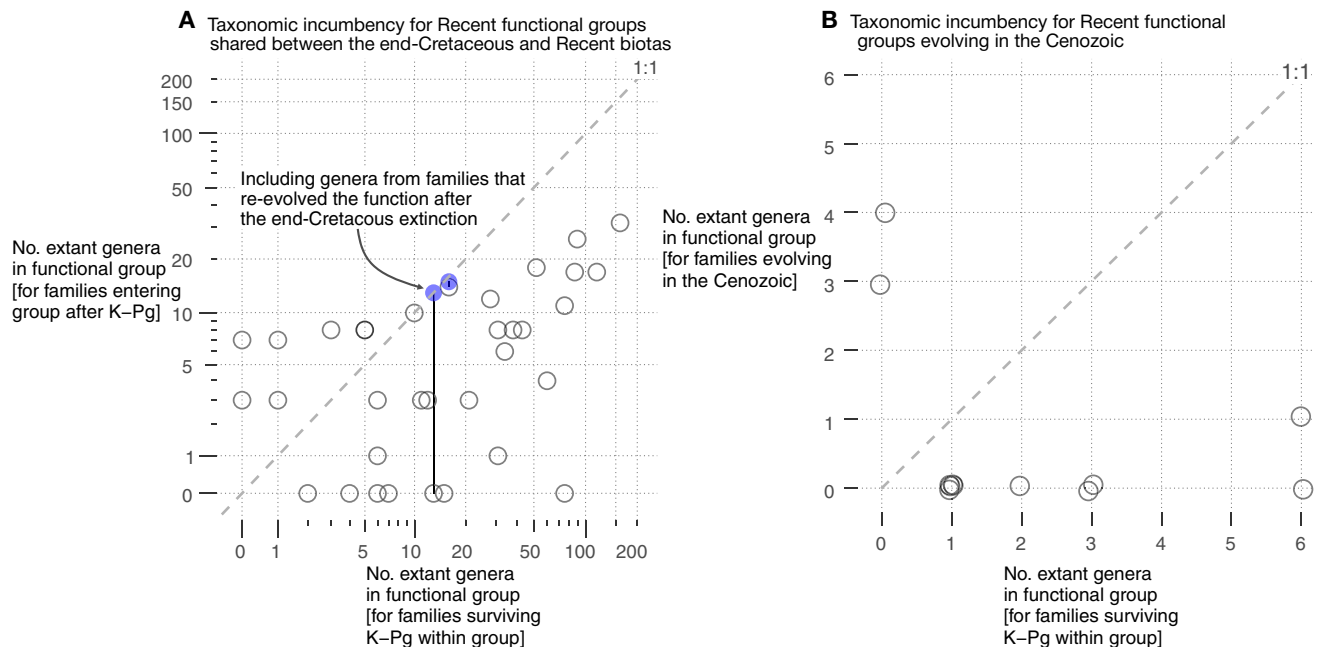


Fig. 5. Taxonomic incumbency from the K-Pg event and its relation to the richness structure of functional groups in the Recent biota. (A) The number of genera today from families surviving the K-Pg event within a functional group compared to the number of genera from families entering the functional group during the Cenozoic. Blue points show genus richness from families that lost a function at the K-Pg event but re-evolved it in the Cenozoic. (B) As in (A), but for functional groups that evolved during the Cenozoic. Data for both axes are integers, but points are jittered slightly to show overlap of multiple functional groups in the space.

groups likely derives from other factors influencing intrinsic diversification rates of lineages, such as genetic population structures or finer subdivisions of functional groups via morphological divergence. Thus, the end-Cretaceous event opened up post-extinction opportunities for diversification within functional groups—and extensive reshuffling of their taxonomic and phylogenetic composition—but incumbency evidently undermined these opportunities and thus underlies most of the present-day richness patterns.

It is notable that functional diversity persists despite individual families losing functions at the K-Pg event 16 times (13% of family-function combinations). Only two families reacquired their lost functions in the Cenozoic, notably in scallops, where swimming was lost and regained (Fig. 5A). This pattern suggests possible preemption by other families (49) or the lasting consequences of losing key phenotypic traits and quite possibly their developmental basis. Two unique functional modes of rudists (if photosymbiotic) have yet to re-evolve, although warm, carbonate-rich shallow seas have occurred in the Cenozoic. The extinction of the rudist clade may have foreclosed the restoration of those functions given that the clade had been separated from the rest of Bivalvia for at least 200 Myr [and possibly as long ago as ~475 Ma via the Ordovician Megalodontoida (26)], and none of the surviving bivalves had similar ontogenies or adult morphologies. One bivalve lineage, the Cardiidae, entered comparable, but not precisely matched, functional groups in the Cenozoic, most impressively as the giant clams of the Indo-West Pacific (subfamily Tridacninae). Such photosymbiotic functional groups appear to be a fatal attractor for bivalves (5), having evolved independently in each of the Phanerozoic eras (24) only to see all associated lineages lost in the end-Permian and end-Cretaceous mass extinctions—and today's giant clams are also under threat from the rapid pace of environmental change.

Future work should begin dissecting how the extensive Cenozoic changes seen in the Earth system have further shaped marine functional diversity. Global climate and oceanography has shifted considerably over the Cenozoic, with a narrowing of the tropics (50), the development of a major biodiversity hotspot in the Indo-West Pacific through a confluence of biotic and abiotic factors (44, 51), and through turnover and diversification of predators and other enemies (47). All of these factors could alter the relative richness of functional groups, and each might provide opportunities for new groups to join the high-diversity ranks. For example, does an over-accumulation of taxa in a function relative to random expectations scale with the number of provinces occupied, perhaps promoted by increasing vicariance driven by continental dispersal and steepening thermal gradients (52, 53)? The next step will be to layer in the effects of phylogenetic and evolutionary contingencies to test the balance of deterministic and random factors in shaping biodiversity rebounds from tight bottlenecks.

Maintaining, recovering, and conserving functional diversity

Functional diversity is also notably persistent through the other Big Five extinctions and smaller events for several major marine animal groups (6–10, 54–57); for an exception in a more narrowly defined clade, see diplobathrid crinoids (1). Bivalves lose more than half of their genera across the both end-Permian and end-Triassic extinctions, but here too their functional richness was virtually unchanged (7–9), also incompatible with random extinction (Fig. 1A) (9). The survival of functional groups is even more notable in light of present-day biogeographic patterns, with functional variety declining from tropics to poles in rough proportion to taxonomic richness in both marine and terrestrial systems, toward a more even structure (12, 58, 59). The contrast with the biogeographic trend is conceptually

important for at least two reasons. First, it shows that our functional scheme founded on discrete categories has sufficient resolution to detect changes in functional richness and evenness. Second, it highlights our poor understanding of the response of functional variety to marked drops in taxonomic richness. The tropics-to-poles latitudinal trends and the era-defining mass extinctions show intriguing contrasts and commonalities that will surely repay further dissection (60).

Even systems showing more extensive losses of functional groups through mass extinctions often rapidly re-evolved them. As many as 17 terrestrial functional groups were lost in the end-Triassic event (perhaps expected given the reported 96% genus-level extinction, also raising sampling questions), with most groups recovered in new or surviving lineages (61). The diversity of insect mouthparts and thus the number of feeding guilds declined around the end-Permian and end-Cretaceous events (62), the latter also showing a loss and resumption of plant-insect damage syndromes (63). The end-Cretaceous removed entire teleost clades with morphologies indicating fast swimming and cruising lifestyles, but surviving teleosts quickly re-occupied this niche during the Paleogene (64). These examples may reflect a greater tendency for terrestrial (and/or vertebrate) mass extinctions to remove broader clades (and therefore entire modes of life), or for functional groups to be less polyphyletic, than in marine invertebrates. In these cases and others [mammals (65); fishes (66); plants (67)], the persistence or recovery of functions has limited impact on how the ecological landscape is ultimately rebuilt.

As shown here, mass extinctions impose ecological parity, nearly equalizing taxon richness among the surviving modes of life. The ecological structure usually returns to a skewed distribution of taxa among functions in most systems (Fig. 2) [(68, 69); but see ref. (70)], albeit on long geological timescales (71). Our results support that view and show that, although a precise recovery of the pre-extinction biota is unlikely, broad aspects of the ecological structure may persist. For example, long-impooverished functional groups with a deep evolutionary history might reflect a limited capacity to accommodate taxa; this has not necessarily been a liability when it comes to extinction risk, but it does suggest that these groups are unlikely to dominate future ecological landscapes. This may be the basis for the failure of most functional groups that were genus-poor prior to the K-Pg event to rise in rank through the Cenozoic (Fig. 2). However, there is limited similarity among these low-diversity functional groups, implying their low diversities cannot be attributed to one or a few functional traits. Alternatively, the clades having the anatomical or physiological capacity for occupying those functional groups might have other intrinsic properties that damp their diversification, for example, by lowering per-capita origination rates. Disentangling extrinsic constraints on the accommodation of taxa from intrinsically low origination and/or extinction rates in these functions will be important here.

Analyzing the interplay between phylogeny and function becomes a critical exercise for sustaining biodiversity in the “Anthropocene.” Low phylogenetic diversity in low-richness functions today could imply a heightened risk of extinction, but the K-Pg bivalves indicate that low richness and/or low phylogenetic diversity are not necessarily liabilities. However, within functions, phylogenetic loss can have profound, long-term consequences, given the apparently limited potential for lineages other than the former dominants to match or exceed previous diversity levels. For example, the near extinction of the trigonioid bivalves was not counterbalanced by a

later diversification of archiheterodonts in that functional group [see also ammonoids versus nautiloids (72, 73)]. This is a particularly acute problem as both anatomical and functional similarity fades with phylogenetic distance so that functional replacements become increasingly less feasible, i.e., the apparently more extinction-resistant gorgonian corals seem ill-equipped to prime a new era of wave-resistant reefs like the ones built by their scleractinian relatives [(5) and see Valentine’s (52) thought experiment on the improbability of re-evolving echinoderm functions in the event of their extinction]. Thus, the phylogenetic context of bivalve functional diversity shows two targets to consider for setting conservation agendas. The first should be the low-diversity functions that represent evolutionarily rare but ecologically important acquisitions (e.g., the phylogenetically isolated and taxon-poor, photosymbiotic bivalves that split from the rest of the cardiid clade at ~50 Ma). The second should be the clades that have repeatedly captured novel functions (e.g., the mussel family Mytilidae, which occupies 11 functional groups today; fig. S5). Past mass extinctions were, if anything, statistically overdispersed relative to marine functional groups given that low-diversity ones persisted, but this is not the case today for exploited species (11), perhaps suggesting that “Anthropocene” declines in taxonomic and functional richness may more closely resemble today’s latitudinal decline than persistence across past extinction events.

The ongoing biodiversity crisis threatens to disrupt the global biota to a degree last seen during ancient mass extinctions (74, 75). In our model system, functional diversity was robust to severe taxonomic loss, a notable mismatch between taxonomic and functional group extinction intensities. However, the genus richness of functional groups and their phylogenetic compositions have been markedly reorganized to the present day. Despite this scrambled rank order, most of the richest bivalve functional groups prior to the K-Pg event are among the richest today (top 25%). Thus, functional innovation in the wake of the extinction has not been the primary driver of the Cenozoic rebound. Rebuilding the phylogenetic structure of functional diversity has also depended more on lineages surviving the K-Pg event than on those originating in its wake. Most of the surviving clades (here, families) maintain their functional roles from before the extinction, with the richest ones tending to be the source for new functional groups. New clades and functions do arise, but few of them now dominate the ecological landscape, even 66 Myr after the last major extinction. The bivalves show that mass extinctions and their rebounds play a major role in the history of life but are neither strictly random nor ecologically deterministic in any simple way. The challenge now is to weigh the roles of phylogenetic and ecological structuring set by the extinction survivors in understanding the dynamics of past and future biodiversity.

MATERIALS AND METHODS

Dataset

Taxon sampling and family-level phylogeny

Three sets of taxa were analyzed here: (i) genera occurring within the Maastrichtian age of the Late Cretaceous epoch (72.2 to 66.0 Ma), termed the “end-Cretaceous biota”; (ii) genera known to survive the Cretaceous-Paleogene mass extinction (K-Pg, or end-Cretaceous event) into the Cenozoic, termed the “survivor pool”; (iii) genera occurring in today’s oceans, i.e., the “Recent biota.” Compared to the operationally instantaneous samples that define the survivor pool and Recent biotas, the end-Cretaceous biota draws taxa from the

Maastrichtian age spanning ~6 Myr, as required for a truly global analysis. Despite the time-averaging and potential inflation of genus richness during this interval, the known diversity is still one-third that of the Recent biota (see below) and likely understates the differences in diversity between the pre-extinction biota and the present day.

The 438 fossil genera occurring in the end-Cretaceous biota and the 172 genera surviving the end-Cretaceous event were compiled from a compendium of first and last stratigraphic occurrences of 3365 fossil marine bivalve genera that has been taxonomically and stratigraphically vetted and expanded using the primary literature and museum collections. The end-Cretaceous dataset contains 111 more genera and more finely resolved stratigraphic ranges than the Paleobiological Database (as queried August 2024); the parent dataset has ~1100 more genera, an expected expansion given that occurrence-based compilations are derived from sources containing fossil assemblages, rather than targeting range endpoints, and cannot be as extensively vetted as a taxon-based range-through database used here (21). The 1349 genera originating post-Cretaceous and occurring in the Recent biota were compiled from a taxonomically updated version of the dataset from ref. (11). All genera were assigned to 108 “operational families” that encounter either the end-Cretaceous or Recent time intervals, spanning all six major branches of bivalve phylogeny (76). These operational families reflect the molecular uncertainty in the family-level topology of ref. (76): Neilonellidae, Tindariidae, Sareptidae, and Yoldiidae were folded into Malletiidae; Phaseolidae, Bathyspinulidae, and Siliculidae into Nuculanidae; Nucinellidae into Solemyidae; Erodonidae into Corbulidae; Condylolardiidae into Carditidae; and Basterotiidae, Galeommatidae, Lasaeidae, and Sportellidae into Galeommatoidae.

The 20 families analyzed here that were not placed in the phylogeny of ref. (76) (all from the end-Cretaceous biota) were grafted to that phylogeny using existing topological or systematic hypotheses in the literature, as detailed for each family in Supplementary Text. As in ref. (76), the branch lengths of the phylogeny were scaled to geologic time using treePL (77), setting the minimum and maximum age constraints on nodes as the boundaries of the stratigraphic intervals for the younger of the two lineages subtending a node (i.e., the budding model of evolution). The “thorough” option was specified to run analyses until the penalized likelihood reached convergence, and the randomcv option set to 1000 so that the cross-validation procedure could determine the smoothing parameter for penalizing rate variation across the phylogeny.

Phylogenetic continuity and fossil preservation potential

All of the operational families (hereafter, families) were directly observed via genus occurrences in the Maastrichtian ($N = 82$). For families with all of their known Maastrichtian genera going extinct at the K-Pg boundary but with genera also known from the Cenozoic [Lazarus taxa (78)], one Maastrichtian genus was chosen to operationally represent the survival of the family, i.e., preserve phylogenetic continuity ($N = 10$ families). In all but one case, the Maastrichtian genera within each of these families were in the same functional group, and thus choosing an operational surviving genus did not affect analyses of functional diversity; Maastrichtian Monopleuridae genera had different functions, so the genus with the same function as the Cenozoic genus was chosen as the family’s operational survivor (cf. *Gyropleura* and *Paramonopleura*).

To assess the potential impact of preservation potential on the relative richness of functional groups in the end-Cretaceous biota, each genus was categorically scored for its primary shell mineralogy

and organic content following (79). Aragonitic mineralogy and high organic content reduce preservation potential (79, 80). Therefore, shell mineralogies were scored from entirely aragonitic (score = 1) to calcitic (3) and shell organic content from high (1) to low (3). Preservation scores were then calculated as the product of the scores for mineralogy and organic content (ranges 1 to 9; see fig. S2). Preservation scores of functional groups were then compared against the rank order of genus richness.

Functional ecologies

Genera were classified into discrete ecological functional categories using a combination of direct observations recorded in the primary literature and aspects of their functional morphology applied in a phylogenetic context. Four functional axes were defined: mobility (3 states), attachment (3 states), substratum use (which reflects tiering; 9 states), and feeding mode (7 states). The resolution of this scheme has detected different responses of functional diversity to taxonomic turnover in other contexts (9, 12). Details and references to functional assignments are provided in ref (81).

Extinction dynamics

Extinction intensity of genera across the K-Pg boundary was calculated as the proportion of all genera occurring in the Late Cretaceous (Maastrichtian) with a known stratigraphic range terminating prior to the Early Paleocene (Danian). Functional groups were considered extinct if all of their constituent genera accounting for phylogenetic continuity were lost at the K-Pg boundary. Simulations were then used to test whether observed extinction intensities of either functional groups or the genera within them differed from random expectation. For each of the 1000 simulations, 172 genera (the surviving 39%) were randomly sampled without replacement to represent a random survivor pool. The frequency of at least three functional groups going extinct per simulation was determined from this distribution of random samples. Buffering of functional trait states against extinction was assessed as the proportion of functional groups with a given trait state showing the observed survivorship or extinction of their constituent genera falling outside the 95% confidence interval generated through the random extinction simulations. The phylogenetic diversity of functional groups was estimated as the mean pairwise patristic distance of their constituent families using our time-calibrated phylogeny.

Comparing functional structures between the end-Cretaceous and Recent biotas

Exceptional over- or underaccumulation of genera between the K-Pg survivor pool and the Recent biota was assessed via random accumulation of genera in functional groups according to their richness at the start of the Cenozoic (plus the observed 12 groups evolving in the Cenozoic). Genera were sampled with replacement from the richness-frequency distribution of genera among functional groups in the survivor pool up to the total Recent genus richness; functional groups originating in the Cenozoic were seeded with a single genus. This simple null sets a baseline expectation for the distribution of genera among functions today that largely mirrors the shape of the distribution for the survivor pool. Exceptional accumulation of genera in functional groups today was determined by having observed richness values fall outside the 95% confidence intervals of the random accumulation simulations.

The timing for the origination of Cenozoic-only functional groups was determined by evaluating the functional morphology of genera in families that originated prior to the oldest known genus in the function occurring in the Recent biota. This approach sets a minimum age

on the origination of these functions given the very small but non-zero probability for genera in families not present in functions today to have occupied different functions from their confamilials in the early Cenozoic.

To evaluate the potential effect of taxonomic and phylogenetic incumbency on the standing taxonomic richness of functional groups today, families within functional groups were categorized as “survivors”—having genera that survived the K-Pg event in that particular function—and “newcomers”—having genera that entered the function following the K-Pg event. Families with the highest genus richness in a given function were considered the “dominant” family per function in each taxon set. To evaluate the phylogenetic structure of any turnover among dominant families in functions, the phylogenetic distance(s)—as patristic distance in Myr and as the number of internodes—of the dominant family(ies) in the end-Cretaceous biota were compared to both the new dominant family(ies) and the nondominant family(ies) in the Recent biota.

All analyses were performed in R v. 4.4.1 (82); all data and codes to reproduce analyses are available as part of the Figshare repository (81).

Supplementary Materials

This PDF file includes:

Supplementary Text

Figs. S1 to S5

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