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Skeletal marine animal biodiversity is built by families with long macroevolutionary lag times

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2020-10

Kroger , B & Penny , A 2020 , ' Skeletal marine animal biodiversity is built by families with long macroevolutionary lag times ' , Nature Ecology & Evolution , vol. 4 , no. 10 , pp. 1410-+ . <https://doi.org/10.1038/s41559-020-1265-8>

<http://hdl.handle.net/10138/326731>

<https://doi.org/10.1038/s41559-020-1265-8>

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Figure #	Figure title	Filename	Figure Legend
	One sentence only	This should be the name the file is saved as when it is uploaded to our system. Please include the file extension. i.e.: <i>Smith_ED Fig1.jpg</i>	If you are citing a reference for the first time in these legends, please include all new references in the Online Methods References section, and carry on the numbering from the main References section of the paper.
Extended Data Fig. 1	Comparison of diversities of the two cohorts with medium lag time cohort, and random sample.	Kroger_Penny_Fig_DE1.eps	Richness estimates calculated with c-r modelling approach. a , C_{long} , genera of families with long macroevolutionary lag time, C_{short} , genera of families with early burst diversification, C_{medium} genera of families with moderate lag-times between 6.05–12.1 Myr. Dataset consists of 8050 genera of C_{long} , 3879 genera of C_{short} , and 1465 genera of C_{medium} . The median longevity of the combined families of C_{long} and C_{medium} is 106 Myr compared with 51 Myr in C_{short} (Mann-Whitney U test, $p < 0.001$). b , C_{sample} , mean richness resulting from 50 bootstrap samples of 200 families taken from the total group of 1414 families of skeletal non-colonial animals used for the analysis. Note the difference of the resulting curve from curves of C_{short} and C_{medium} : the random samples preserve the rising Palaeozoic and Mesozoic-Cenozoic trend of the total group (see Fig. 2). Vertical bars are 95% confidence intervals. Blue hatched

			lines mark from left to right end-Ordovician, end-Devonian, end-Permian, end-Triassic, and end-Cretaceous mass extinctions. Based on a download from the PaleobioDB from 16.04.2020.
Extended Data Fig. 2	Waxing and waning of genus richness of families.	Kroger_Penny_Fig_DE2.eps	All family longevities are standardized ranging from 0-100%. Based on c-r richness estimates of n=1414 non-colonial skeletal marine metazoan families. The pattern predicts that maximum diversification of families occurs within the first two-fifths of the duration of a family regardless of the absolute length of the duration, and it also predicts that in families with longer durations the time from first appearance to peak diversification is longer than in families with shorter durations. The hat-shaped pattern is a common feature of clade evolution ¹² .
Extended Data Fig. 3	Comparison of ecological modes of life of the two cohorts.	Kroger_Penny_Fig_DE3.eps	Diagrams depict relative frequencies of ecological life modes of genera within the two cohorts. Based on categorisations of 1653 genera of C _{short} and 3247 genera of C _{long} . Categories of ecological modes of life from ²⁹ , and categorisations of genus life modes from ³⁰ . C _{long} , cohort with long macroevolutionary lag;

			C_{short} , cohort with short macroevolutionary lag.
Extended Data Fig. 4	Results of the autocorrelation function (ACF) for the richness curves of C_{long} (cohort with long macroevolutionary lag) and C_{short} (cohort with short macroevolutionary lag).	Kroger_Penny_Fig_DE4.eps	Autocorrelations not significantly different from zero are similar to autocorrelation functions of random walks ⁵⁶ . Random walk dynamics have been previously identified and analysed for Phanerozoic time series of diversity and evolutionary rates ⁵⁶ . Dotted line: 95 % confidence interval.
Extended Data Fig. 5	Richness curves of a reduced set of skeletal marine metazoans at genus level.	Kroger_Penny_Fig_DE5.eps	Families with maximum diversification during one of the stages with duration twice of maximum short-lag duration (= 12.1 Myr, Emsian, Famennian, Tournaisian, Viséan, Norian, Aptian, Albian, Campanian, marked in red) were filtered out. C_{long} , genera of families with long macroevolutionary lag time (dotted line) and C_{short} , genera of families with early burst diversification (solid line). Dataset consists of 1398 families, 16 families less than in the complete analysis. The filtering has a minor effect on the curves but does not change the strongly diverging trend between C_{short} and C_{long} (comp. Figure 2). Vertical bars are 95% confidence intervals.

			Richness estimates calculated with c-r modeling approach. Blue hatched lines mark from left to right end-Ordovician, end-Devonian, end-Permian, end-Triassic, and end-Cretaceous mass extinctions. Apt., Aptian, Alb., Albian, Camp., Campanian, Fam., Famennian. Based on a download from the PaleoBioDB from 16.04.2020.
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Item	Present?	Filename	A brief, numerical description of file contents.
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Supplementary Information	Yes	Kroger_Penny_SI.pdf	Supplementary Tables 1-6
Reporting Summary	Yes	nr-reporting-summaryBK.pdf	

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4 **Skeletal marine animal biodiversity is built by families with long**

5 **macroevolutionary lag-times**

6

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16

17 **Introductory Paragraph**

18 The clade dynamics of marine animals have changed markedly over the Phanerozoic.
19 Long-term diversification is associated with decreasing origination and extinction
20 rates, and with increasing taxon longevity. Here, we use the diversification
21 trajectories of skeletal non-colonial marine families to infer the mechanisms which
22 generated these trends. Suggested mechanisms behind these trends include stochastic
23 extinction of taxa with high evolutionary volatility, and selection for traits that buffer
24 against extinction. We find an increasing predominance of Phanerozoic families with
25 long lag times between first appearance and peak diversity, over those with ‘early
26 burst’ diversification trajectories. Long-lag families persisted for longer, had lower
27 evolutionary volatilities, higher genus-level occupancies, and genera with larger
28 niche breadths than early-burst families. However, they do not preferentially show
29 ecological modes known to protect against extinction. We interpret the rise of the
30 long lag families to reflect an intensification of ecosystem-level mechanisms
31 supporting both long-term coexistence and transient dynamics, which increased the
32 capacity of marine ecosystems to accommodate highly diverse communities.

33

34 **Introduction**

35 Global rates of origination and extinction in marine taxa have declined markedly over
36 the Phanerozoic Eon^{1 2}. This trend in turnover rates is real and not a result of
37 sampling bias^{2,3}. It may result from stochastic sorting of clades for stability, whereby
38 over geological time scales high-turnover (volatile) clades tended to become extinct
39 more rapidly than stable clades with low turnover^{4 5}. According to this model,
40 modern marine diversity results from the successive accumulation of genera in long-
41 lived, low-volatility clades⁶. Moreover, the relationship between genus richness and
42 turnover rates in marine Linnean classes has changed over geological time; high
43 genus richness was associated with high turnover rates until the late Mesozoic, and
44 with low turnover rates afterwards⁶.

45 Previous research has also identified physiological and ecological traits that are
46 protective against extinction and led to increased resilience against environmental
47 stressors, such as a fully motile habit, predatory feeding, and pelagic habitat⁶. Hence,
48 resistance to extinction, tied to clade-specific traits and low volatility, has been
49 identified as a major factor in taxonomic diversification in the marine realm.

50 Here, we focus on taxon longevity (at family and genus level) and family specific
51 diversity trajectories as key to understanding the Phanerozoic marine diversification.

52 The longevities and diversity trajectories of families are a result of their species
53 durations. All families originated with species with specific sets of physiological and
54 ecological traits within specific ecological communities, and subsequently persisted
55 and became accommodated within other communities in space and time. The
56 evolutionary process whereby organisms integrate into novel environments and
57 persist in novel association with other taxa as a result of the traits that they carry is
58 known as ecological fitting^{7,8}. Here we use this concept in a macroevolutionary

context, where genera and families persist and consecutively colonize novel ecosystems in geological time.

Family longevities and their diversity trajectories are determined by family-specific properties (both traits and volatility) that allow, what we would call “macroevolutionary ecological fitting”, and buffer against extinction. Similarly, though not independently, the higher-level properties of the ecosystems (e.g., spatial extent, spatial and temporal heterogeneity, niche structure, and invasibility^{9 10}), which the families are part of during geological time scales, are potential determinants of family longevity and diversity. The success of families relies on both a) the potential of their lower taxa to initially invade an ecosystem and resist extinction, and b) the capacity of ecosystems to allow invasion and to accommodate their members. Herein, we assess these two aspects of family success, and use them to infer mechanisms which might have generated the changing Phanerozoic relationship between genus richness and turnover rates.

Our analysis is based on a generalized and simplified model for diversity curves of families (and higher taxa in general). Based on the timing of the peak diversification in the curves, the model allows an evaluation of the relative importance of the family properties at time of origination versus changing ecosystem properties later in the life histories of the respective families.

Results and Discussion

A generalized model for within-lineage diversity curves. Species and higher taxa originate and disappear in a waxing and waning pattern of abundance, occupancy, and diversity^{11–13} (Figure 1b). The canonical view on this scenario is that new clades arrive by chance, increase in abundance, diversity, and occupancy because their novel

84 traits confer a selective advantage, and eventually go extinct because that selective
85 advantage is lost ¹⁴. The interval between each taxon's expansion and decline can
86 differ in timing and duration, but on average follows a symmetrical pattern with a
87 climax at approximately mid-range ¹². A taxon's longevity and the duration of its
88 waxing and waning are therefore generally correlated ¹⁴.

89 An early burst pattern often (but not exclusively ¹⁵) reflects adaptive radiation, where
90 new adaptations and ecological roles are triggered by ecological opportunity, either
91 through a key innovation, extinction of an antagonist, or by entry into a new
92 environment ¹⁶⁻¹⁸. In the case of an early burst, the fate of a clade is tightly connected
93 to an initial relaxation of selection ¹⁷. In early burst scenarios, novel organismic
94 features (i.e. morphological or functional characters) simultaneously rise toward
95 ecological significance and often allow for the rise of a new higher taxon ¹⁸.

96 However, species and higher taxa may instead originate and persist for a long
97 evolutionary interval with low abundance, occupancy and diversity. A change within
98 the ecosystem, temporally and causally decoupled from the appearance and initial
99 persistence of these taxa, triggers their rise to high abundance and diversity (e.g. via
100 exaptations ¹⁹) eventually resulting in what has been termed a long phylogenetic fuse
101 ²⁰, or macroevolutionary lag-time ^{21,22}. These taxa gained ecological opportunities on
102 geological time scales, triggered by adaptive zone changes ^{23,24}. Thus, in this model,
103 short macroevolutionary lag time is associated with organismic novelty causing an
104 initial rise of these families in occupancy and diversity, and long macroevolutionary
105 lag times with ecosystems' changing capacities to accommodate members of older,
106 pre-existing families.

107 The model is based on the assumption that fossil families and genera of skeletal
108 marine animals adequately represent evolutionary clades with their respective
109 aggregate properties, such as evolutionary rates, occupancies, and niche breadth.
110 Paraphyly and variation among classifications has been identified as a source of error
111 for diversity estimations (²⁵, see also ²⁶ for a recent review). Statistical comparisons,
112 however, indicate that the effects of taxonomic errors and practices of taxonomic
113 standardization ²⁷, and the impact of “wastebasket” ²⁸ taxa for estimations of diversity
114 are minor.

115

116 **Two cohorts of families.** We used data from the Paleobiology Database
117 (PaleoBioDB, downloaded 16.04.2020) to calculate the genus level diversity curves
118 for 1414 well documented, non-colonial skeletal marine metazoan families
119 (comprising 15437 genera) spanning the whole Phanerozoic at chronostratigraphic
120 stage resolution. This is c. 63% the number of extant marine animal families in the
121 Global Biodiversity Information Facility (accessed via <https://www.gbif.org/> at
122 30.04.2020) and represents c. 55% of all marine metazoan families in the
123 PaleoBioDB. For each family, we calculated the time span from first appearance to
124 estimated peak diversification in genus richness and termed it diversification lag-time
125 (hereafter referred to as “lag-time”). The median lag-time for peak diversification of
126 families is 6.05 Myr, which represents only c. 6% of the average family longevity (c.
127 109 Myr). This is slightly more than the mean length of our stage time bins (c. 5.7
128 Myr) and we cannot rule out that this reflects the limits of our time resolution
129 scheme. Regardless, the relative brevity of the median lag-time qualifies it
130 conveniently as the upper limit for our short lag-time cohort (C_{short}). Families with a
131 lag-time of at least twice the median lag time (12.1 Myr) are assigned to the long lag-

time cohort (C_{long}). Although, our distinction is arbitrary with regard to the specific lag-time durations, we chose these boundaries to focus our analysis on the two extremes of the complete spectrum of existing lag-times. We disregarded families with moderate lag-times between 6.05–12.1 Myr. This cohort comprises c. 12% of the families and 11 % of the genera (173 families, 1465 genera) of the total sample. Results from capture-recapture (c-r) modelling approach indicate that families of this cohort are only minor contributors to the total diversity and their exclusion has no effect on the significance of the results (Extended Data Fig. 1). In contrast, the C_{short} sample comprises 710 families and 3879 genera and the C_{long} sample has 530 families with 8050 genera.

As expected, the two cohorts differ significantly in longevity (median C_{long} = 132 Myr, median C_{short} = 51 Myr, Mann-Whitney U test, $p \ll 0.001$). This difference is real and not just an effect of the arbitrary filter that we set at 12.1 Myr for the minimum lag diversification time of C_{long} , because the skew toward shorter longevity in C_{short} persists even when families with durations less than 12.1 Myr are removed (Figure 1a), and when strictly families with lag time < 6.05 Myr (C_{short}) and families with lag time > 6.05 Myr (C_{long} + families with median lag time) are compared (Extended Data Fig. 1). The difference is in agreement with expectations from the model of symmetrical waxing and waning pattern of family diversity, which is also observed in our data, following the analytical protocol of Foote¹² (Extended Data Fig. 2). Hence, C_{long} predominantly represents long-lived families, and C_{short} families with short longevity.

The two cohorts differ in taxonomic composition, with differences largest in molluscs (44% molluscan genera in C_{short} vs. 56% in C_{long}) and chordates (8% chordate genera in C_{long} vs. 18% in C_{short}), reflecting a bias towards bivalves and

157 gastropods within C_{long} and towards actinopterygian fish and mammals within C_{short}
158 (Supplementary Table 1, 2). This difference is also reflected in differences in the
159 relative abundances of “ecological modes of life”²⁹ within the two cohorts. We
160 categorized the genera of the two cohorts using published genus level categorizations
161³⁰. Freely moving, pelagic and predatory genera, including cephalopods, are
162 overrepresented within C_{short} and non-motile, surficial, suspension feeders
163 overrepresented within C_{long} (Extended Data Fig. 3) (Fisher’s Exact Tests for
164 motility, feeding, and tiering are all with $p < 0.001$). Hence, the two cohorts are not a
165 random taxonomic sample of modes of life of all skeletal marine animals in the
166 PaleoBioDB. Nor do they represent subsamples dictated by taxon membership within
167 one of the predominant classes or phyla of time specific faunas, such as the three
168 evolutionary faunas of the Phanerozoic^{31,32}, because e.g. gastropods, bivalves,
169 mammals and actinopterygians all belong to the modern evolutionary fauna but are
170 distributed across the two cohorts.

171

172 **Divergent cohort diversity trajectories.** The Phanerozoic richness curves for C_{short} ,
173 C_{long} and for all taxa were estimated with the capture-recapture (c-r) approach at
174 genus level (Figure 2)³³. The resulting curves for the two cohorts are distinct: The
175 richness of C_{long} can be best described as a succession of distinct growth curves, each
176 with a major period of diversification (Figure 2). The end-Permian and the end-
177 Cretaceous mass extinctions stand out as singular events with drastic richness
178 incursions. The richness of C_{short} differs from a random subsample of the total group
179 of families and from C_{long} in being less volatile and in having the dynamics of a
180 random walk with drift with less than 10% increase from the late Cambrian onward

(Figure 2, Extended Data Fig. 1b, see also Extended Data Fig. 4, and Supplementary Table 3 for an analysis of randomness of the time series). This pattern is consistent with expectations from models of stochastic sorting for stability ⁴, i.e. declining volatility. Sorting for long-lived families and genera occurs via preferential extinction of highly volatile short-lived families, while families with low volatility have relatively higher extinction resistance and so persist for longer, accumulating richness. ⁶ Supporting evidence for declining volatility at family level comes from our analysis of evolutionary rates. We used the c-r method to calculate mean genus level per-million-year rates of origination (r_p), extinction (r_q), and turnover ($r_p + r_q$) for each family. As expected, the evolutionary volatility (i.e. genus level turnover) is higher in families of C_{short} (mean turnover = 0.79, $n = 498$) than in families of C_{long} (mean turnover = 0.40, $n = 439$) (Mann-Whitney U test, $p < 0.001$, Supplementary Table 4).

Determinants of cohort diversity trajectories. Genera which are fully motile, predatory and/or pelagic, and which are physiologically buffered against environmental stressors have a lower extinction risk ⁶ and therefore should be expected to be relatively more abundant within C_{long} . However, in our study, these ecological modes and their underlying family- and genus-specific extinction protective traits are not associated with membership in C_{long} (Extended Data Fig. 3). Instead, fully motile, predatory and/or pelagic genera are relatively more abundant within the C_{short} cohort (see above).

The families of the two cohorts differ in occupancy (i.e. for each family, the number of PaleoBioDB collections with genus occurrences from that family relative to the total number of collections with skeletal, non-colonial animal genera in the family's

time range). Occupancy is a clade property known to be a significant determinant of extinction risk ³⁴. The occupancy of the families of C_{long} (mean = 0.018) is larger than that of the families of C_{short} (mean = 0.013) (Mann-Whitney U test, $p < 0.001$), which is consistent with the lower extinction rates of the former (Supplementary Table 4, 5). Moreover, the occupancy of families of C_{long} is significantly larger in the time range after the macroevolutionary lag (mean occupancy before maximum diversification = 0.013 vs. after maximum diversification = 0.025, Mann-Whitney U test, $p < 0.001$). Additionally, we estimated, based on co-occurrences in geological formations, the mean per family generalist-specialist metric θ , or niche breadth ³⁵ of the genera of the two cohorts. We assumed θ to be a proxy for the ability of a family to occur in different ecological communities, following previous studies in which fossils within geological formations are interpreted as constituents of past metacommunities ³⁶. The two cohorts differ significantly with respect to their relative niche breadth; genera in C_{long} families generally have larger θ and thus can be interpreted as being relatively more generalist compared with C_{short} (Mann-Whitney U test, $p < 0.001$, Supplementary Table 5).

Broad scale change of macroevolutionary lag time. These differences among the two cohorts can be interpreted in two ways, which are not mutually exclusive. First, they could result from different organismic properties of the genera of the two cohorts, such as dispersal capability and tolerance against stressors. Our analysis provides no positive evidence for this interpretation. Second, varying properties of marine ecosystems, such as spatial pattern ³⁷, gross production ³⁸ or nutrient exchange ³⁹ are factors that potentially determine longevities, occupancy, and relative niche

230 breadth (e.g.^{40, 41}). Ecosystem changes can occur independently from genus and
231 family originations and could allow or impede diversification of a wide range of
232 skeletal marine animals long after their origination and hence change the relative
233 diversities of C_{short} and C_{long} within ecological communities. Throughout the
234 Phanerozoic the macroevolutionary lag time of skeletal marine animal families
235 increased dramatically across a wide range of marine ecological communities. The
236 relative number of genera of C_{long} occurring within geological formations (interpreted
237 as reflecting a record of past ecological communities³⁶) tripled during the Palaeozoic
238 and almost doubled during the Mesozoic-Cenozoic eras (Figure 3A). And the relative
239 abundance of formations that contain more than 75% genera belonging to C_{long} more
240 than tripled since the beginning of the Mesozoic (Figure 3B). This relative increase in
241 C_{long} could just be an aggregated effect of the mechanism of stochastic sorting, where
242 clades with high evolutionary volatilities, narrow niches and low occupancies
243 increasingly became filtered out, and ecosystems became increasingly dominated by
244 long lived clades. However, the main intervals of richness increase of C_{long} , the early
245 Palaeozoic and late Mesozoic-Cenozoic eras, coincide with intervals of major
246 diversification and restructuring of marine ecosystems^{42, 43}. These temporal
247 correspondences suggest that structural changes in marine ecosystems during these
248 diversifications broadly increased the ecosystems' capacities to allow families to
249 persist for longer and to give opportunities to families to diversify long after their
250 first appearances. It is a subject for future research to identify specific ecosystem-
251 level mechanisms which promoted ecological opportunity and high diversity during
252 these transitions.
253

254 **Mechanisms for diversification with increasing lag times.** The increasing
255 dominance of marine skeletal animal biodiversity by families with predominantly
256 generalist genera, with long durations and macroevolutionary lags is consistent with a
257 declining role for ecological specialisation within families in determining
258 evolutionary fitness. Several complementary mechanisms could explain this trend,
259 and we examine them below.

260 One potential mechanism that could allow families to accumulate species and genus
261 diversity under regimes of increasing lag time, niche breadth and occupancies is
262 ecosystem dynamics in steady rapid transition, i.e. in ecosystems with transient
263 dynamics, facilitated by dispersal among connected local communities.

264 Metacommunity diversification models with transient dynamics predict increased
265 species longevities and delayed peak diversifications^{44 45}. Conversely, in these
266 models, shorter longevities, early burst diversification and decelerating richness
267 accumulation are associated with ecological differentiation of species. Although our
268 results reflect higher taxonomic levels, they are consistent with these predictions
269 insofar as short macroevolutionary lag times of families are here equated with
270 diversification generated by ecological differentiation and opportunity at origination.

271 Higher levels of ecological differentiation in C_{short} are also consistent with lower
272 average genus θ (i. e. more specialist genera) and smaller family sizes (i.e. higher
273 phylogenetic distinctiveness) in this cohort compared with C_{long} (median per-million-
274 year family size $C_{\text{short}} = 0.10$ genera, $C_{\text{long}} = 0.49$ genera, Mann-Whitney U test,
275 $p < 0.001$).

276 In addition to an increase in transient dynamics, long-term intensification of
277 mechanisms which promote long-term coexistence of increasing numbers of species
278 within ecosystems are also consistent with our results. Equalizing processes, which

279 reduce fitness differences between members of a community, and stabilizing
280 processes, which increase the intensity of negative intraspecific interactions relative
281 to interspecific interactions, can work together to promote high community diversity
282 ⁴⁶. Our global analyses do not allow us to infer the nature and relative importance of
283 these ecosystem-level mechanisms. However, we note that more intense intraspecific
284 competition might be expected for C_{short} genera, which are on average more specialist
285 than C_{long} genera, while reductions in fitness differences might reduce the need for
286 ecological differentiation or organismic novelty, and favour accommodation of
287 generalists into new ecosystems (C_{long}).
288 The increasing proportion of long-lived families and families with long
289 macroevolutionary lag times among skeletal marine animals throughout the
290 Phanerozoic thus can be interpreted as a result of multiple mechanisms, including a
291 rise in transient dynamics and long-term coexistence in marine communities. This
292 interpretation is consistent with previous analysis of diversity partitioning among
293 benthic communities, which revealed a decreasing coupling of beta and gamma
294 diversity throughout the Phanerozoic ³⁶.

295

296 **Conclusions**

297 Throughout the Phanerozoic, the flux of novel genera from marine skeletal animal
298 families with early burst diversification was relatively stable, without a substantial
299 increase in diversity from the early Palaeozoic onward. Small per family genus
300 numbers, low occupancy and narrow relative niche breadth in the cohort of families
301 with early burst diversification suggest that early burst diversification is associated
302 with organismic novelty and ecological differentiation. In contrast, families with long
303 macroevolutionary lag times, and with high longevities constitute a progressively

304 larger fraction of marine diversity over the Phanerozoic. Families with long lag times
305 have high per family genus numbers, and wide niche breadths of genera, suggesting
306 that their diversification may have resulted from ecological processes which reduce
307 the role of ecological specialisation in determining evolutionary fitness, and instead
308 allow generalist families to persist over long timescales.
309 Macroevolutionary lag time, longevity and relative niche breadth of families are also
310 determined by ecosystem level properties, such as temporal fluctuation, spatial
311 heterogeneity and areal extent. Although our study does not allow us to identify
312 specific ecosystem level properties associated with the diversification, our results
313 reveal that marine ecosystems increased their capacity to accommodate a broad range
314 of skeletal animal genera giving opportunity to allow increasing niche breadth among
315 genera, and long macroevolutionary lag time within families.

316

317 **Methods**

318 The focus of our analysis was at genus and family level, because genera and families
319 are traditionally excellently documented in the paleontological literature, such as in
320 the *Treatise of Invertebrate Paleontology* and in the Paleobiology Database
321 (PaleoBioDB). We based our analysis on fossil genus occurrences of brachiopods,
322 echinoderms, molluscs and arthropods, agnathans, and marine gnathostomes from the
323 Paleobiology Database (PaleoBioDB) (downloaded 16th April 2020) (Supplementary
324 Table 1, 2). Colonial skeletal metazoans, such as anthozoans, sponges, and bryozoans
325 were excluded from our analyses, because we assumed they contain a larger
326 percentage of wastebasket, ambiguous and potentially non-monophyletic families.
327 The download comprises 745880 occurrences ranging from the base of the Cambrian
328 to the Holocene and includes extant taxa. We filtered the download for occurrences

329 identified to at least genus level, and assigned the stratigraphic ages of the
330 occurrences to time bins at the resolution of chronostratigraphic stages. We did not
331 filter for possible “wastebasket taxa”, i.e. groups resulting from inadequate
332 systematic attention or determination. Although these may be abundant in the dataset
333 of long ranging taxa, previous analyses showed that their impact on diversity
334 estimations is minimal to statistically insignificant^{28 47}. We excluded all occurrences
335 with less than chronostratigraphic stage time resolution from the analysis. The
336 absolute age boundaries were taken from the International Chronostratigraphic Chart
337 (v2018/08)⁴⁸. The median absolute time range of the chronostratigraphic stages is 4.8
338 Myr, and the mean 5.7 Myr. The filtering procedure left us with 459945 occurrences
339 of a total of 20805 genera and 2988 families at chronostratigraphic stage resolution.
340 Genus and family longevities were estimated from the filtered dataset as time range
341 from first to last occurrences. We calculated genus level richness curves of all
342 families with occurrences in more than two chronostratigraphic stages with the
343 capture-recapture (c-r) modelling approach⁴⁹ which results in 1414 individual family
344 richness curves. The method was conceptually transferred from ecology to fossil data
345 following Connolly and Miller⁵⁰, and Liow and Nichols³³ and allows for an explicit
346 estimation of sampling probability, which in fossil data is a mixed effect of
347 preservation and sampling. A presence-absence matrix was constructed based on the
348 filtered and binned PaleoBioDB occurrences. This matrix served for the fitting of
349 explicit models for richness estimation with time varying probabilities of survival,
350 sampling/preservation, and origination. We fitted the Jolly-Seber model following the
351 POPAN formulation⁵¹.

Evolutionary rates were estimated by using the Pradel seniority model ⁵². We
 estimated survival, seniority and sampling probabilities, along with diversification
 rates of genera, which are transformed into per-million-year extinction (r_q),
 origination (r_p) rates. This transformation is necessary, because probabilities between
 time-intervals of different lengths cannot be compared directly ⁵³. For a detailed
 description of the transformations see ⁵³. Additionally, we estimated instantaneous
 extinction and origination rates of genera with Alroy's ⁵⁴ statistical estimator and as
 per-capita rates ¹¹using the R package divDyn, version 0.70 ⁵⁵. For each family we
 calculated the genus level r_q and r_p curves and calculated the means for a comparison
 of the evolutionary volatility. The divDyn calculation is based on the 10-Myr time
 bin scheme and thus the results are not directly comparable. However, the
 calculations consistently resulted in lower mean extinction rates for C_{long}
 (Supplementary Table 4).

We filtered the time binned PaleoBioDB download for genus occurrences of families
 assigned to the two cohorts (C_{long} 257387 occurrences; C_{short} 74272 occurrences) and
 estimated a richness curve for each of the two data sets individually, and for the total
 dataset, using the c-r modeling approach. We limited the time range of our analysis in
 order to minimize boundary effects. A potential boundary effect toward the present is
 caused by the declining number of taxa of C_{long} in the younger time bins, because
 longevities ranging from origination to extinction cannot be projected into the future.
 Taxa originating e.g. in the Pleistocene can only have maximal longevities that range
 through the Holocene. This shifts longevities toward lower estimates. Similar
 problems occur with taxa that went extinct at the lowermost Cambrian. We therefore

375 limit the analysis of our c-r results to an interval ranging from Cambrian Stage 3 –
376 the late Paleogene Chattian Stage.

377 We tested the resulting time series of the richness for random walk dynamics,
378 following ⁵⁶, and or stationarity, drift and trend with the Augmented Dickey-Fuller
379 test for the null hypothesis of a unit root ⁵⁷ (Supplementary Table 3).

380 We decided to compare longevity and lag-time on a continuous time scale and not on
381 a discrete time scale that would be based on the number of stages. Although the
382 occurrences are binned within discrete stage level units, the length of the individual
383 stages varies considerably. This introduces a bias, towards longer durations where
384 stage-level time resolution is low and towards shorter durations where time resolution
385 is high, because short ranging taxa are covered in the binning scheme in a varying
386 degree. Within a discrete time scale this bias would be obstructed. In our continuous
387 time scale the bias is present (Supplementary Table 6), but explicitly quantifiable by
388 comparing time bin length with our estimates. We find that the variation within our
389 estimates is large enough to overprint the expected dependence with time bin length
390 and we find no correlations between time bin length and lag time (Supplementary
391 Table 6).

392 As an additional test for the bias introduced by intervals with poor time resolution,
393 we filtered out all families of C_{long} which have their maximum diversification within
394 one of the six stage bins with durations more than twice as long as the median $t_{\text{r}\Delta\text{max}}$
395 (Emsian, Famennian, Tournaisian, Viséan, Norian, Aptian, Albian, Campanian). In
396 these exceptionally long stage bins detection of C_{short} is impossible. The resulting
397 diversity curves preserve the divergent trends of C_{long} and C_{short} (Extended Data Fig.
398 5).

399 We used the tabulated genus level assignments of marine genera to ecological modes
400 of life of ³⁰, defined in ²⁹ into tiering position relative to sea floor, degree of motility
401 and feeding mode to compare the life-modes of the two different cohorts (Extended
402 Data Fig. 3).

403 For our analysis of the waxing and waning pattern of family richness we followed a
404 procedure slightly modified from Foote ¹². We standardized the family longevity by
405 dividing each family range into equal time bins ranging from 1-100. We standardized
406 the estimated c-r richness of each family to 100 and calculated the percentage of
407 genera in each chronostratigraphic stage, rounded toward its nearest integers. We
408 then calculated the relative duration of each family range through chronostratigraphic
409 stages. Next, we assigned the standardized genus number to each of the respective
410 standardized time bins. The frequency distribution of numbers of genera within the
411 standardized longevity for all families gives our hat-shaped waxing and waning
412 pattern (Extended Data Fig. 2).

413 Additionally, for each family of C_{long} and C_{short} we filtered the PaleoBioDB download
414 for occurrences within the family time range, counted the number of collections with
415 genus occurrences of the respective family and divided it by the total number of
416 collections with genera in this subset. This ratio is our proxy for occupancy.

417 The average niche breadth of a family was calculated using the generalist-specialist
418 metric θ ³⁵, applied to each genus in a family. The metric is based on an analysis of
419 community difference (presence-absence beta diversity) across sites where a taxon
420 occurs. Taxa which occur at a number of sites which show high levels of community
421 difference are considered generalists, while taxa which occur at few sites and/or
422 consistently occur alongside a similar assemblage of other taxa are considered

specialists. We used the pairwise Jaccard dissimilarity to calculate beta diversity among genera in formations as a turnover estimate following the suggestions of⁵⁸.

Data Availability

The data downloaded from the PaleoBioDB (<https://paleobiodb.org>) and the URLs for retrieving data used to generate the results are available in the accompanying R code, which is available on <https://doi.org/10.5281/zenodo.3901507>

Code Availability

The R code for all analyses is available on <https://doi.org/10.5281/zenodo.3901507>

Competing interests

The authors declare no competing interests.

Acknowledgments

We are grateful for discussions and commentaries on earlier versions of the manuscript from Indrė Žliobaitė, Mikael Fortelius, and Stefan Geritz (all Helsinki, Finland). This is official Paleobiology Database Publication 374.

Author Contributions

A.P. and B.K. contributed to the design and implementation of the research, to the analysis of the results and to the writing of the manuscript.

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591

592 **Figure legends**

593

594 **Fig. 1: Distinction of two cohorts of families of skeletal marine metazoans.**

595 C_{long} , families with long macroevolutionary lag time (grey), C_{short} , families with early
596 burst diversification (black). **a**, Frequency distribution of families with longevities >
597 12.1 Myr. Note the skew of C_{short} toward shorter longevities. Mann-Whitney U test
598 between the two samples with $p \ll 0.001$. Mode of C_{short} at 20-40 Myr, Mode of
599 C_{long} at 40-60 Myr. **b**, Illustrative examples of early Palaeozoic families of trilobites
600 with early burst and long macroevolutionary lag diversification pattern. Spindle
601 width = relative genus richness. Based on a download from the PaleoBioDB from
602 16.04.2020. For abbreviations see Figure 2.

603

604 **Fig. 2: Richness curves of skeletal marine metazoans at genus level**

605 C_{long} , genera of families with long macroevolutionary lag time (dotted line) and C_{short} ,
606 genera of families with early burst diversification (solid line). Vertical bars are 95%
607 confidence intervals. Compare the different trajectories of the two cohorts. Richness
608 estimates calculated with c-r modeling approach. Blue hatched lines mark from left to
609 right end-Ordovician, end-Devonian, end-Permian, end-Triassic, and end Cretaceous
610 mass extinctions. Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C,
611 Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene.
612 Based on a download from the PaleoBioDB from 16.04.2020.

613

614 **Fig. 3: The increasing abundance of C_{long} genera in the fossil record.**

615 **a**, Mean number of genera belonging to C_{long} in a geological formation relative to all
616 skeletal non-colonial marine animals in the formation. Vertical bars are 95%

617 confidence intervals. **b**, Number of formations containing more than 75% genera
618 belonging to C_{long} relative to the total number of formations per stage. Based on
619 18040 genus occurrences in 6477 formations. Based on a download from the
620 PaleoBioDB from 16.04.2020. For abbreviations see Figure 2.
621