ECOLOGICAL SPECIATION

Ecologically diverse clades dominate the oceans via extinction resistance

Matthew L. Knope¹*, Andrew M. Bush²†, Luke O. Frishkoff³†, Noel A. Heim⁴†, Jonathan L. Payne⁵†

Ecological differentiation is correlated with taxonomic diversity in many clades, and ecological divergence is often assumed to be a cause and/or consequence of high speciation rate. However, an analysis of 30,074 genera of living marine animals and 19,992 genera of fossil marine animals indicates that greater ecological differentiation in the modern oceans is actually associated with lower rates of origination over evolutionary time. Ecologically differentiated clades became taxonomically diverse over time because they were better buffered against extinction, particularly during mass extinctions, which primarily affected genus-rich, ecologically homogeneous clades. The relationship between ecological differentiation and taxonomic richness was weak early in the evolution of animals but has strengthened over geological time as successive extinction events reshaped the marine fauna.

ore than half a century ago, Hutchinson (1) asked "Why are there so many kinds of animals?" and answered that adaptive ecological divergence permits coexistence of species and leads to taxonomic diversification. Indeed, ecological differentiation and taxonomic diversity are tightly correlated in many modern ecosystems (2-5). Ecological differentiation can permit the exploration of additional niches, reducing competition and fueling speciation (4-7). However, a similar correlation between ecological differentiation and taxonomic diversity would also be generated if causation were reversed, and a greater number of speciation events provided additional opportunities for ecological divergence (6, 7). Furthermore, taxonomic diversification occurs as a result of the difference between origination and extinction rates (Fig. 1A), but the contribution of extinction to the coupling between ecological differentiation and taxonomic diversification has received relatively little attention (8). Thus, the nature of the relationship between ecological differentiation and taxonomic diversification remains a central unanswered question in biology.

Here, we use a comprehensive dataset of both living and fossil marine animal genera to examine how the coupling between ecological and taxonomic diversity has evolved over the past 500 million years, leading to the modern relationship between ecological differentiation and taxonomic diversity on a global

*Corresponding author. Email: knope@hawaii.edu †These authors contributed equally to this work. scale. The fossil record provides a distinctive perspective on this question; the relationship between the two parameters can be tracked through time, and the influences of origination and extinction can be explicitly separated.

In the modern oceans, taxonomic diversity (referred to as genus richness) is highly correlated with differentiation into varied ecological modes of life (referred to as ecological diversity) (Fig. 2A), which are defined by a genus's tiering position relative to the seafloor, degree of motility, and feeding mode (9, 10) (class level: coefficient of determination $R^2 = 0.64$, P < 0.0001, Fig. 2A and fig. S1; phylum level: $R^2 = 0.90, P < 0.0001$, fig. S2). The slope of the regression relationship has increased over time (Fig. 2A and tables S1 and S2), and Cenozoic stages (66 million years ago to present) are not significantly different from the modern fauna (Fig. 2B). This steepening is primarily attributable to shifts associated with successive mass extinction events (Fig. 2 and fig. S3) rather than a simple continuous increase over time (multiple linear regression; continuous year-before-present effect: F = 0.06, P = 0.80; interval effect: F = 4.66, P = 0.002; full model $R^2 = 0.75$) (tables S1 and S2). These shifts indicate that the cumulative effects of mass extinctions played a key role in generating the currently strong correlation between ecological diversity and genus richness. This change in slope over time is a primary biological signal and not attributable to agedependent properties of the fossil record or effects of clade age (fig. S4). The quantity of unmetamorphosed marine sedimentary rocks does not increase toward the present (11, 12), and sampling standardization does not remove the drastic Cenozoic biodiversification event from raw diversity estimates (13), nor can the increase in slope be attributed to a greater proportion of genera assigned to ecological modes toward recent time intervals (14) or to the taxonomic scale of inquiry (compare Fig. 2 with fig. S3). Thus, the relationship that characterizes the living marine fauna and the more recent fossil record is a geologically recent development, shaped over hundreds of millions of years of evolutionary dynamics (Fig. 2).

In the Cenozoic, the most genus-rich classes are associated with lower origination rates (averaged across all prior time intervals) rather than higher rates, and their overall greater taxonomic net diversification rates result from their even lower extinction rates (Fig. 1B). However, before the end-Cretaceous mass extinction (66 million years ago), the most genus-rich classes tended to have much higher origination and extinction rates with greater taxonomic turnover (Fig. 1B). The most important determinant of genus richness in classes has therefore shifted over time from a propensity toward origination to resistance against extinction.

What led to this long-term shift in the relationship between diversity, origination, and extinction? It is often suggested that ecological differentiation either results from or promotes speciation (6, 7), but the results from the fossil record of marine animals contradict this hypothesis in several ways. First, ecologically diverse higher taxa tend to be characterized by lower, not higher, instantaneous probabilities (fig. S5 to S7) and rates of genus origination across time (Figs. 1C and 3). Thus, there is no evidence that high ecological diversity drives greater origination on these time scales (Fig. 3). Ecologically diverse clades also display lower instantaneous probabilities (fig. S5 to S7) and rates of genus extinction (Figs. 1C and 3). Across the Phanerozoic, greater ecological diversity is significantly associated with higher net diversification rates, whereas greater genus richness is significantly associated with lower net diversification rates across time (fig. S8), ultimately leading to the lowered taxonomic turnover rates in genus-rich classes in the Cenozoic (Fig. 1B).

The era-bounding mass extinctions resulted in massive loss of taxonomic diversity but little loss of functional groups (fig. S9) (14-16). The most genus-rich functional groups were hit hardest on a per-genus basis (14), whereas the most ecologically diverse groups were relatively spared (Fig. 1 and figs. S5 to S7), resulting in the evening out of taxonomic diversity across ecological modes (fig. S10). Further, although ecological diversity and taxonomic diversity within classes were not significantly correlated during the Paleozoic (541 million to 252 million years ago), standing ecological diversity during the Paleozoic does predict standing genus richness for almost every stage for the past ~150 million years (fig. S11) as well as aggregate genus richness across the Phanerozoic (14). In contrast, standing genus richness

¹Department of Biology, University of Hawaii, Hilo, Hil, 96720, USA. ²Department of Geosciences and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA. ³Department of Biology, University of Texas at Arlington, Arlington, TX 76019, USA. ⁴Department of Earth and Ocean Sciences, Tufts University, Medford, MA 02115, USA. ⁵Department of Geological Sciences, Stanford University, Stanford, CA 94305, USA.



Fig. 1. For clades with similar origination times, greater standing diversity will be associated with faster net diversification

rates. The net diversification rate represents the difference between the rates of origination and extinction. Consequently, greater net diversification can be associated with a higher or lower origination rate, depending on the relationship between extinction rate and diversity (**A**). Mean origination and extinction rates across all prior stages versus standing taxonomic richness (**B**) and ecological diversity (**C**) in the final stage of each period. BC, boundary-crosser extinction metric; Ma, million years ago. See figs. S13 and S14 for all underlying data points and net diversification rates.

during the Paleozoic does not predict either coeval or later ecological diversity (fig. S11), indicating that high genus richness does not lead to greater evolution of new modes of life. Rather, clades that had greater ecological diversity early were positioned to achieve greater taxonomic richness across time, because they weathered mass extinctions better than ecologically homogeneous clades did (Fig. 1 and figs. S5 to S7).

The dynamics revealed in the analysis of the fossil record suggest an alternative mechanism by which the modern correlation between ecological diversity and taxonomic richness developed through time. Clades that have high probabilities of origination on geologic time scales also have high probabilities of extinction (17, 18) (figs. S5 to S7), a correlation that has strengthened over time (fig. S12). Taxa that contain many modes of life tend to experience low intensity of both origination and extinction (Figs. 1C and 3) and display low volatility (Fig. 4), meaning that their diversity tends to change more slowly. Volatile taxa (i.e., those with higher origination and extinction rates) are more likely to go completely extinct, either through random chance (17) or during mass extinctions (18), when extinction intensity increases for all taxa and can be extremely high for volatile clades. Several highly volatile taxa diversified rapidly during the Paleozoic but were hit hard during mass extinctions, leading to a long-term shift in dominance toward lowvolatility taxa (18), which tend to be ecologically diverse.

Why do ecologically diverse taxa tend to have low volatility? To investigate the possibility that ecologically diverse classes have physiological or ecological traits that are protective against extinction at the genus level, we coded all genera by their physiological buffering capacity (the sophistication of the respiratory and circulatory systems, which are documented to have differential sensitivity to well-known ocean acidification and anoxic events in the geologic record) (19, 20), motility, habitat, and feeding mode (9). Extinction probability (in a general linear mixed-effects model) (10) was significantly lower for genera that were fully motile (P = 0.005), predatory (P = 0.01), pelagic (P = 0.01), or physiologically buffered and motile (buffered, fully motile: P < 0.001; buffered, facultatively motile: P = 0.02). Even after controlling for the effects of these traits, genera belonging to ecologically diverse classes still had a lower extinction risk (table S3), indicating the existence of additional, unidentified reasons that ecologically diverse clades have constituent members that are more resistant to extinction.

Motility and physiological buffering are associated with lower extinction risk during a number of major and minor mass extinctions, possibly because they impart a greater ability to cope with physiological stressors, such as ocean acidification and warming (21) (motility and buffering are related because unbuffered





Fig. 2. The relationship between taxonomic richness and ecological diversity in marine animal Linnaean classes in modern oceans and over the **past 444 million years.** (A) The abovementioned relationship for living and fossil faunas from individual geologic stages. Living marine animals demonstrate a strong, positive, and statistically significant power-law relationship [$R^2 = 0.64$;

P < 0.0001; slope 0.31; 95% confidence interval (CI), 0.27 to 0.36]. Paleo, Paleogene; Neo, Neogene; Jur, Jurassic; Cret, Cretaceous; Carb, Carboniferous; Perm, Permian; Sil, Silurian; Dev, Devonian. (**B**) The slopes of the regression lines in (A), with 95% CI plotted across time. Dashed vertical lines indicate mass extinction events.



Fig. 3. The slopes of the regression models for all stages since the end of the Ordovician period of the (log₁₀) number of modes or genera versus extinction and origination rates. Histograms on the right display the frequency of stage-specific slopes with mean and 95% Cl and examine the origination or extinction rate of single stages (thus maintaining statistical independence for hypothesis testing). Lines on left are cumulative curves of the time-averaged origination or extinction rate for all stages up to the focal stage for illustration of trends if assessed at different points in time, and the slope across all stages is indicated by a thick black line. See Fig. 2A for color legend.

physiology is often associated with a heavy carbonate skeleton, which limits motility). Motility is also necessary for many ecological modes of life, and movement permits access to food and habitats that are unavailable to nonmotile animals (9). Additionally, many nonmotile animals may have been negatively affected by increasing disturbance and predation intensity as motile animals diversified (22, 23). Thus, the morphological and physiological traits that permit a clade to explore greater amounts of ecospace also convey to its individual members added resilience against some of the most common and severe environmental stressors in the oceans.

The classes that had high taxonomic richness and low ecological differentiation during the Paleozoic, such as rhychonelliform brachiopods and crinoids, consisted largely or entirely of nonmotile suspension feeders that mostly cannot occupy infaunal or pelagic habitat tiers. In contrast, the classes and phyla that are genus-rich in the Cenozoic (e.g., mollusks, arthropods, and vertebrates) are generally motile, feed in a variety of ways, live across many habitat tiers, have more control over gas exchange with the environment, and have weathered mass extinctions well.

Contrary to the hypothesis that ecological differentiation is required to explain increases in taxonomic diversity via increased origination rates (6, 7), the classes that are the most ecologically diverse and taxonomically rich in the modern oceans have not had significantly higher average origination rates over time (Fig. 1). Instead, ecologically diverse classes have become genus-rich owing



Fig. 4. Volatility across time as a function of the number of genera and the number of ecological modes in Linnaean classes. Histograms (right) display distributions of correlation coefficients for volatility across all geologic stages. Overall Phanerozoic mean plotted with 95% CI to far right for volatility versus

genus richness = 0.07 ± 0.02 (top panel) and overall Phanerozoic mean plotted with 95% Cl to far right for volatility versus ecological modes = -0.04 ± 0.01 (bottom panel). C, Carboniferous; D, Devonian; J, Jurassic; K, Cretaceous; Ng, Neogene; O, Ordovician; P, Permian; Pg, Paleogene; S, Silurian; Tr, Triassic.

to lower background rates of evolutionary turnover and resistance to mass extinction (Figs. 1 and 3 and figs. S5 to S7). The fable of the tortoise and the hare applies well to marine animal diversification; some clades jumped out to an early diversity lead in the Paleozoic, only to be surpassed by those that combined low volatility, steady diversification, and strong physiological resistance to mass extinctions.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/367/6481/1035/suppl/DC1 Materials and Methods Figs. S1 to S15 Tables S1 to S5 References (25–33)

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Resisting extinction

Prevailing evolutionary wisdom tells us that ecological differentiation leads to speciation. Whether this pattern can be seen over paleontological time, however, has been difficult to test. Knope *et al.* looked at a dataset of thousands of modern and extinct marine groups and found the relationship to be more complex than expected. Ecological diversification is associated with lower rates of origination, and the taxonomical richness seemingly associated with these groups is due to resistance to extinction. Furthermore, the researchers found that the strong association between ecological differentiation and taxonomic diversity is a recent development shaped by extinction events over time. *Science*, this issue p. 1035

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