PALEONTOLOGY

Selectivity and the effect of mass extinctions on disparity and functional ecology

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Selectivity of mass extinctions is thought to play a major role in coupling or decoupling of taxonomic, morphological, and ecological diversity, yet these measures have never been jointly evaluated within a single clade over multiple mass extinctions. We investigate extinction selectivity and changes in taxonomic diversity, morphological disparity, and functional ecology over the ~160-million-year evolutionary history of diplobathrid crinoids (Echinodermata), which spans two mass extinctions. Whereas previous studies documented extinction selectivity for crinoids during background extinction, we find no evidence for selectivity during mass extinctions. Despite no evidence for extinction selectivity, disparity remains strongly correlated with richness over extinction events, contradicting expected patterns of disparity given nonselective extinction. Results indicate that (i) disparity and richness can remain coupled across extinctions even when selective extinction does not occur, (ii) simultaneous decreases in taxonomic diversity and disparity are insufficient evidence for extinction selectivity, and (iii) selectivity differs between background and mass extinction regimes.

INTRODUCTION

Mass extinctions are catastrophic events characterized by the loss of more than 75% of Earth's species and have occurred on only five occasions during the past half-billion years (1, 2). In addition to widespread species loss, mass extinctions change the trajectory of evolution by restructuring ecosystems, altering the dominant types of functional ecological groups, and affecting patterns of morphological evolution (3–6). Because changes in morphological and ecological diversity are major components of extinction events and their subsequent recoveries, examining changes in taxonomic, morphological, and ecological diversity in concert provides a more comprehensive view of mass extinctions and can illuminate underlying evolutionary processes.

Disparity, the overall diversity of morphological form, has been used extensively to investigate patterns of morphological evolution in both living and fossil groups (7, 8). Further, morphological features with inferred ecological functions (ecomorphological traits) can be used to study patterns of ecological disparity [e.g., (9–13)]. Although the accumulation of morphological and/or ecological disparity may covary with that of taxonomic diversity, peak taxonomic diversity and morphological disparity are often reached at different times in a clade's evolutionary history, and decoupling of taxonomic diversity and morphological disparity has been identified in numerous clades [e.g., (8, 14–20)]. Likewise, discordance between functional/ecological diversity and taxonomic richness has been identified in many cases across both mass extinctions and recovery events (21) as well as in modern ecosystems (22). Foote (14) summarized a number of scenarios that can result in discordance between disparity and taxonomic diversity. Extinction plays an important role in many of these decoupling scenarios, because morphologically/ecologically selective removal of taxa will often decrease disparity in concert with taxonomic diversity, whereas random extinction will maintain it (14, 18, 23). Further, selectivity of extinction can affect recovery of

clades following mass extinctions. For example, mass extinctions may result in bottlenecks that restrict the potential of some clades to undergo subsequent morphological evolution, resulting in suppressed disparity relative to taxonomic diversity (19, 24). Alternatively, extinction events may open ecological niches, resulting in adaptive radiations and increases in disparity as ecological opportunities are exploited through morphological and/or ecological innovation (20, 25, 26). Morphological disparity, ecological disparity, and taxonomic diversity are best evaluated jointly to fully understand how extinction events have shaped patterns of taxonomic diversity and disparity through time (27). However, few studies to date have evaluated the interplay between these three components of diversity (9), and to our knowledge, none have evaluated them within a single clade over multiple mass extinction events. Here, we investigate changes in morphological disparity, ecological disparity, and taxonomic diversity over the ~160-million-year evolutionary history of diplobathrid crinoids (Echinodermata), a major order of Paleozoic marine invertebrates. Diplobathrids persisted through two mass extinction events, the Late Ordovician (LOME; ~445 Ma ago) and the Late Devonian (~383 Ma ago), so their fossil record provides a framework for investigating the effect of mass extinction selectivity and taxonomic losses on patterns of morphological and ecological disparity (Fig. 1).

Crinoids (feather stars and sea lilies) are a class of marine invertebrates that originated during the Early Ordovician (~485 Ma ago) and still persist in modern oceans. Because of their well-sampled fossil record and multi-elemental skeletal construction, crinoids have been used extensively as a model group for investigating morphological radiations and patterns of disparity through time [e.g., (15, 16, 20, 28–32)]. Previous investigations of crinoid disparity have never explicitly included characters that capture functional ecology in crinoids, although some have inferred ecological function for subsets of character data (29) or identified potential ecological drivers of morphological disparity patterns (20, 28). However, studies of fossil and extant crinoids have established a suite of criteria by which crinoids partition niches through differences in feeding ecology, many of which directly correspond to skeletal morphology (33–35). As a result, these ecomorphological characters can be used to reconstruct fossil crinoid ecology with a high degree of fidelity.

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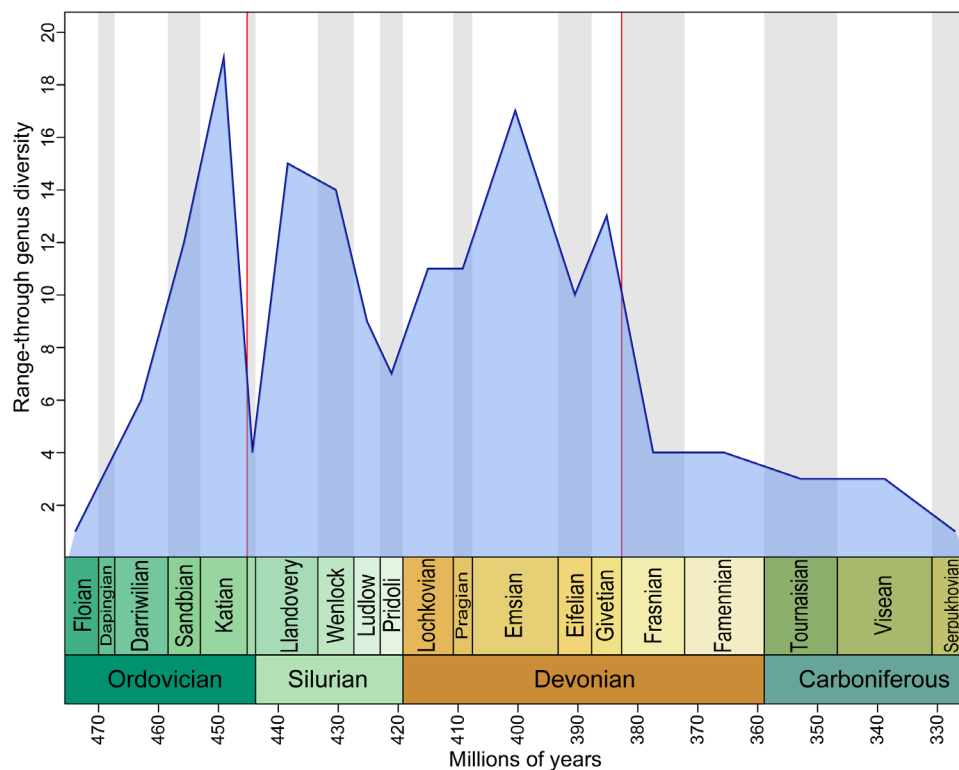*Corresponding author. Email: colesr@si.edu

Fig. 1. Diplobathrid diversity. Diplobathrid genus diversity through time calculated using the range-through method.

This study characterizes crinoid morphological and ecological disparity using separate morphological and ecological character matrices, which allows us to (i) document both ecospace and morphospace occupation through time, (ii) explore the interplay between morphological disparity, ecological disparity, and taxonomic diversity, and (iii) evaluate the effect of mass extinctions on patterns of morphological disparity and functional ecology. To further investigate the role of extinctions in driving the evolution of diplobathrid disparity, we test for morphological, ecological, and phylogenetic selectivity across mass extinction events and evaluate the long-term morphological and ecological effects of extinctions by examining disparity during post-extinction recovery periods. Combined, these approaches allow us to better understand fundamental processes underlying patterns of extinction and evolution, including the selective nature of mass extinctions, the long-term effects of mass extinctions on functional ecology and morphological evolution, and the interplay between different types of biodiversity over geological time scales.

RESULTS

Disparity and diversity through time

Matrices of morphological and ecological trait data were analyzed to investigate covariation and changes in morphology and ecology through time. Three primary indices were used to summarize different aspects of disparity. Sum of ranges (SOR) captures the total amount of morphospace/ecospace occupied and thus reflects patterns of overall expansion and contraction of trait space. Sum of variances (SOV) measures the dispersion of taxa around the centroid and reflects the density of taxa within the occupied region of morphospace/

ecospace. Shift in centroid was calculated to capture change in the overall position of taxa within morphospace/ecospace.

Patterns of morphological and ecological disparity are strikingly similar throughout the evolutionary history of diplobathrids, and both correlate significantly with each other and with taxonomic diversity for all disparity indices ($P < 0.05$ for all comparisons; Fig. 2 and table S1). Increases and decreases in disparity are similar across all indices, although they are most pronounced for SOR. This is likely due, in part, to the greater sensitivity of SOR to sample size compared to that of SOV. Following a rapid rise in disparity during the Middle to Late Ordovician, the first major decrease in morphological and ecological disparity occurred during the Late Ordovician in response to the LOME. Disparity then rebounded during the early-middle Silurian. Throughout the remainder of the Silurian, all measures of diversity declined, although taxonomic losses did not approach mass extinction levels. Following increases in disparity and taxonomic diversity during the Early-Middle Devonian, a third disparity decrease occurred during the Late Devonian. This consisted of an initial sharp drop over the Givetian-Frasnian stages, corresponding to the Late Devonian mass extinction, followed by a subsequent drop over the Devonian-Carboniferous boundary (Fig. 2). Shifts in centroid were largest during the Ordovician and across both mass extinctions, particularly the Late Devonian (Table 1).

Despite the overall correlation between measures of disparity and richness, there are two minor instances of decoupling. The first occurred during the Late Ordovician, when ecological and morphological SOR continued to increase from the Sandbian to Katian while SOV plateaued, indicating that total morphospace/ecospace occupation increased, while the relative distribution of taxa within
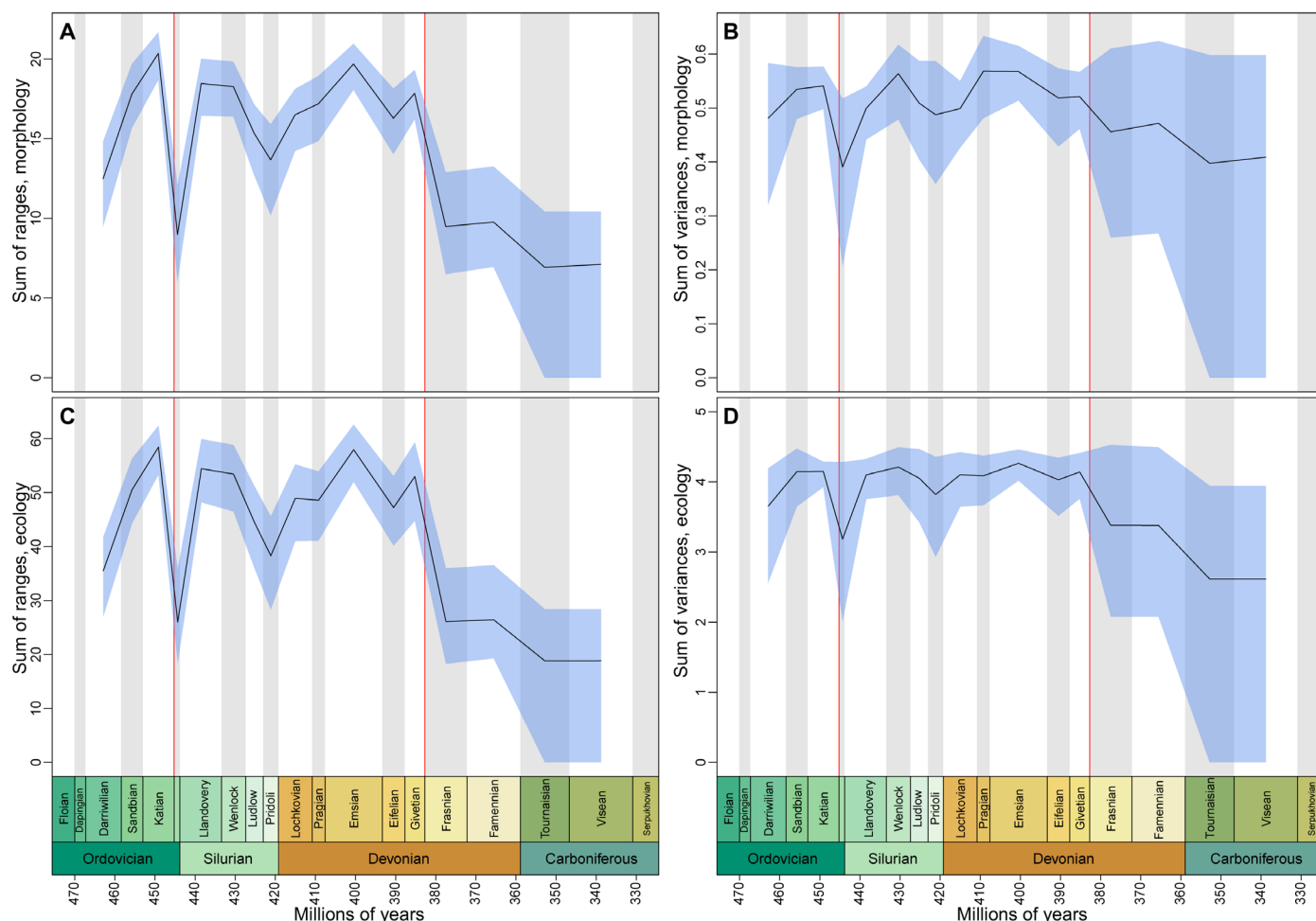
Fig. 2. Morphological and ecological disparity through time. (**A** and **B**) Morphological disparity. (**C** and **D**) Ecological disparity. Disparity is summarized using both sum of ranges (A and C) and sum of variances (B and D). Solid lines are mean values from 1000 bootstrap replicates, and shaded areas represent 95% confidence intervals.

morphospace/ecospace remained stable. The second instance of decoupling occurred during the Silurian, when taxonomic diversity and SOR decreased slightly from the Llandovery to the Wenlock, while SOV increased, resulting in differences in the timing of maximum SOR and SOV during the Silurian (Fig. 2). In contrast to decoupling during the Ordovician, this reflects increased density of taxa within morphospace/ecospace during the mid-Silurian, although the total amount of morphospace/ecospace occupied remained relatively stable.

Results are generally robust to resampling as reflected by bootstrapped confidence intervals, although low richness following the Devonian extinction results in broad confidence intervals, and evolutionary interpretations of these time bins should be made with care (Fig. 2). Although richness is relatively low throughout diplobathrid evolutionary history, it is still possible for disparity measures (including those like SOR that are more sensitive to sample size) to remain high or even increase during proportionally large decreases in richness [e.g., (*18*)]. As a result, the parallel decreases in disparity and richness that are observed here should not be driven by low richness alone.

Occupation of morphospace and ecospace through time

For the morphological dataset, the first two principal coordinate (PCO) axes account for 8.27% and 6.13% of the total variation. For the ecological dataset, the first two PCO axes account for 6.12% and 4.5% of variation. There is some correspondence between morphospace occupation and phylogeny, where both higher clades [defined from the phylogenetic analysis of Cole (*36*)] and traditional family groups tend to be clustered in morphospace, although there is substantial overlap especially among families (fig. S1). In contrast, ecospace occupation shows no correspondence with either clade- or family-level groups (fig. S1). Although the low amount of total variation accounted for by the first two PCO axes of morphospace and ecospace (Fig. 3) is typical for disparity analyses (*37*), interpretations of these plots should be integrated with measures that reflect total variation in the datasets like shift in centroid, SOR, and SOV.

Morphospace and ecospace occupation plots (Fig. 3) are largely consistent with disparity curves and relative shifts in centroid estimated across all axes but highlight changes between the morphological and ecological data that are captured only by very subtle differences in slopes of disparity curves (Table 1 and Fig. 2). During the Middle

Table 1. Shifts in centroid for morphological and ecological data. Shifts in centroid are calculated between adjacent time bins with >1 taxon and between pre- and post-extinction recovery intervals (Katian versus Llandovery for the Ordovician extinction, Givetian versus Famennian for the Devonian extinction). Mean shift in centroid is 0.24 for morphology and 0.66 for ecology.

Time bins compared	Shifts in centroid, morphology	Shifts in centroid, ecology
Darriwilian-Sandbian	0.315	0.837
Sandbian-Katian	0.287	0.649
Katian-Hirnantian	0.370	1.001
Hirnantian-Llandovery	0.318	0.920
Llandovery-Wenlock	0.268	0.678
Wenlock-Ludlow	0.195	0.531
Ludlow-Pridoli	0.200	0.536
Pridoli-Lochkovian	0.244	0.708
Lochkovian-Pragian	0.274	0.676
Pragian-Emsian	0.157	0.398
Emsian-Eifelian	0.190	0.503
Eifelian-Givetian	0.179	0.492
Givetian-Frasnian	0.301	0.893
Frasnian-Famennian	0.239	0.732
Famennian-Tournaisian	0.368	1.074
Tournaisian-Visean	0.000	0.000
Pre-/post-Ordovician extinction	0.254	0.659
Pre-/post-Devonian extinction	0.323	0.936

to early-Late Ordovician, major increases in morphospace and ecospace occupation occurred, most notably during the Darriwilian-Sandbian; these correspond with increasing measures of disparity and taxonomic diversity (Fig. 2). However, expansion of morphospace slowed during the Sandbian-Katian when taxonomic diversity peaked, while ecospace occupation contracted slightly. Over the LOME, both morphospace and ecospace occupation decreased sharply. During the subsequent early Silurian recovery, morphospace and ecospace returned to similar pre-extinction levels in terms of total occupation and regions occupied. By the Wenlock, new regions of both morphospace and ecospace had become occupied, which corresponded to moderate shifts in centroid compared to the mean (Table 1). Throughout the remainder of the Silurian and Middle Devonian, there was a prolonged period of relative stability in morphospace and ecospace occupation. Taxonomic losses from the Devonian mass extinction affected morphospace and ecospace differently. Initially, the distribution of taxa in morphospace remained relatively broad after the extinction, allowing relatively high morphospace occupation to be maintained, and a sharp decrease occurred later over the Devonian-Mississippian boundary along with the second-highest shift in centroid. By contrast, ecospace contracted dramatically as a result of the Devonian extinction and ecospace occupation remained low throughout the remainder of diplobathrid history.

Selectivity of extinction

We used the simulation-based "extinction space" approach of Korn et al. (23) as a diagnostic for distinguishing between random selectivity, selectivity for marginal taxa, or selectivity for subgroups ("lateral extinction"; see Materials and Methods for further details). Diplobathrid extinction events fall within the region of extinction space that corresponds with random extinction for morphological and ecological datasets over both the Late Ordovician and Late Devonian mass extinctions. These results indicate that taxonomic losses over both extinction events were random with regard to ecology and morphology.

For the LOME, we find no evidence for phylogenetic clustering of extinction ($P < 0.05$) and are unable to reject a random model of extinction ($P > 0.05$) in more than 1400 of 1500 trees (Table 2). For the Late Devonian extinction, we are unable to reject either the random model or the BM model ($P > 0.05$). These statistically ambiguous results for the Devonian extinction are likely due to low taxonomic diversity during this time, which is well below typical thresholds for calculating the D-statistic (38). Although standard deviation (SD) is high, the mean D-statistics for the Devonian extinction are negative, suggesting that random extinction is likely (Table 2).

Notably, simulation studies have suggested that intense extinction events can mimic selective extinction when sample sizes are small (39). Although diplobathrids had relatively low generic richness and underwent major taxonomic losses over the LOME and late Devonian extinctions, we still recover no evidence for selective extinction over these events. This further substantiates our findings that mass extinction events were nonselective in diplobathrids.

DISCUSSION

Correspondence between morphological disparity, functional ecology, and taxonomic diversity

Although this study is the first to evaluate diplobathrid disparity throughout the entire evolutionary history of the group, we recover some similar patterns to previous studies, such as rapid morphological evolution during the initial Ordovician diversification of crinoids (15, 16, 20, 31). Notably, our results reveal that functional ecology increased simultaneously during this major interval of diversification.

Our finding that both morphological and ecological disparity were significantly correlated with each other and with taxonomic diversity (Fig. 2 and table S1) contrasts with numerous studies that have identified decoupling between taxonomic diversity and disparity (14–20). However, concordance between diplobathrid disparity and diversity is consistent with a scenario of morphological diffusion or adaptive radiation based on the idealized diversification models of Foote (14, 40). The relationship between morphological and ecological disparity in the fossil record has received comparatively less attention than that of disparity and taxonomic diversity, but there is a general expectation that overall morphological form will correspond to ecological diversity (9, 10, 12, 40).

With few exceptions, morphological disparity and functional ecology were closely linked throughout the evolutionary history of diplobathrids, which may raise the question of whether structural linkages between morphological and ecological characters could be driving this covariation. However, the morphological and ecological matrices were constructed using nonoverlapping characters that come from structurally independent regions of the crinoid, and
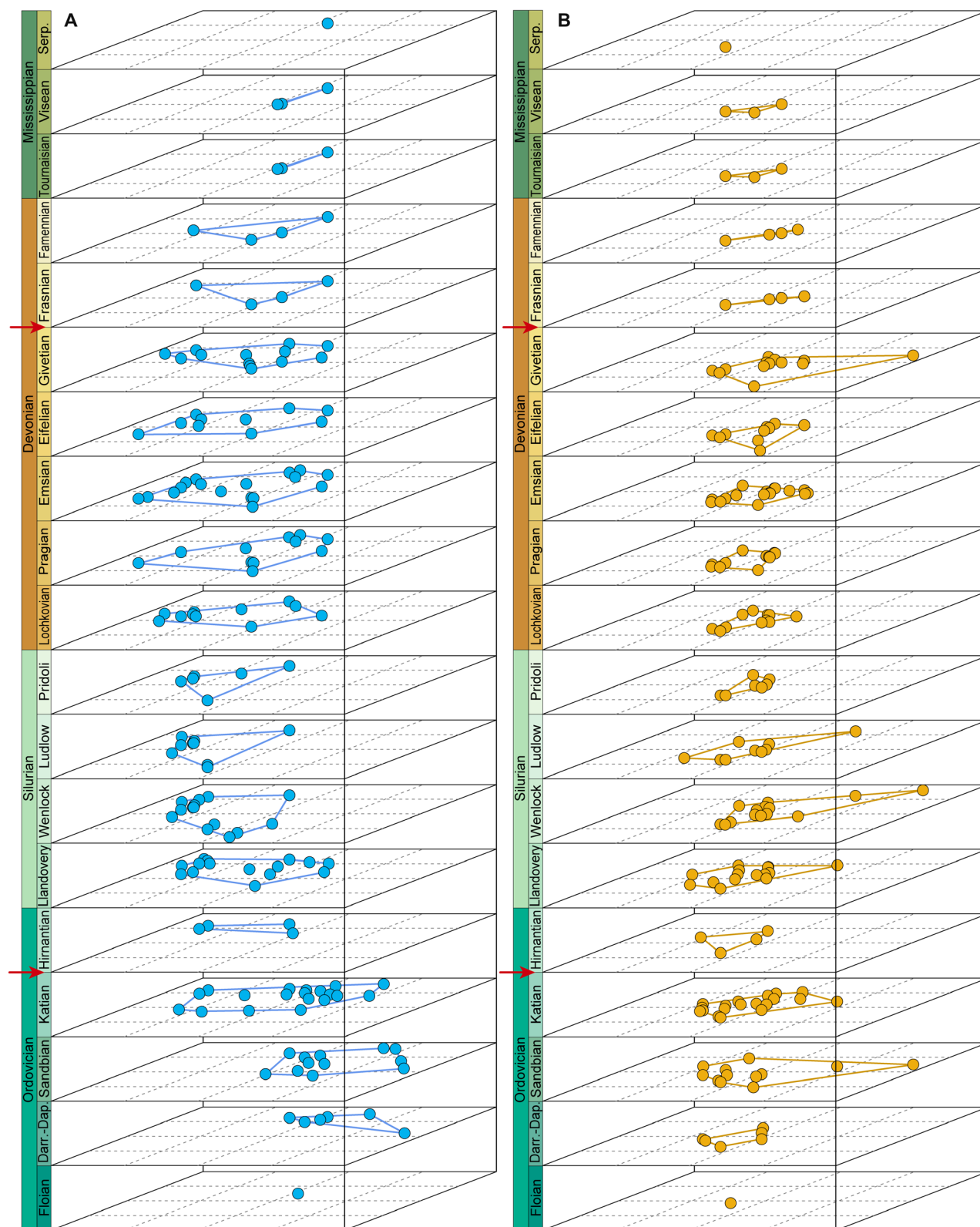
Fig. 3. Morphospace and ecospace occupation through time. (**A**) Morphospace occupation. (**B**) Ecospace occupation. Occupation of morphospace and ecospace is summarized from results of principal components analyses. Each plot represents all taxa present within a time bin; spacing of time bins is not scaled to time. Mass extinction boundaries are marked by red arrows. The first two axes (shown) for morphological and ecological datasets represent 14.4% and 10.62% of the variation, respectively. See the Supplementary Materials for plots with centroid and taxon labels (figs. S5 and S6).

Table 2. Phylogenetic clustering (*D*) of mass extinctions summarized over 1500 time-scaled trees. Mean *P* values indicate whether extinction scenarios deviate significantly from models of random ($D \geq 1$) versus BM phylogenetically structured extinction ($D \leq 0$); statistically significant values indicate that the model can be rejected. The number of trees out of a sample of 1500 for which random and phylogenetic structuring models can be rejected is also given.

Extinction scenario	Mean extinct taxa	Mean extant taxa	Mean *D*	SD of *D*	Mean *P* value, random model	*N* trees rejecting random model (*P* < 0.05)	Mean *P* value, BM model	*N* trees rejecting BM model (*P* < 0.05)
Ordovician: end-Katian	14.941	42.739	2.244	0.723	0.928	8	0.011	1436
Ordovician: end-Katian and end-Hirnantian	17.132	42.543	1.980	0.907	0.958	6	0.009	1446
Devonian: end-Givetian	3.361	3.989	−36.577	1302.165	0.536	20	0.318	219
Devonian: Givetian-Frasnian	4.607	2.914	−0.271	26.807	0.365	7	0.480	92

thus, covariation of the two datasets should not be an artefact of character sampling (see the Supplementary Materials for further discussion). Rather, we interpret the covariation of the two datasets to be the result of correlation of both morphology and ecology with taxonomic richness. As a result, overall morphology serves as a surprisingly effective proxy for functional ecology in diplobathrid crinoids.

Two intervals when morphological disparity, ecological disparity, and/or taxonomic diversity measures were asynchronous provide insight into unusual periods of diplobathrid macroevolutionary history. First, differences in SOR and SOV during the Sandbian-Katian suggest that total occupation of morphospace and ecospace increased while still maintaining the same general relationship to the centroid. For morphological data, this pattern is reflected in the morphospace plots (Fig. 3) and the minor shift in centroid (based on relative ranking of values for shift in centroid throughout the study interval; Table 1). For ecological data, there was a moderate shift in centroid (Table 1) and apparent contraction of ecospace from the Sandbian to Katian, particularly along the first PCO (Fig. 3). Thus, although SOR and SOV are very similar for both ecological and morphological disparity during the Late Ordovician, diplobathrid ecology underwent greater change during this time and contracted along at least its primary axis of variation. Crinoid communities underwent notable increases in complexity during the Katian (*35*), so this shift in functional ecology may reflect ecological restructuring in response to increasing competition and species packing within communities. Second, during the early Silurian recovery following the LOME, taxonomic diversity and SOR decreased slightly from the Llandovery to the Wenlock, while SOV increased. These changes were accompanied by occupation of new regions of morphospace and ecospace along with moderate shifts in centroid for morphology and ecology. An evaluation of stratigraphic ranges of Wenlock diplobathrids reveals that about 42% of taxa have their first occurrences in the Wenlock, and about 58% carried over from the Llandovery or earlier. Thus, this brief decoupling of diversity and disparity reflects a period of high taxonomic turnover during the Middle Silurian when the distribution of taxa became increasingly dense both morphologically and ecologically (as reflected by the increase in SOV), despite the

evolution of many new morphological and ecological forms. Similar patterns of innovation have been documented for other crinoid groups during the Middle Silurian, including morphological diversification of existing lineages and the evolution of many novel morphological forms [e.g., (*41*)]. Notably, the taxa occupying new regions of morphospace during this time differ almost entirely from those occupying new regions of ecospace (figs. S5 and S6).

Selectivity and the effect of mass extinctions on disparity
A number of factors have been identified that correspond to extinction selectivity in crinoids during background extinction intervals. A study including diplobathrids and other crinoid groups found evidence for selective extinction of morphologically specialized taxa during background extinction intervals (*42*). Selective extinction has also been identified in multiple crinoid clades for ecological traits like habitat breadth (*43*) and the structure of the filtration fan (*44*). Similarly, an investigation focusing exclusively on diplobathrids found that background extinction was selective for ecological factors including habitat preference and aspects of feeding ecology (*45*). Combined, these case studies provide abundant evidence for selective extinction of crinoids during background intervals across a range of traits. In contrast, we find no evidence for ecological or morphological selectivity in diplobathrid crinoids over mass extinctions. Whereas extinction during background intervals is commonly selective, mass extinctions tend to be nonselective with regard to ecological and morphological traits (*23*, *46*–*49*), although there are notable exceptions (*50*). Our results support the presence of selectivity differences during background versus mass extinction regimes with regard to both ecological and morphological selectivity in crinoids. In particular, results from the present study and those of Cole (*45*) indicate that diplobathrids underwent ecologically selective extinction over background regimes and nonselective extinction during mass extinctions.

A prevalent expectation in the study of morphological diversity is that disparity will be maintained when extinction and/or origination are random with respect to morphology, whereas disparity will tend to decrease when extinction and/or origination are morphologically

selective. This correspondence between morphological variance and selectivity was summarized by Foote [figure 1 of (*14*)] in the context of idealized clade histories [note that this is discussed in terms of morphological variance but also applies to SOR and centroid shift (*23*)]. On the basis of expected correlations between variance and extinction selectivity, many studies have used concomitant decreases in variance and taxonomic diversity as evidence for selective extinction without directly testing for selectivity [e.g., (*12*, *28*, *46*)]. This relationship between variance and selectivity has been supported by simulation studies of extinction space (*23*) and empirical investigations that directly tested for selectivity (*17*, *51*). Further, recent simulations evaluating the effect of selective extinction and other factors on disparity recovered results that are broadly consistent with previous expectations, where SOV typically decreases in response to strongly selective extinctions but may remain relatively unchanged or even increase during nonselective extinctions (*39*). In contrast, our empirical results conflict with this expected relationship between disparity and extinction selectivity. In diplobathrids, SOV decreases over mass extinction events despite no evidence for morphological or ecological extinction selectivity from extinction space plots (Fig. 4) and no notable shift in centroid occurs over extinction events (Table 1). However, many of the simulations by Puttick *et al.* [figure S3 of (*39*)] show that SOV can decrease when selective extinction is weak or absent, as long as certain conditions are met for variables like background extinction intensity, mass extinction severity, and the number of taxa. These results suggest that even if selective extinction results in decreases in SOV as a general rule, there are instances where nonselective extinctions may still produce similar patterns. As a result, coincident decreases in disparity and diversity should not be

used in isolation as evidence for selective extinction, and instead, methods that directly test for extinction selectivity should be used [e.g., (*17*, *23*, *38*, *52*)].

Nonadaptive recovery and decline following mass extinctions

Widespread removal of taxa from mass extinctions may reduce morphological diversity to such a degree that subsequent taxonomic and/or morphological diversification is hampered, resulting in evolutionary bottlenecks with long-term consequences for diversification (*19*, *24*). Alternatively, mass extinctions commonly create conditions for adaptive radiations through widespread removal of taxa followed by promotion of diversification through increased ecological opportunity (*25*, *26*). Although adaptive radiations can be challenging to identify, they are expected to comprise increases in both taxonomic and morphological diversity, with the latter typically serving as a proxy for functional diversity.

Superficially, rapid increases in diplobathrid taxonomic richness and disparity following the LOME appear consistent with a model of adaptive radiation driven by ecological opportunity. However, diversification during the recovery interval was not accompanied by morphological or ecological innovation. Although shifts in centroid were relatively large across the LOME, diplobathrids that evolved in the wake of the LOME were largely restricted to pre-extinction regions of morphospace and ecospace, with comparatively small shifts in centroid relative to the mean between pre-extinction (Katian) and post-extinction (Llandovery) intervals (Fig. 3 and Table 1). Thus, early Silurian diplobathrids were both ecologically and morphologically similar to their Ordovician predecessors and predominantly returned to formerly occupied niches rather than expanding into newly vacated niche space. By contrast, previous studies have documented the radiation of other crinoid groups into new areas of trait space following the LOME and other extinction events (*15*, *16*, *20*, *31*). Thus, although the rapid increase in diplobathrid taxonomic diversity does indicate that the group underwent a substantial diversification following the LOME, this was more consistent with a pattern of nonadaptive radiation (*53*) where morphological diversification follows a more diffusive pattern rather than an "early burst" pattern. This is equivalent to the type 3 diversification of Jablonski (*27*), where increases in richness are not associated with evolution of anatomical features tied to novel ecological functions. However, the LOME did not permanently suppress diplobathrid evolution as the group was able to subsequently diversify both morphologically and ecologically during the early-middle Silurian.

By contrast, the Devonian extinction was a major evolutionary bottleneck for diplobathrids. Along with generic diversity, morphological and ecological disparity dropped precipitously over the Devonian extinction and continued to decline throughout the Mississippian. A sharp decrease in ecospace occupation and a large (greater than mean) shift in centroid for ecology occurred over the Givetian-Frasnian extinction boundary, whereas a relatively large region of morphospace remained occupied into the Famennian before decreasing over the Devonian-Mississippian boundary (Table 1 and Fig. 3). The timing of decreases in morphospace versus ecospace occupation indicates that Late Devonian and Mississippian diplobathrids were especially restricted in terms of ecological strategies, although morphological forms retained a moderate degree of variability. This marked ecological bottleneck over the Devonian extinction may have been severe enough to prevent subsequent
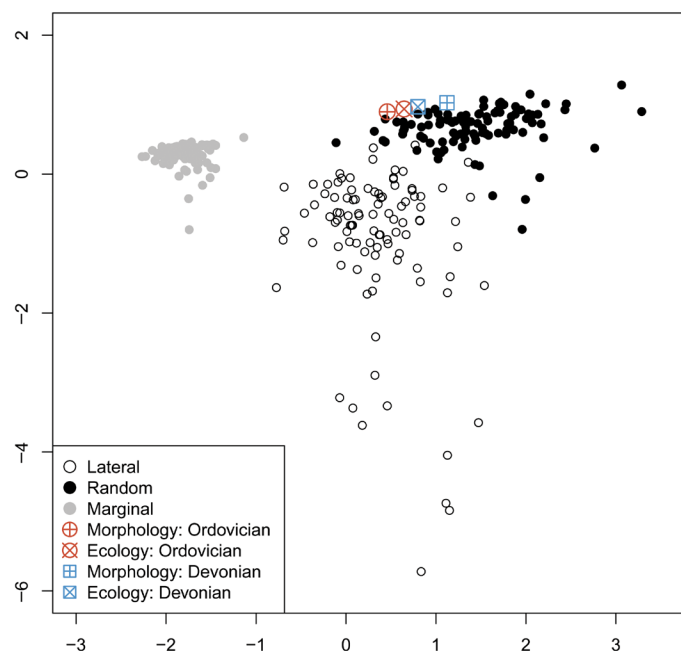

Fig. 4. Locations of diplobathrid extinction events in extinction space. Empirical data from diplobathrid extinctions are compared to those of lateral, random, and marginal extinctions simulated under 75% extinction intensity (*23*). Diplobathrid extinction events are divided into morphological and ecological datasets for both the Late Ordovician mass extinction and the Late Devonian mass extinction.

morphological diversification and the evolution of new genera, leading to the steady decline of diplobathrids and their ultimate extinction at the close of the Mississippian. Although the sample size for Late Devonian and Mississippian diplobathrids is small, it reflects the actual known generic diversity at the time (three genera included in the dataset of four known genera, with one genus excluded because arms have not been preserved).

Patterns of Paleozoic crinoid disparity

We recover evidence for rapid morphological evolution during the initial Middle Ordovician diversification of crinoids, which is broadly comparable to previous findings (*15*, *31*). Further, results of this study establish that functional ecology increased simultaneously during this major interval of diversification and during subsequent diversifications such as that occurring in the wake of the LOME (Fig. 2). Although this study is the first to evaluate diplobathrid disparity throughout the entire evolutionary history of the group, diplobathrid disparity was previously summarized using a more restricted Ordovician-Silurian dataset (*31*). We recover similar patterns of morphological disparity over this time interval, although there are some notable differences. In the analysis of Deline and Ausich (*31*), diplobathrid disparity (as measured by mean pairwise dissimilarity) peaked during the late Middle Ordovician and then declined through the Late Ordovician with only a slight decrease and subsequent recovery over the LOME [figure 9B of (*31*)]. By contrast, our results indicate that high disparity was reached during the early Late Ordovician (Sandbian), remained high until it dropped dramatically over the LOME, and recovered rapidly during the Early Silurian, eventually exceeding pre-extinction levels by the middle Silurian [Fig. 2; see also fig. S2 for disparity curves using mean pairwise dissimilarity]. The more pronounced LOME drop and Silurian recovery of our study are likely due to more extensive character sampling and larger taxonomic sample size, attributable, in part, to a recent notable increase in the known taxonomic diversity of Late Ordovician and early Silurian diplobathrids [e.g., (*54*–*56*)].

Conclusions

Morphological disparity is a nuanced measure of biodiversity. Care should be taken when interpreting drivers of disparity, because similar patterns can be produced by multiple generating processes (*20*, *57*). Here, we emphasize that although morphology is often used as a proxy for ecological diversity, evaluating both morphological and ecological disparity permits a deeper understanding of the nature of diversification. Further, our results demonstrate that simultaneous decreases in taxonomic and morphologic diversity cannot be used as evidence for selective extinction and highlight the importance of explicitly testing for selectivity and incorporating other dimensions of diversity into disparity studies.

MATERIALS AND METHODS
Data preparation

Data for morphological disparity were compiled from the phylogenetic character matrix of Cole (*36*), which was comprehensive across order Diplobathrida at the genus level (*N* = 100 genera). The dataset was vetted to exclude invariable characters, and characters with ecological functions were reassigned to a second ecological matrix. To capture character dependencies occurring in complex or nested character suites, we reevaluated all remaining morphological characters and subdivided several that represented character complexes.

In total, 121 morphological characters were used to capture overall morphological disparity of diplobathrid crinoids.

The ecological dataset was compiled from 18 characters taken from Cole (*36*) that were inferred to have ecological function and 10 continuous characters from the dataset of Cole (*45*) that were originally collected to summarize diplobathrid functional ecology for a total of 28 ecological characters. Crinoid functional morphology has been studied extensively, and a suite of characters have been identified that directly correspond to ecological functions, especially relating to feeding ecology (*33*, *34*). A detailed summary on inferring functional ecological traits in crinoids is provided by Cole *et al.* (*35*). For characters included in the ecological matrix for this study, examples of discrete characters include arm number, branching type, construction of the brachials, and pinnule arrangement. Examples of continuous ecological characters include brachial width, pinnule spacing, and density of the filtration fan. Because ecological characters are restricted to regions of the body that do not overlap with morphological characters, the two matrices are structurally independent (see the Supplementary Materials for additional details).

A $\log(x + 1)$ transformation was applied to continuous ecological characters before analysis. Several poorly preserved taxa (e.g., those without arms preserved) had extensive missing data for the ecological matrix, with some preserving too few characters to differentiate them from other taxa. As a result, 22 taxa were removed from both the ecological and morphological matrices, leaving a total of 78 genera considered for all analyses.

Character dependencies can result in inapplicable character codings that are typically treated as missing data by dissimilarity metrics such as Gower's coefficient. However, inapplicable characters can be accounted for using a recently developed dissimilarity metric (*58*). To investigate the effect of inapplicable characters on disparity measures, we created of list of character dependencies outlining these nested relationships for both morphological and ecological datasets by identifying each character as primary or secondary (see the Supplementary Materials for an example). A total of 22 secondary characters were identified in the morphological dataset, and six secondary characters were identified in the ecological dataset; all others were primary characters.

Following Cole (*36*), genus-level diversity was calculated using the range-through method based on first and last appearances of all known species within a genus. Stratigraphic ranges of genera were based on the compilation by Webster and Webster (*59*) with updates to ranges added from more recent taxonomic descriptions and stratigraphic revisions (see the Supplementary Materials). Taxa were binned using the finest level of stratigraphic resolution that could be applied across all sampled genera, which was stage level for the Ordovician, Devonian, and Mississippian and series level for the Silurian. Because no diplobathrids are known from the Dapingian stage of the Ordovician, the Dapingian was combined with the subsequent stage, the Darriwilian, for analyses.

Analysis of morphological and ecological disparity

Disparity analyses were conducted in R using the package Claddis (*37*). Dissimilarity matrices of both the ecological and morphological datasets were constructed using Gower's coefficient as the dissimilarity metric. Dissimilarity matrices were arcsine-transformed (*37*), and a Cailliez correction was applied to correct for negative eigenvalues that are produced when principal coordinates analysis is applied to matrices with missing data. Gower's coefficient treats inapplicable characters as missing, which can lead to erroneous rank

ordering of pairwise dissimilarities, and a recently developed family of dissimilarity metrics has been proposed that avoids this problem (58). Using character dependency lists of primary and secondary characters, we constructed dissimilarity matrices using the metric of Hopkins and St John (58) but found that applying this method did not substantially alter the results of downstream analyses (figs. S3 and S4), likely because of the small proportion of inapplicable characters within the morphological and ecological matrices (4.6% and 8.3% of the character states, respectively).

Multiple disparity indices have been developed to capture different aspects of trait distributions; as a result, consideration of multiple indices is necessary to fully characterize changes in disparity (37, 60), especially over mass extinction events (39). We quantified morphological and ecological disparity using three standard indices, which were chosen to capture different aspects of disparity: SOR, which reflects the total amount of morphospace/ecospace occupied in a given time bin; SOV, which provides a measure of dispersion of taxa around the centroid of the group; and shift in centroid, which measures change in the position of taxa within morphospace/ecospace independent of SOR and SOV [for further interpretations of disparity indices, see (7, 60–62)]. SOR and SOV are not redundant with one another (7, 60) but may change in a coordinated fashion in certain scenarios (23, 62). SOR and SOV were calculated from PCO scores across all axes to capture total variation of the data. To generate confidence intervals for disparity through time, 1000 bootstrap replications were run for SOR and SOV with taxa resampled with replacement in each time bin. To allow direct comparison with past studies of crinoid disparity, we also calculated the mean pairwise dissimilarity, an index that is calculated directly from the dissimilarity matrix and summarizes the average distance between every possible pair of taxa. Although this index may be preferred for avoiding problems with disparity indices calculated from ordinations (37, 60), it is typically very similar to SOV, as is the case here (fig. S2).

To test for covariation between disparity and diversity, we analyzed the correlation between ecological disparity, morphological disparity, and genus diversity using Pearson's coefficient and first differences to remove potential correlations induced by temporal autocorrelation (applied by taking the time series at time t minus the series at time $t − 1$). Correlation was assessed using mean bootstrapped values for all three disparity indices. Last, to visualize morphological and ecological change through time, morphospace and ecospace occupation plots were generated using the first two PCO axes for each time bin. Because visualizations only reflect the first two axes of variation, which are relatively small for both morphological and ecological datasets, we further summarized change in morphospace and ecospace occupation by calculating the centroid for each time bin over all PCO axes. Centroid values were then used to calculate shift in centroid between time bins and between pre- and post-extinction recovery intervals.

Morphological and ecological extinction selectivity

To determine if there was morphologically or ecologically selective extinction of diplobathrids during the Ordovician and Devonian mass extinctions, we used the simulation-based extinction space approach of Korn et al. (23) as a diagnostic for distinguishing between random selectivity, selectivity for marginal taxa, or selectivity for subgroups (lateral extinction). Briefly, Korn et al. (23) generated morphospaces by sampling different initial distributions (e.g., random versus normal) and then subsampling these for each of the

three modes of extinction (random, lateral, or marginal) at different extinction intensities (50%, 75%, and 87.5% loss of taxa). The change in the range was calculated as the percentage ratio of the SOR of the "post-extinction" dataset to the SOR of the "pre-extinction" dataset. The change in the variance was calculated as the percentage ratio of the SOV of the post-extinction dataset to the SOV of the pre-extinction dataset. The change in the centroid was calculated as 100 minus the percentage ratio of the change in the position of the centroid of the pre- and post-extinction datasets to the SOR of the pre-extinction dataset. These disparity indices were calculated for all simulated datasets, and a principal components analysis was used to graphically summarize the effect of different modes of extinction, where the distribution of variation along the components is indicative of the degree of selectivity and asymmetry in selectivity (extinction space).

To compare our results to those predicted by Korn et al. (23) for each kind of extinction selectivity, we calculated the percent change in the SOR, the percent change in the SOV, and the percent change in the position of the centroid for diplobathrid morphology and ecology across the LOME (78.9% of genera lost) and the Late Devonian extinction (69.2% of genera lost). We then generated an extinction space by running a principal components analysis of the empirical results from the diplobathrid datasets with the simulated results of Korn et al. (23) for a similar extinction intensity (75% loss in both cases). Extinction space analyses were conducted in R.

Phylogenetic clustering of extinction

Extinctions may be random or may selectively eliminate taxa that have certain traits. Many case studies have found evidence for selective extinction for a variety of intrinsic traits (e.g., ecology and life history) and/or emergent traits (e.g., geographic range size). Because many of these traits are phylogenetically structured, selective extinction may, in turn, be correlated with phylogeny, where taxa that go extinct over a given time interval are more closely related than would be expected given random extinction (i.e., phylogenetically clustered). To determine whether mass extinction events were phylogenetically clustered, we calculated the Fritz-Purvis D-statistic for diplobathrid crinoids over the Late Ordovician and Late Devonian mass extinctions (38) and evaluated support for phylogenetic clustering assuming a Brownian motion (BM) model versus random extinction. The Fritz-Purvis D-statistic tests for clustering of a binary trait on a phylogenetic tree (38) and can be applied to studies of extinction selectivity by assigning "extinct" and "not extinct" as binary states.

For each extinction event, we trimmed 1500 time-scaled trees from Cole (45) to include only pre- and post-extinction taxa using the R package motmot (63) and calculated the Fritz-Purvis D-statistic using the R package caper [(64); code adapted from (52)]. We then summarized the mean P values and the proportion of trees for which D indicates phylogenetic clumping of extinction under a BM model ($D ≤ 0$) versus random extinction ($D ≥ 1$). Pre- and post-extinction taxa were identified based on two extinction scenarios for each of the mass extinctions. For the late Ordovician extinction, these scenarios were a single-pulse extinction at the end Katian (an interval from 453 to 445.2 Ma ago) and a two-pulse extinction from the Katian to Hirnantian (an interval from 453 to 443.8 Ma ago). The scenarios considered for the Devonian were a single end-Givetian event (an interval from 387.7 to 382.7 Ma ago) and a prolonged Givetian to Frasnian extinction (an interval from 387.7 to 372.2 Ma ago). Because of the low number of taxa present during the Middle and Late Devonian, some of the time-scaled trees for the late Devonian

extinction contained only taxa that went extinct before the end of the interval(s) considered, preventing calculation of the D-statistic. These trees were excluded from the study. A total of 103 trees were discarded for the single-pulse Givetian extinction, and 53 trees were discarded for the prolonged Givetian-Frasnian extinction scenario. The D-statistic was calculated for all remaining trees and summarized as a mean D value for each extinction event. Support for random versus clustered extinction was evaluated by calculating the mean P value for random extinction ($D \geq 1$) and phylogenetic clumping of extinction under a BM model ($D \leq 0$) and by summarizing the proportion of trees for which a significant P value was recovered. Note that for tests of the D-statistic, significant P values indicate that the model being tested can be rejected (*38*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/19/eabf4072/DC1

View/request a protocol for this paper from *Bio-protocol*.

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Selectivity and the effect of mass extinctions on disparity and functional ecology

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