Low-Latitude Origins of the Four Phanerozoic Evolutionary Faunas

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Abstract: Sepkoski's hypothesis of Three Great Evolutionary Faunas that dominated Phanerozoic oceans represents a foundational concept of macroevolutionary research. However, the hypothesis lacks spatial information and fails to recognize ecosystem changes in Mesozoic oceans. Using a multilayer network representation of fossil occurrences, we demonstrate that Phanerozoic oceans sequentially harbored four evolutionary faunas: Cambrian, Paleozoic, Mesozoic, and Cenozoic. These mega-assemblages all emerged at low latitudes and dispersed out of the tropics. The Paleozoic–Mesozoic transition was abrupt, coincident with the Permian mass extinction, whereas the Mesozoic–Cenozoic transition was protracted, concurrent with gradual ecological shifts posited by the *Mesozoic Marine Revolution*. These findings support the notion that long-term ecological changes, historical contingencies, and major geological events all have played crucial roles in shaping the evolutionary history of marine animals.

One Sentence Summary:

Network analysis reveals that Phanerozoic oceans harbored four evolutionary faunas with variable tempo and underlying causes.

The hypothesis of the Three Great Evolutionary Faunas postulated that the major groups of marine animals archived in the Phanerozoic fossil record were distributed non-randomly through time and could be grouped into Cambrian, Paleozoic and Modern mega-assemblages (*1*). Jack Sepkoski formulated this hypothesis based on a factor analysis of family-level diversity within taxonomic classes (*2*). This hypothesis became a foundational concept of macroevolutionary research, used as a framework-setting assumption of studies on large-scale trends in diversity (*3, 4*), extinction (*5–7*), and evolution of marine animals (*8–10*). However, the three-phase model fails to account for ecosystem changes in Mesozoic oceans, which point to a later emergence of the modern marine faunas than was predicted by the model (*11–13*). Moreover, the geographic origin, timing, and causative drivers of the major biotic transitions between successive evolutionary faunas are still debated (*14–16*). This lack of clarity raises a fundamental question: How does Phanerozoic marine diversity structure into these discrete, global-scale mega-faunal assemblages that persist over extended intervals of geological time? Using a multilayer network framework, we unveiled the dynamic spatiotemporal organization of marine life during Phanerozoic times.

In the network analysis employed here (Fig. S1), we aggregated accepted genus-level occurrences of the dominant fossil groups of marine invertebrates (trilobites, decapods,

40 brachiopods, bryozoans, corals, echinoderms, and mollusks) (*17*) from the Paleobiology Database (*18*) into spatially and temporally explicit grid cells. We used the aggregated data to generate a multilayer network where each layer represents a geological stage in the geological timescale (*19*) and consists of grid cells and taxa that occur in each stage. The taxa connect both to stage-specific grid cells through intra-layer links with weights adjusted for sampling effort

45 (*20*) and to grid cells in adjacent stages through inter-layer links (*21*). The assembled network comprises 4,906 spatiotemporal grid cells and 18,297 genera, distributed into 99 stages (Data S1). This multilayer network representation simultaneously captures geographical and temporal relationships between taxa, which enables integrative spatiotemporal analysis of the Metazoan macroevolution.

50   Using the multilevel network clustering algorithm Infomap (21–23), we found that the assembled network is best described by four significant supermodules of highly interconnected taxa and grid cells (Data S2). These supermodules capture fundamental structure and dynamics of the Phanerozoic benthic marine faunas in two ways (Fig. 1). First, the supermodule grid cells divided the Phanerozoic rock record into four successive intervals: The Phanerozoic domains.

55 Second, the supermodule taxa define four partially overlapped sets of marine animals that characterize each Phanerozoic domain and sequentially shift dominance patterns over time: The four evolutionary faunas. These faunas represent marine mega-assemblages that vary in the composition and proportional representation of major animal groups, which we define as those taxa that represent ≥ 5 % of the supermodule genera (Fig. S2). Although our analysis identified

60 four mega-assemblages, in contrast to three assemblages discriminated in the classic analyses (1), the classes of marine invertebrates that contribute the most to our Cambrian, Paleozoic, and combined Mesozoic—Cenozoic mega-assemblages match those from the hypothesis of the Three Great Evolutionary Faunas, suggesting that these macroevolutionary units are unlikely to represent an artifact of the factor (12) or network analyses.

65   The Phanerozoic domains are slightly different from standard geological eras (Adjusted Mutual Information, AMI = 0.71). They show that Phanerozoic oceans sequentially harbored the four evolutionary faunas, as follows (Fig. 1): Cambrian (Fortunian to Paibian, 541-494 Ma), Paleozoic (Jiangshanian to Changhsingian, 494-252 Ma), Mesozoic (Induan to Hauterivian, 252-129 Ma), and Cenozoic (Barremian to Holocene, 129-0 Ma). However, the three mega-

70 assemblage shifts that define four evolutionary faunas vary in timing and causative drivers. The Cambrian—Paleozoic faunal shift appears to be an abrupt transition at the base of the uppermost Cambrian stage (Fig. 2A-C), although the limited number of fossil occurrences from that interval prevents a better understanding of the faunal transition (Supplementary Materials and Methods). The Paleozoic—Mesozoic faunal shift is also abrupt (Fig. 2C-D); the two consecutive domains

75 overlap in one geological stage that lasted ~2.5 Ma, and the mega-assemblages share a few taxa (Jaccard similarity index = 0.03). This faunal transition coincided with the Earth's largest mass extinction event (*6, 24*), which is viewed as the cause of the global shift in ocean life at that time (*2, 25*). In contrast, the Mesozoic—Cenozoic faunal transition is protracted, with a gradual shift in dominance among mega-assemblages, which share more taxa (Jaccard similarity index = 0.11)

80 (Fig. 1), and substantially overlap in geographic space (Fig. 2D-E). In addition, the two consecutive domains overlap in two geological stages that lasted ~8.0 Ma.

       The protracted Mesozoic—Cenozoic biotic transition is reminiscent of the gradual Mesozoic restructuring of the global marine ecosystems, which included changes in food-web structure, functional ecology of dominant taxa, and increased predation pressure (*11, 13*). These

85 changes in marine ecosystems started early in the Mesozoic era and continued throughout the Cenozoic era (*26, 27*). However, changes in Mesozoic oceans were particularly notable in the mid-Cretaceous (*28, 29*). Our results suggest that such changes in the global marine ecosystems may have been responsible for the gradual emergence of the modern evolutionary fauna. However, regardless of the transition mechanism, the gradual emergence of the Cenozoic

90 evolutionary fauna indicates that modern benthic biota first emerged during the early Mesozoic already, but did not became dominant until the mid-Cretaceous (~130 Ma) (Fig. 2A). In this way, the quadripartite structuring of the Phanerozoic marine fossil record revealed by multilayer network analysis resolves the conflict between the Three Great Evolutionary Faunas and the Mesozoic Marine Revolution hypothesis (*15*), which postulates the gradual diversification of

95 Sepkoski's modern evolutionary fauna during the late Cretaceous and Cenozoic (*11*).

The multilayer network framework provides a platform for studying the geographic distribution of the evolutionary faunas over time. The spatial distribution of the taxa shows that Mesozoic (Fig. 2D) and Cenozoic (Fig. 2E) evolutionary faunas were concentrated preferentially in lower latitudes before they became globally dominant by establishing their respective domain.

100 Taxa from both Paleozoic (Fig. 2C) and Mesozoic (Fig. 2D) evolutionary faunas preferentially persisted in low-latitude areas after a new fauna became globally dominant. Furthermore, the latitudinal extent of the Phanerozoic domains shows that evolutionary faunas became dominant first at low (< 12°, Cambrian, Paleozoic, and Mesozoic) and low-to-mid latitudes (< 40°, Cenozoic) and then experienced extratropical spread (Fig. 2A). Overall, these findings are

105 consistent with the Out of the Tropics hypothesis, which postulates tropical origin, poleward dispersal, and low-latitude persistence of the marine taxa (*30*).

The nested hierarchical structure of the multilayer network of Phanerozoic benthic marine faunas suggests that biogeographic structure underlies evolutionary faunas. The supermodules identified in the assembled network consist of lower-level modules that capture

110 internal structure of the faunas. Overall, modules from the second hierarchical level delineate shorter temporal units consistent with periods in the geological timescale (AMI = 0.83) (Fig. S3A). Moreover, some lower-level modules form geographically coherent units that change over time (Fig. S4) (*17, 20*). We were unable to map such bioregions through the entire Phanerozoic, which may reflect resolving limitations of existing data. Nevertheless, the presence of bioregions

115 suggests that evolutionary faunas scale up from localized geographic areas (Fig. 3; Fig. S4). Testing this hypothesis – mapping the complete Phanerozoic marine bioregions in a consistent fashion that links them explicitly to evolutionary faunas – will require improved paleontological data with finer chronostratigraphic constraints and improved spatial coverage.

Our analysis of the marine fossil record in a multilayer network framework demonstrates

120 that Phanerozoic oceans sequentially harbored four marine evolutionary faunas, which emerged at low latitudes and then persisted as globally dominant mega-assemblages. The major transitions between successive evolutionary faunas varied in tempo and underlying causes, ranging from abrupt global perturbations to protracted ecological shifts. In addition, we show that biogeographic structure underlies the evolutionary faunas in the dynamic organization of the

125 Phanerozoic marine diversity. Overall, these findings highlight the evolutionary importance of historical contingencies and support the notion that long-term ecological interactions, as well as global geological perturbations, have played a critical role in the shaping evolutionary history of marine animals (*16*).

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Supplementary Materials:

Materials and Methods

Figs. S1-S4

Tables S1-S2

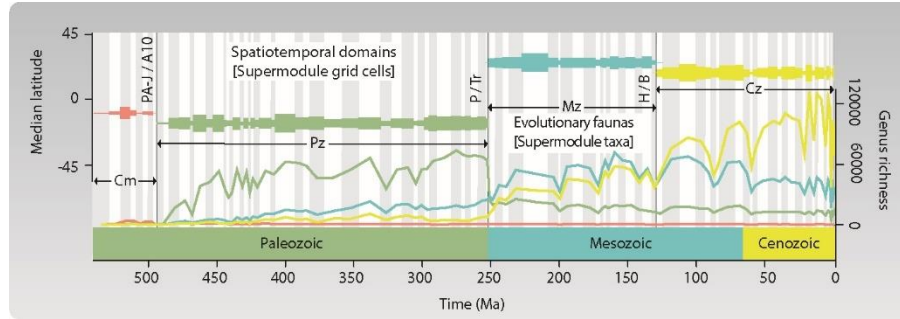Caption for Data S1-S2

References (*30-39*)

Figure 1. Modular configuration of the multilayer network of Phanerozoic benthic marine faunas.

210   The four evolutionary faunas and domains delineated by multilayer network analysis. Lines represent the genus richness of each evolutionary fauna. Mega-assemblages shift dominance patterns over time, but transitions are either abrupt (Paleozoic—Mesozoic faunal shift) or protracted (Mesozoic—Cenozoic faunal shift). Horizontal bars represent the Phanerozoic domains, with the bar width indicating the number of grid cells. The domains are temporally

215   coherent units describing the successive dominance of the four evolutionary faunas. Abbreviations: Cambrian (Cm); Paleozoic (Pz); Mesozoic (Mz); and Cenozoic (Cz). Domain boundaries: combined Paibian-Jiangshanian—Age10 (PA-J/A10); Permian—Triassic (P/Tr); and Hauterivian—Barremian (H/B). Supermodule robustness: Cambrian, $P_{0.7} = 1.00$; Paleozoic, $P_{0.7} = 0.99$; Mesozoic, $P_{0.7} = 0.25$ and $P_{0.5} = 1.00$; and Cenozoic, $P_{0.7} = 1.00$.
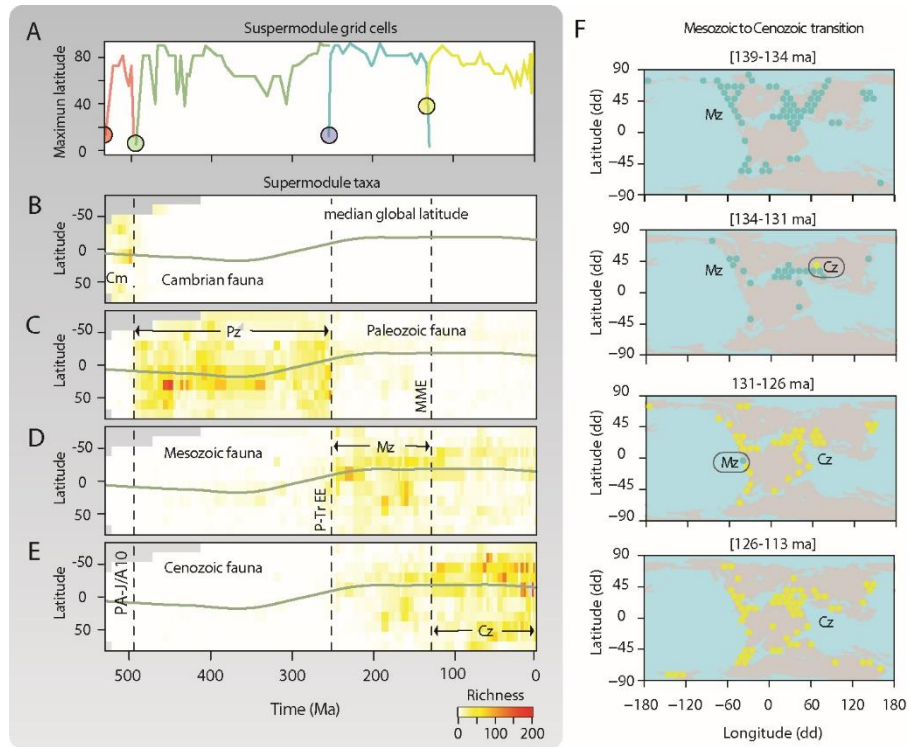
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Figure 2. Geographic distribution of the four evolutionary faunas over time.

(A) Latitudinal extent of the Phanerozoic domains. Lines represent the maximum latitude of the grid cells delimiting each domain. The domains emerge at low latitudes and experience rapid extratropical spread. (B-E). Genus richness maps of the four evolutionary faunas. Mega-assemblage shifts are either abrupt global perturbations (Cambrian—Paleozoic and Paleozoic—Mesozoic faunal shifts) or protracted changes with substantial temporal and spatial overlap (Mesozoic—Cenozoic faunal shift). (F) Maps across the Mesozoic—Cenozoic domain transition.
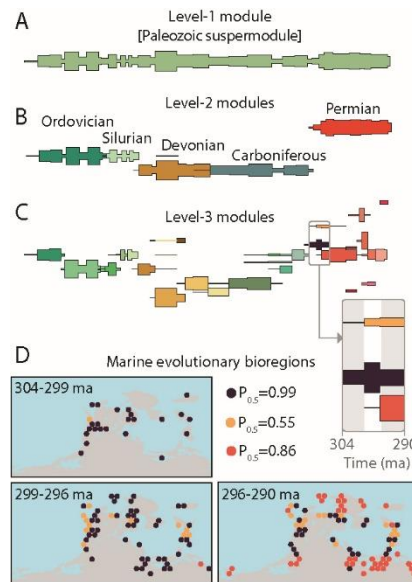
Figure 3. Nested hierarchical structure of the multilayer network of Phanerozoic benthic marine faunas.

235   (A) Supermodule. (B) Second hierarchical level. Modules are consistent with geological periods (all modules $P_{0.7} \geq 0.94$). (C) Third hierarchical level (all modules $P_{0.7} \geq 0.95$). (D) Bioregions around the Carboniferous/Permian boundary (all modules $P_{0.7} \geq 0.97$). Lower-level modules delineate geographically coherent units (*20*) that change throughout time (*17*). The nested hierarchical structure of the assembled network suggest that geographic structure underlies the

240   evolutionary faunas.