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Response of beta diversity to pulses of Ordovician-Silurian mass extinction

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Abstract. Ecologists are increasingly using the fossil record of mass extinction to build predictive models for the ongoing biodiversity crisis. During mass extinctions, major depletions in global (i.e., gamma) diversity may reflect decrease in alpha diversity (i.e., local assemblages support fewer taxa), and/or decrease in beta diversity (such that similar pools of taxa are common to a greater number of local areas). Contrasting the effects of extinction on alpha and beta diversity is therefore central to understanding how global richness becomes depleted over these critical events. Here we investigate the spatial effects of mass extinction by examining changes in alpha, beta, and gamma diversity in brachiopod communities over both pulses of Ordovician-Silurian extinction (~445.2 and ~438.8 million years ago), which had dramatically different causal mechanisms. We furthermore reconstruct geographic range sizes for brachiopod genera to test competing models for drivers of beta diversity change. We find that: (1) alpha and beta diversity respond differently to extinction; (2) these responses differ between pulses of extinction; (3) changes in beta diversity associated with extinction are accompanied by changes in geographic range size; and (4) changes in global beta diversity were driven by the extinction of taxa with statistically small and large ranges, rather than range expansion/contraction in taxa that survive into the aftermath. A symptom of ongoing biotic crisis may therefore be the extinction of specific narrow- or wide-ranging taxa, rather than the global proliferation of opportunistic and “disaster” forms. In addition, our results illustrate that changes in beta diversity on these longer timescales may largely be dictated by emplacement and removal of barriers to dispersal. Lastly, this study reinforces the utility of the fossil record in addressing questions surrounding the role of global-scale processes (such as mass extinctions) in sculpting and assembling regional biotas.

Key words: beta diversity; brachiopods; climate change; glaciation; mass extinction; Ordovician; Silurian.

INTRODUCTION

Mass extinctions have a profound effect on the history of life. These are commonly studied in terms of the rise and fall of major taxonomic groups (e.g., Jablonski 1986a, Sepkoski 1986, Erwin 1993) and shifts in basic ecological systems (e.g., (Bambach et al. 2002, Wagner et al. 2006). By contrast, paleontologists have paid less attention to the effects of mass extinction on the spatial organization of biota (Jablonski 2001, 2008) despite the fact that studies focused on the current biodiversity crisis show strong biogeographic patterns to ecological stress (Parmesan et al. 1999, Scott et al. 2002, Thomas 2010). In the context of this crisis (the “6th mass extinction” [see Erwin 2009, Barnosky et al. 2011, Harnik et al. 2012, Hönisch et al. 2012, Hull and Darroch 2013]), both ecologists and paleontologists focusing on conservation and monitoring efforts require

historical data pertaining to how (and on what scales) these biogeographic changes will become manifest. Examining biogeographic changes over intervals of mass extinctions in the fossil record are therefore an invaluable and underused source of information (Jablonski 2001).

One of the most basic biogeographic patterns is beta diversity, i.e., the variation in taxonomic composition across space (Whittaker 1960). In the simplest formulations, beta diversity is the ratio between global richness (gamma diversity), and local richness (alpha diversity). More recently, beta diversity has been used to describe rates and patterns of ecological differentiation at any given scale, and is central to addressing processes underlying the formation of local and regional biotas. Correspondingly, beta diversity studies already underpin much of conservation theory and practice (McKnight et al. 2007). Studies examining changes in beta diversity through time are less common, and typically investigate change on relatively short temporal scales (i.e., 10^1 – 10^2 years; see Collins et al. 2000, Korhonen et al. 2010). Although these studies are extremely valuable, there is

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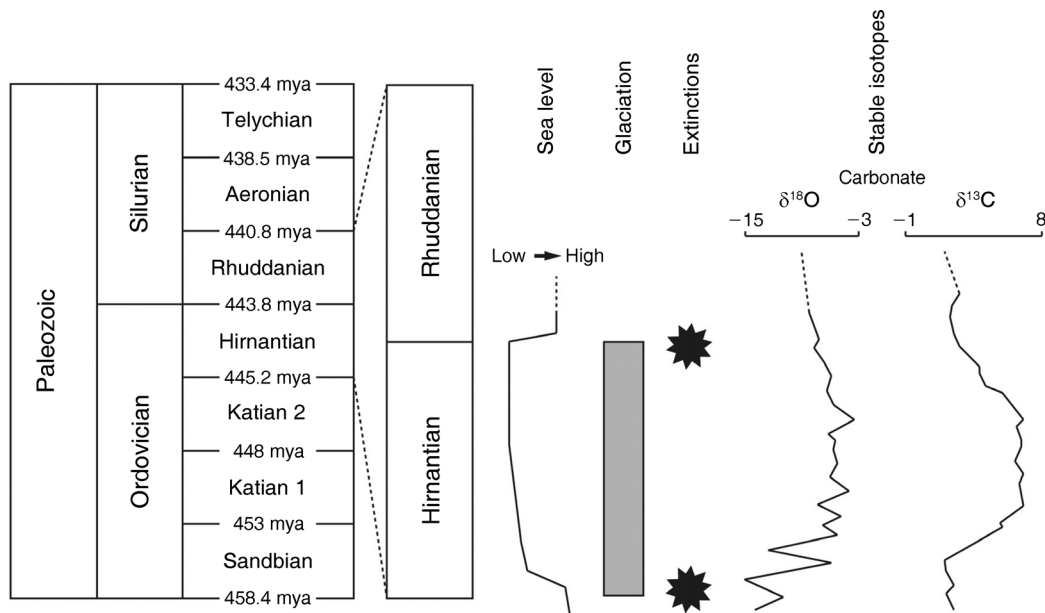


FIG. 1. Composite figure illustrating the time interval studied (official stage nomenclature and radiometric ages from ICS stratigraphic chart, see Cohen et al. [2013]; dates are million years ago [mya]), schematic sea level, and isotope profiles (data from Copenhagen Canyon, Nevada), and duration of glaciated intervals, with pulses of extinction marked as multi-pointed stars. Figure modified from Brenchley et al. (2003).

still a need to investigate changes on longer geological and evolutionary timescales (see Davis 2005, Gaston et al. 2007, Belmaker et al. 2008, Buckley and Jetz 2008, Darroch et al. 2014), especially given the recognition that spatial patterns in biodiversity have been profoundly influenced by large-scale ecological, historical, and evolutionary processes (Ricklefs 2004, Harrison and Cornell 2008, Thomas 2010), and mass extinctions in particular (Jablonski 2008). During extinctions, the shifts in gamma diversity measured by paleontologists might reflect different responses of alpha and beta diversity (e.g., Sepkoski 1988); on one extreme, alpha diversities might generally drop without beta diversity changing, whereas on another extreme beta diversity might decrease while alpha diversities remain unchanged. Paleontological studies provide many examples of decreased alpha diversity in association with mass extinctions (e.g., Twitchett 2006, Webb and Leighton 2011). However, few studies of mass extinctions quantify changes in beta diversity. Quantifying beta diversity is therefore central to assessing different ideas for why global diversity decreases.

Geographic range size is an ecological property of taxonomic groups, linked with beta diversity (e.g., Darroch et al. 2014), which also has implications for extinction studies. Previous studies (Jablonski and Hunt 2006, Payne and Finnegan 2007, Foote et al. 2008, Jablonski 2008) indicate that extinction risk rises as range size decreases, such that across extinction events taxa with smaller ranges tend to be more severely affected than those with larger ranges. In tandem with this, post-extinction rebounds are associated with

“blooms” of opportunistic and generalistic taxa that proliferate in response to the removal of incumbents and relative ecological “specialists” (e.g., Harries et al. 1996, Rodland and Bottjer 2001, Twitchett 2006). Both of these processes could potentially produce changes in overall patterns of beta diversity at any given scale.

The End-Ordovician (445.2–443.8 mya [million years ago]) mass extinction occurred in two distinct pulses, that are both associated with periods of rapid climate change (Brenchley et al. 1994, 1995, 2003; see Fig. 1). The changes in climate and ocean state over this interval are thought to resemble those occurring in the present day (e.g., Armstrong 2007), and so can be used as a modern analogue for predicting the responses of biota to continuing global change. The first pulse at the onset of the Hirnantian (~445.2 million years ago) coincides with the onset or intensification of ice accumulation, which led to a ~100-m sea level fall, widespread occurrences of oceanic anoxia in paleotropical and subtropical localities (Melchin et al. 2013), and up to 6°C cooling (Brenchley et al. 1994, Sheehan 2001, Finnegan et al. 2011). These processes likely drove extinction by a combination of habitat loss in shallow epicontinental seaways, thermal stress from rapid cooling, and deep-water anoxia (Finnegan et al. 2011, 2012, Hammarlund et al. 2012, Hull and Darroch 2013). During the Hirnantian, a widespread eponymous *Hirnantia* fauna occurs all over the globe, suggesting that beta diversity was extremely low after the first extinction pulse (Temple 1965, Wright 1968). The second pulse of extinction coincides with the termination of peak glaciation, pronounced global warming, and re-

flooding of continental seaways (Brenchley et al. 2003, Hammarlund et al. 2012). The causal mechanisms of this second pulse are less clear than those of the first pulse (Finnegan et al. 2012), although changing depth distribution of anoxic bottom waters is a suggested kill mechanism (Bambach 2006, Zhang et al. 2009, Melchin et al. 2013). More recently, data from nitrogen isotopes indicate that both pulses of extinction were influenced by redox-driven changes in nutrient cycling and primary production (Melchin et al. 2013). This interval therefore provides an ideal opportunity to compare the spatial fabric of extinction and recovery in response to different sources of environmental stress.

Brachiopods represent one of the best-studied and most ubiquitous marine invertebrate groups during this interval. Consequently, in this study we use Ordovician-Silurian brachiopod data to ask: (1) do alpha and beta diversity behave in similar fashion over an interval of extinction? (2) Do the responses of alpha and beta diversity change between pulses of extinction with different causal mechanisms? (3) Are changes in beta diversity associated with significant shifts in geographic range size? (4) If beta diversity decreases after extinction intervals, to what extent is this decrease driven by the extinction of taxa with small/large ranges? Alternatively, to what extent is decrease driven by the expanded ranges of surviving taxa, for which the new environments represent ecological opportunity (hereafter referred to the “extinction” and “expansion” hypotheses, respectively)? And finally, (5) Does variation in sampling intensity over time and over biogeography affect our ideas about the interplay between alpha, beta, and gamma diversity?

Addressing these questions using the fossil record of mass extinction has the potential to aid in identifying the biogeographic symptoms of ecological crisis, albeit on longer than human timescales. Specifically, these data help in linking change in biogeographical patterns with specific processes, and identifying spatial scales (i.e., local, regional, global) at which changes in beta diversity in the modern oceans may be easily detected.

DATA AND METHODS

Occurrences, collections, and formations

We use brachiopod occurrence data spanning the late Ordovician to middle Silurian from the Paleobiology Database (Holland et al. 2013).⁴ Our analyses use 10 961 occurrences from 2422 collections (i.e., particular fossiliferous localities) from 265 formations. These occurrences yield 433 genera from 127 families. Because we use genera as our metric of “shared taxa” and to avoid possible issues of over-splitting or over-lumping of species within genera, we count only one occurrence per genus per collection. This reduces the total occurrences to 10 234. A total of 182 references contributed to these

occurrences, with the most prominent including Holland and Patzkowsky (2007), Layou (2009), Cooper and Prouty (1943), Liberty (1968), Klingensmith (2011), Gillette (1947), and Hurst and Pickerill (1986) (see the Appendix for remaining citations).

We include occurrences without species identifications (e.g., “*Rhynchonella* sp.”) Such occurrences might reduce extinction and origination rates over time (Wagner et al. 2007), as “genus sp.” assignments often reflect nonexperts putting specimens into wastebasket genera. Correspondingly, this practice could artificially elevate similarities among formations if confamilial species are lumped into the type genus (e.g., specimens of the Orthidae being counted as “*Orthis* sp.”) However, this will affect our results only if “casual taxonomy” is more common in some intervals than others. There is no prior reason to think this: brachiopods are thoroughly studied throughout the Paleozoic for a host of reasons, and the same individuals frequently classify both Ordovician and Silurian brachiopods. Moreover, because the intervals in question have been subject to more intense scrutiny than other intervals, this might even introduce a conservative bias: “casual” taxonomy elevating beta diversity should be more typical of “background” intervals rather than the ones immediately preceding and following extinctions.

We use stratigraphic formations as our units of beta-diversity comparison (see Peters and Foote 2001). Formations represent the most fundamental unit in stratigraphy, and ideally an individual formation represents a discrete environment in space and time similar to a modern biome. Realistically, this is not always the case: formations sometimes are over “split” because of historical contingencies (e.g., geopolitical boundaries) or over “lumped” due to lack of investigation (Peters and Foote 2001, Benton et al. 2013). However, this creates a problem for our analysis only if formations in individual substages differ wildly in their diagnostic criteria. Our formation data are vetted extensively, with two primary “corrections.” First, we standardize the formation taxonomy. In many cases, this simply involves providing a single name for formations with multiple spellings. In other cases, we replace outdated formation names with current “senior synonyms.” Many different workers have considered some rock units to be both formations and members within formations. We standardize those to one status or the other based on the most recent opinions we could find. Second, we correct the chronostratigraphic assignments of many formations (or localities within formations). In most cases, the disagreements reflect historical changes between regional chronostratigraphic scales (e.g., those for North America or Europe) and global chronostratigraphic scales (see Gradstein et al. 2012). In other cases, the original publication uses age assignments that subsequent chronostratigraphic work has changed.

⁴ <http://www.paleobiodb.org/>

We partition the data into chronological ages (=stratigraphic stages): the Sandbian, Katian, Hirnantian, Rhuddanian, Aeronian, and Telychian (Fig. 1). Because the Katian stage is appreciably longer in duration than the other five stages, we split that stage into lower (“Katian-1”) and upper (“Katian-2”) subdivisions, with the latter corresponding to the *Amorphognathus* conodont zone (see Gradstein et al. 2012). Our resulting chronostratigraphic time slices nonetheless vary slightly in terms of overall duration; the longest (Sandbian) lasts ~5.3 million years, while the shortest (Hirnantian) lasts ~2.1 million years.

Accounting for unequal sampling over time and space

It is well known that sampling from the fossil record varies over time (Raup 1972, 1976, Foote 2001) and space (Smith 2001, McGowan and Smith 2008, Dunhill et al. 2012). There are two basic ways in which variable sampling affects diversity estimates that we use here. One is that as sampling intensity of specimens and localities increases, observed alpha diversity within formations or other assemblages (Hurlbert 1971) and observed gamma diversity within substages also will increase (Alroy 1996, 2010, Miller and Foote 1996, Connolly and Miller 2001). Sampling intensity also affects observed beta diversity by affecting the observed shared taxa between two formations, particularly if shared taxa tend to be rare in one or both assemblages (Chao et al. 2000).

Sampling also can vary among different biogeographic regions in the same time interval (e.g., Vilhena and Smith 2013, Wagner and Marcot 2013). Suppose that Regions A and B have similar numbers of formations in Interval 1 but that Region A has many more formations than Region B in Interval 2. Even if individual taxa have independent bounds on their ranges, spatial autocorrelation still predicts that formations from Region A should share more taxa with each other than they do with formations in Region B (see Nekola and White 1999, Lyons 2005, Dormann et al. 2007, Soininen et al. 2007, Belmaker et al. 2008, Qian et al. 2009). Thus, if we randomly sample X formations from both Intervals 1 and 2, then we frequently will sample a greater proportion of geographically adjacent formations and thus taxonomically similar formations from Interval 2. This in turn will artificially decrease average beta diversity among formations in Intervals 2. As a corollary, this will also depress gamma diversity in Interval 2 simply because of “redundant” sampling of similar faunas.

Both of these sampling issues affect our data. Both numbers of occurrences and numbers of collections (=localities) vary substantially from one stage to the next (Appendix: Fig. A1-A). Numbers of formations also vary over time, but unlike occurrences and localities, there is not a particularly strong correlation between formations and either localities or occurrences (Appendix: Fig. A1-B). In particular, Katian-1 and Katian-2

both average many more occurrences and localities per formation than in other intervals. Moreover, the average distance between formations (as given by the centroid of all localities within a formation) also varies considerably over time (Appendix: Fig. A3). Katian-1, in particular, shows particularly closely clustered formations with similar faunas. Conversely, intervals such as the Hirnantian and Rhuddanian show a greater proportion of geographically distant formations. As seen in studies of modern communities (e.g., Belmaker et al. 2008, Morlon et al. 2008), faunal dissimilarities between formations typically increase as distances between formations increase (Appendix: Fig. A4).

We use a two-tiered subsampling routine to accommodate variable sampling over time and space. Many of the well-sampled formations considered in this study possess between 10 and 20 occurrences; we therefore first randomly subsample (without replacement) 6 formations with a minimum of 10 occurrences or 5 formations with a minimum of 15 occurrences (hereafter referred to as “6-by-10” and “5-by-15” analyses, respectively). To accommodate different sampling intensities among formations, we then subsample 8 occurrences from the 6-by-10 formations, and 13 occurrences from the 5-by-15 formations. In this fashion, we can guarantee that identical samples are never repeatedly taken from formations (even those with exactly 10 or 15 occurrences). We repeat these subsampling routines for 500 iterations, and calculate the average alpha diversity from each formation, the average beta diversity among formations, and the average gamma diversity from all 5 or 6 formations (see *Diversity metrics*). Raw diversity patterns for the entire data set are seen in just those formations used in the 6-by-10 or even 5-by-15 analyses: for example, global gamma diversity patterns are essentially the same (Appendix: Fig. A2). Thus, our analyses are not predisposed to showing radically different results simply because we are excluding major portions of the data.

We accommodate spatial autocorrelation by repeating these analyses so that formations were subsampled only if each of the 5 or 6 formations was 500 or 1000 km apart from the other 4 or 5 subsampled formations (see Appendix: Fig. A5). We calculate distances between formations based on the centroids of the paleolatitudes and paleolongitudes of the localities (collections) within those formations. Paleolatitudes and paleolongitudes themselves are based on continental reconstructions for the Late Ordovician and Early Silurian utilized by the Paleobiology Database⁵ (see also, Scotese [2011]).

Diversity metrics

We calculate alpha diversity as the average number of unique genera found from each formation after subsampling. We calculate gamma diversity in two ways.

⁵ <http://paleobiodb.org/navigator/>

One is simply the total number of genera subsampled over all 5 or 6 formations. The second is the Chao-2 estimate of “true” richness based on numbers of taxa with 1, 2, 3, etc., occurrences (Chao 1984, 1987, Chao and Lee 1992) based on all occurrences from the 5 or 6 subsampled formations. We measure beta diversity using Simpson’s dissimilarity metric (β_{sim} [Simpson 1960]). Simpson’s beta represents turnover independent of nestedness (Baselga 2010), and is robust to gradients in richness (Koleff et al. 2003). In each subsampling, we calculate β_{sim} in two ways. First, we calculated beta diversity among subsampled formations using mean pairwise β_{sim} dissimilarity. Here, shared richness and observed richness for Formations A and B were based on 8 of 10+ or 13 of 15+ subsampled occurrences. In addition, we use Chao et al.’s (2005) extrapolations of faunal similarity based on estimates of true shared richness and true total richness for two assemblages given the distributions of observed shared and unshared taxa with single and duplicate occurrences.

Geographic ranges of taxa

We first project all unique paleolatitude and paleo-longitude coordinates for all brachiopod-bearing collections in our database into the Behrmann equal-area projection; we then calculate area of geographic range using a convex-hull algorithm (Fig. 2; see also Darroch et al. 2014). Range-size estimates are sensitive to changes in sampling effort; because range size estimates are unreliable when few collections are sampled, we use only genera with >4 occurrences in each interval. Range size estimates calculated using this method are also sensitive to unequal sampling of geographic areas through time; we therefore use a null model in which the observed number of records for each genus within a time slice are randomly assigned to sites. Observed range size is then compared to the results of 1000 permutations of the null model and an effect size calculated as standard normal deviations of observed values from the null. Using this framework, range sizes that fall more than two standard deviations (either positive or negative) away from mean value of the null model are therefore significant, being statistically smaller, or larger, than expected from random occupation of localities (Darroch et al. 2014).

We test whether changes in beta diversity are driven by the removal of small-/large-ranged taxa, or alternatively by sudden range expansion/contraction in opportunistic “disaster” taxa (the “extinction,” and “expansion” hypotheses, respectively). To do this we examine the range size trajectories of individual genera through the studied interval; we split treated genera into “Ordovician fauna” (i.e., genera with stratigraphic ranges beginning in the Ordovician), “*Hirnantia* fauna” (as defined by Rong and Harper 1988), and “Silurian fauna” (genera with stratigraphic ranges beginning in the Silurian). The “extinction” hypothesis predicts a change in mean range size (and consequently change in

beta diversity) over extinction boundaries due to the removal of genera with small or large ranges belonging to the Ordovician fauna. It also allows us to assess whether changes in the geographic ranges of individual genera are associated with major change in beta diversity. The “expansion” hypothesis predicts change in mean range size either due to dramatic range size expansion or contraction in members of the Ordovician fauna, or the appearance of members with small or large ranges of the “*Hirnantia*” or “Silurian” faunas.

All analyses were performed using the statistical software R (R Development Core Team 2010) and programs written by the authors in C.

RESULTS

The subsampled and unsampled analyses show key differences in alpha and beta diversity patterns (see Fig. 3 and Figs. 4–6). In terms of alpha diversity, the raw data recover decrease in alpha over both pulses of extinction, but also decrease from the Rhuddanian into the Aeronian (i.e., delayed recovery), before minor increase in the Telychian. Subsampled analyses recover the same basic pattern when sampling 8 of 10+ occurrences. However, subsampling 13 of 15+ occurrences (i.e., more intensive sampling) suggests that alpha diversity is lowest in the Rhuddanian, and recovers to pre-extinction levels through the Aeronian and Telychian. Differences between subsampled and “raw” analyses are more severe when looking at beta; the raw data recover large decreases in beta diversity over both pulses of extinction, followed by recovery from the Rhuddanian onwards. Subsampled analyses, however, reveal a very different pattern. After accounting for spatial autocorrelation (i.e., only using formation centroids 500+ km apart), beta diversity decreases over the first pulse of extinction, but then increases sharply over the second, before peaking in the Aeronian and decreasing into the Telychian.

Focusing purely on the subsampled results, the different subsampling routines reveal two strong patterns for gamma diversity related to geography and sampling (Fig. 4; see also Appendix: Fig. A6). One is that geography has a much greater effect on subsampled richness from the Sandbian and Katian than it does on the Hirnantian through Aeronian. As we limit subsamples to distant formations, subsampled richness increases much more in the Sandbian and Katian (particularly in the Katian-1) than it does in the Hirnantian through the Aeronian (see Appendix: Table A1 listing first differences in mean calculated diversity indices between successive stages). Similarly, increasing the sampling of individual formations has a much greater effect on subsampled richness from the Sandbian and Katian than it does on the Hirnantian through Aeronian. Increasing subsampling from 8 of 10+ occurrences to 13 of 15+ occurrences increases generic richness in the Sandbian and Katian genera much more markedly than it does in the Hirnantian, Rhuddanian, or Aeronian. Using the

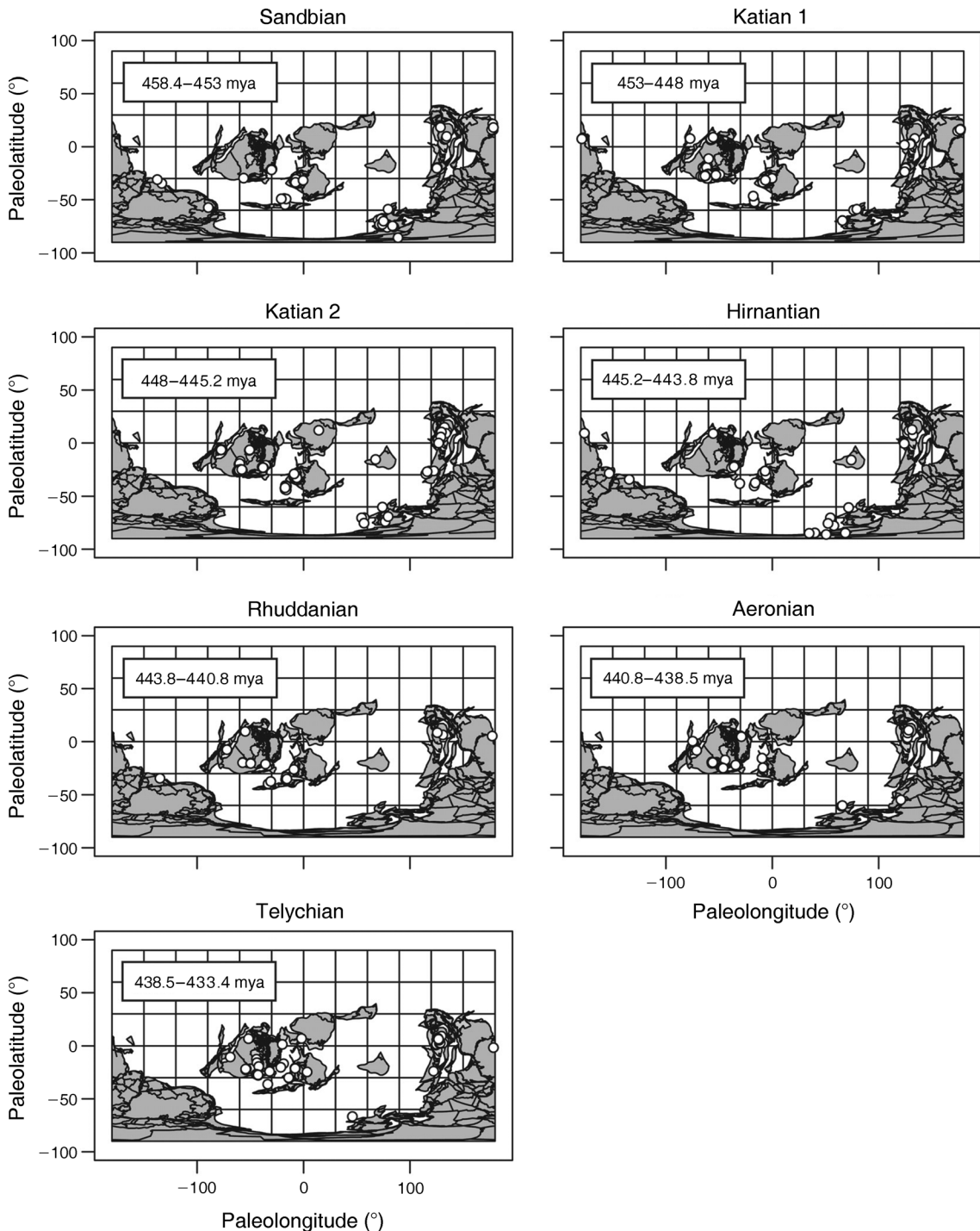


FIG. 2. Paleogeographic reconstructions (Mercator projection) showing the distribution of localities within each stage. Reconstructions from Scotese (2011).

Chao-2 estimators of richness yield patterns intermediate between the raw and subsampled patterns (Appendix: Fig. A6); Rhuddanian richness is again lower than Hirnantian richness, but not as drastically decreased as the raw data imply. Thus, decreases in generic richness

after the Katian are much steeper when we sample more occurrences and restrict sampling of those occurrences to distant formations. Under all analyses, brachiopods return to pre-Hirnantian gamma diversity by the Telychian (~438.5–433.4 million years ago).

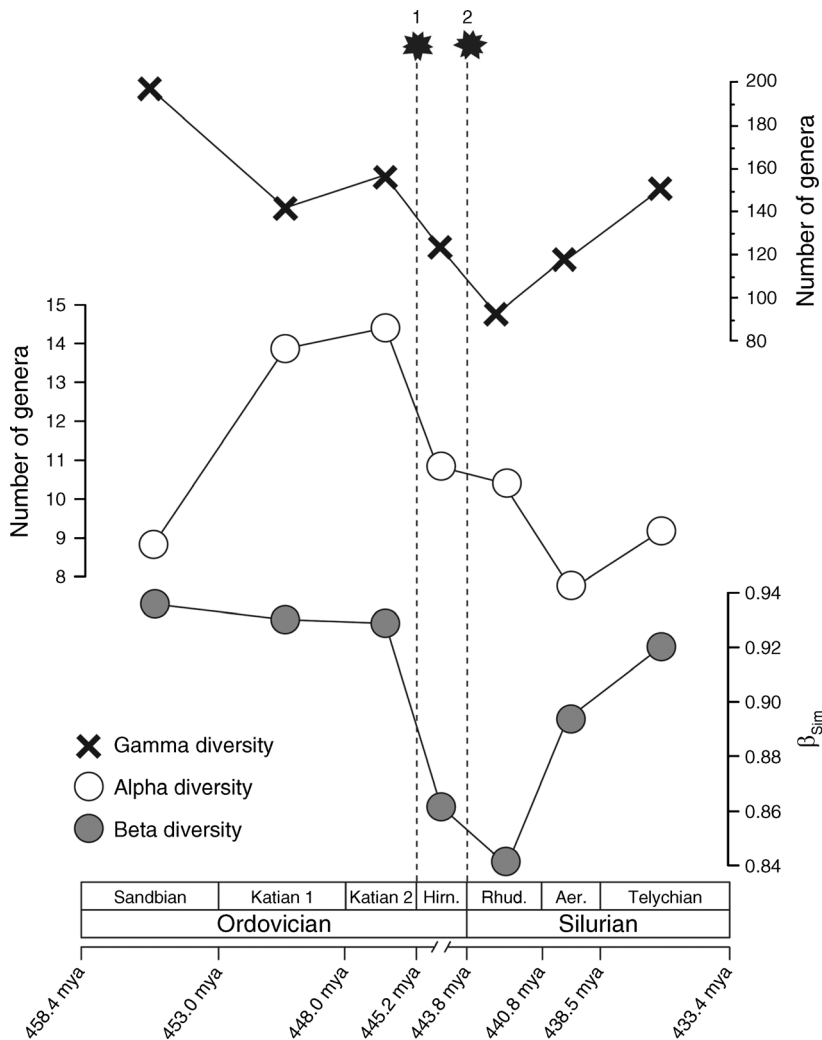


FIG. 3. Raw (i.e., without applying subsampling routines) values for gamma, alpha, and beta (Simpson's) diversity over the studied interval. First (1) and second (2) pulses of extinction are marked by multi-pointed stars. Rhud. represents Rhuddanian; Aer. represents Aeronian; Hirn. represents Hirnantian.

Both sampling intensity and breadth of geographic sampling also affect alpha diversity (Fig. 5). Subsampling 13 occurrences in the 5-by-15 analyses instead of 8 occurrences in the 6-by-10 analyses increases alpha diversity somewhat more for Sandbian and Katian formations than it does for Hirnantian, Rhuddanian, and Aeronian formations. However, when formations are all 500+ or 1000+ km apart, this effect increases, so that the biggest differences between pre-Hirnantian and post-Katian alpha diversity are found when subsampling 13 of 15+ occurrences from 5 formations 1000+ km apart. Under all analyses, alpha diversity rebounds to pre-Hirnantian levels by the Telychian.

After subsampling and controlling for spatial autocorrelation, the behavior of the different diversity indices over the two pulses of extinction can be summarized as follows. (1) Gamma: significant decrease over the first pulse of extinction in the Hirnantian (to the

lowest values seen over the entire interval), followed by negligible change/slight increase over the second pulse (although still exhibiting significant faunal turnover). Recovery to (approximately) pre-extinction levels of gamma diversity occurs in the Telychian. (2) Alpha: decrease over both the first and second pulses of extinction (significant over the second pulse in the 5-by-15 analysis), reaching a minimum in the Rhuddanian. Recovery to (approximately) pre-extinction levels of alpha diversity occurs in the Telychian. (3) Beta: dramatic decrease over the first pulse of extinction in the Hirnantian (to the lowest values seen over the entire interval), followed by immediate return to pre-extinction levels over the second pulse. Beta diversity continues to increase into the Aeronian, and then decreases in the Telychian.

As expected, beta diversity shows strong effects from sampling distant formations (Fig. 6; see also the

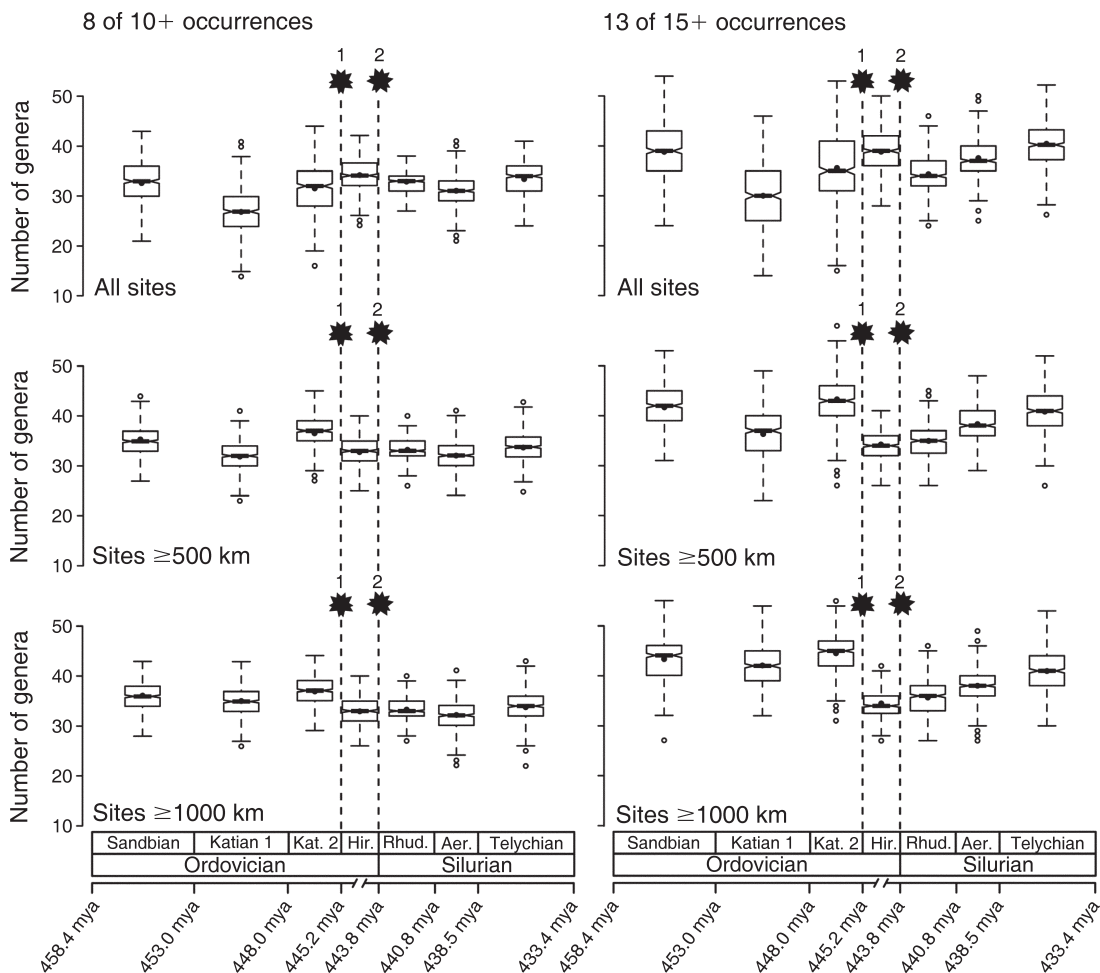


FIG. 4. Rarified estimates of gamma diversity (total number of unique genera within each stage) based on 500 subsamplings. Plots on the left denote subsampling 8 occurrences from 6 formations with 10+ occurrences; those on the right denote subsampling 13 occurrences from 5 formations with 15+ occurrences. Area between whiskers represents the full spread of data, while boundaries of the box mark the upper and lower quartiles; statistical outliers (falling outside whiskers) are shown as small, open circles. Within boxes, black lines represent medians, with “notches” indicating 95% confidence intervals around the median. Mean values (solid black circles) are superimposed on each box. The first row illustrates analyses sampling formations 500+ and 1000+ kilometers apart based on estimated paleogeography. Notches represent 95% confidence intervals around median values. Pulses of extinction are marked by multi-pointed stars. Rhud. represents Rhuddanian; Aer. represents Aeronian; Hir. represents Hirnantian.

Appendix: Figs. A3 and A4). However, it also shows strong sampling intensity effects. When looking only at formations 500+ or 1000+ km apart, beta diversity is appreciably lower among formations in the Hirnantian than among formations from other intervals. The pattern becomes more striking when subsampling 13 occurrences in the 5-by-15 analyses instead of 8 occurrences in the 6-by-10 analyses, indicating that shared Hirnantian genera become more rather than less common when we look at less common taxa. This corresponds with an unusually high number of genera being found in multiple formations (see Appendix: Fig. A8). Conversely, the low beta diversity of the Katian-1 appears to be an artifact of numerous geographically adjacent formations from that interval (see Appendix:

Figs. A3 and A4). Thus, when sampling distant formations, beta diversity during Katian-1 is indistinguishable from the Sandbian or Katian-2. Correspondingly, genera known from more than one formation go from unusually high, given all formations, to very typical when looking only at distant formations. Finally, a rebound in beta diversity in the Silurian is nearly identical in all treatments, with beta diversity dropping perceptibly in the Telychian. Extrapolated beta diversity (following Chao et al. [2005]) yields similar patterns (Appendix: Fig. A7), with the exception of suggesting a greater decrease in beta diversity in the Telychian.

The distributions of geographic ranges change little between the Sandbian and Katian-1. Ranges then

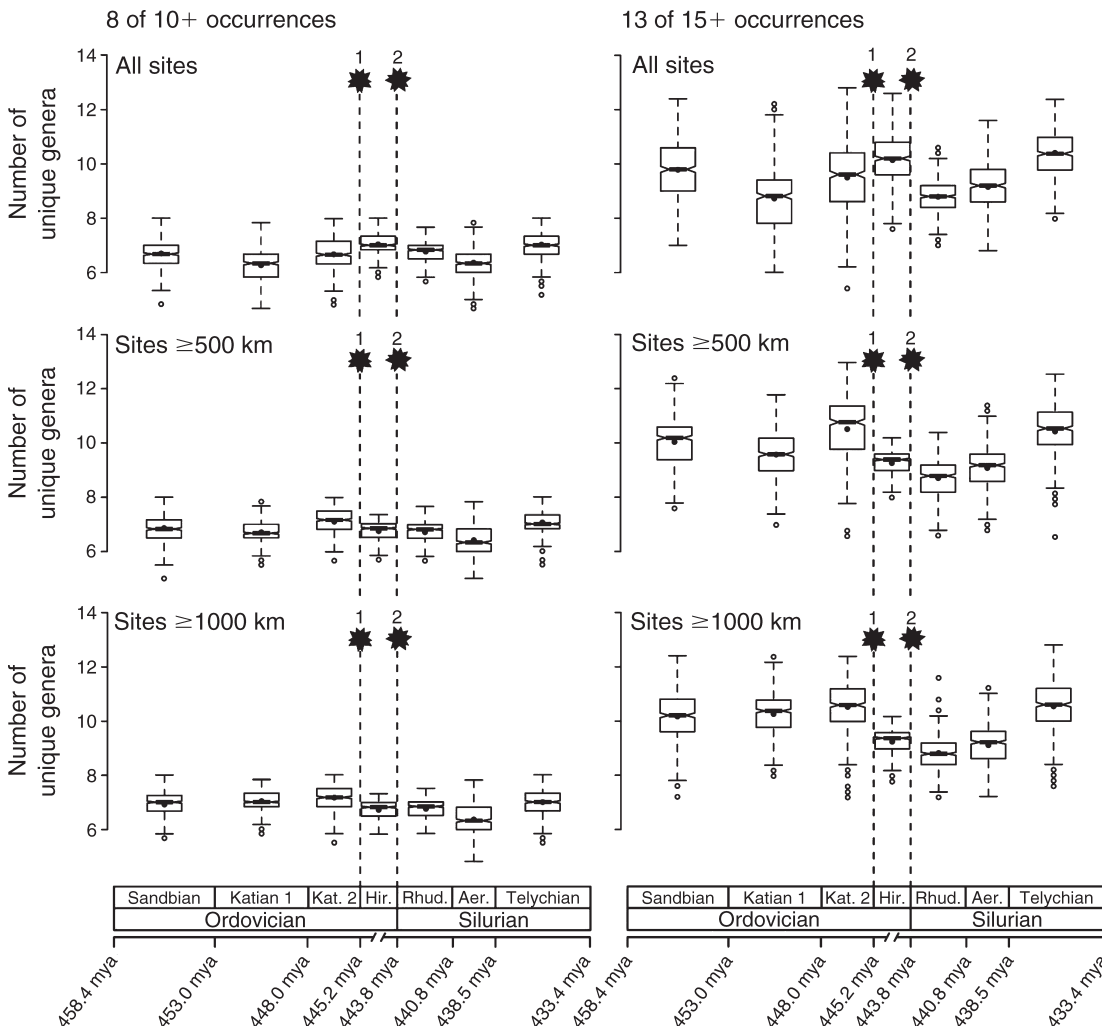


FIG. 5. Rarefied estimates of average per-formation alpha diversity based on 500 subsamplings. See Fig. 4 for description of boxplots. Rhud. represents Rhuddanian; Aer. represents Aeronian; Hir. represents Hirnantian.

increase in Katian-2 and again more sharply in the Hirnantian, where we see the highest values (Fig. 7a). Ranges crash in the Rhuddanian, with a partial rebound in the Aeronian creating distinctly bimodal distribution (see also Appendix: Fig. A14). By the Telychian, the distribution of ranges recovers to pre-Hirnantian levels. In general the data show a clear pattern of large range sizes in the Ordovician (and highest in the Hirnantian), and small range sizes in the Silurian (given by the fact that both mean and median range sizes in Silurian time slices are unanimously smaller than Ordovician). Effect sizes reinforce this clear distinction between the pre-Hirnantian Ordovician and post-Hirnantian Silurian intervals (Fig. 7b). The Sandbian and Katian are characterized by both numerous ranges deviating significantly from the results of the null model, with many examples of both narrow and broad ranges. The first extinction pulse eliminates numerous taxa with small and large ranges (see also Appendix: Figs. A6 and

A7). In the surviving Hirnantian fauna, none of the generic geographic ranges deviate significantly from null expectations. The second pulse of extinction is similar, with range sizes in the Rhuddanian falling within those predicted by the null model (albeit with a smaller effect size than seen in the Hirnantian). In the Aeronian and Telychian a wider spread of range sizes (both small and large) is developed, with some being significantly smaller than expected given the null model. Some of these shifts could potentially be an artifact of the changing spatial distributions of sites through time; across two time intervals where the later interval includes a wider geographic spread of sites, the effect sizes of genera could potentially decrease (i.e., be smaller than expected) even if there is little or no change in actual range sizes. However, the overall distribution of localities actually changes extremely little over the critical Katian-2 to Rhuddanian interval, especially in terms of maximum reconstructed distance (see Appendix: Fig.

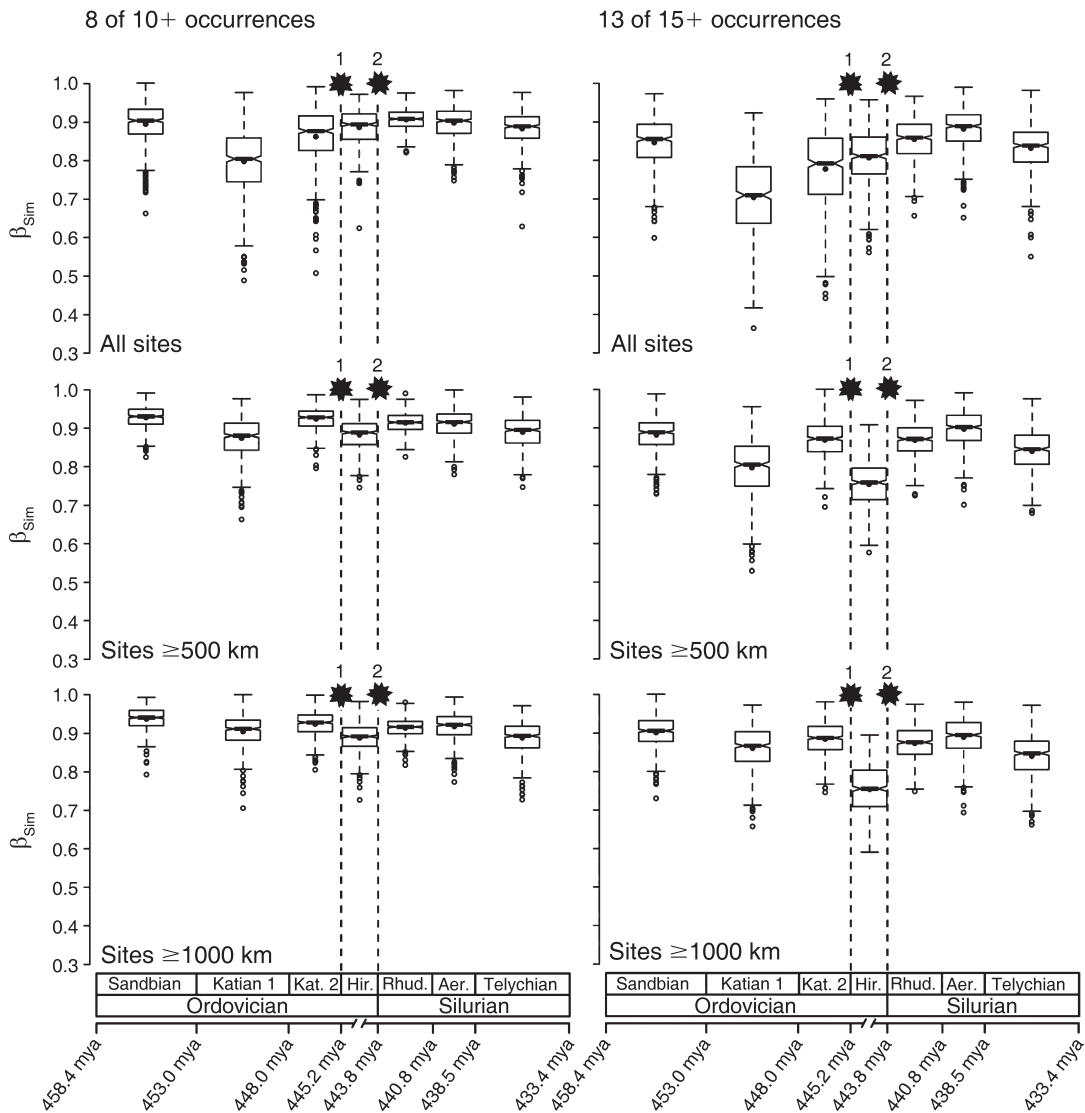


FIG. 6. Rarified estimates of average among-formation beta diversity based on 500 subsamplings. Beta diversity uses Simpson’s dissimilarity, which is the compliment of the shared taxa divided by the possible shared taxa. See Fig. 4 for description of boxplots. Rhud. represents Rhuddanian; Aer. represents Aeronian; Hir. represents Hirnantian.

A3), and so our observed changes in range size likely reflect a genuine paleoecological signal, rather than an artifact of paleogeographic sampling.

Splitting genera into “Ordovician,” “Hirnantian,” and “Silurian” faunas (Fig. 7c, d) illustrates differences between these groupings. Genera belonging to the “*Hirnantia* fauna” are present in assemblages from the Sandbian through to the Telychian, but at no point achieve range sizes that deviate significantly from the results of null models. “Ordovician genera” include all of the taxa with unusually small and large ranges in the Sandbian and Katian, all of which disappear after the first pulse of extinction. Finally, although genera from all three faunas comprise the recovery interval (Rhuddanian-Telychian), holdover “Hirnantian” genera typically occupy wider ranges than do either newly

originated “Silurian” genera or holdover “Ordovician” genera.

DISCUSSION

Abiotic factors

Before discussing the macroecological and macroevolutionary implications of our findings, we will first consider whether they might somehow represent an artifact of the fossil record. We explicitly deal with uneven sampling over space and time. However, fossil accumulations are typically time averaged, such that fossil material from any given horizon can represent organisms that lived over a period spanning 10^2 – 10^3 years (Kowalewski et al. 1998). This has been viewed in the past as a severe barrier to using paleontological

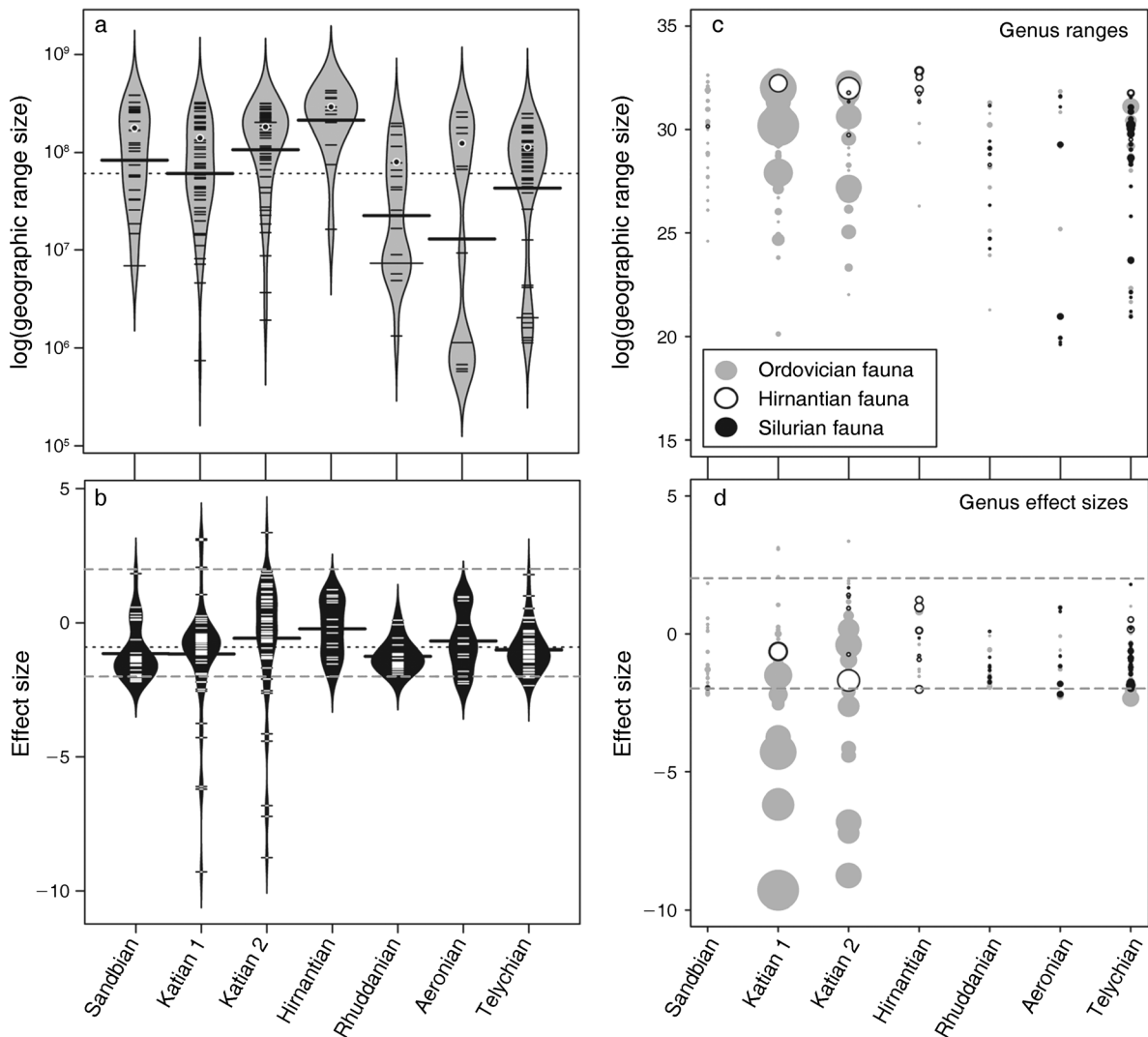


FIG. 7. (a) Composite range size and (b) effect size plots for sampled brachiopod genera, illustrated as beanplots (combined one-dimensional scatterplot and density trace), where width of “beans” corresponds to density of observations within a given range of values. (a) Individual ranges indicated by horizontal black lines; mean range sizes for each stage are superimposed as points. Overall mean range size for the entire studied interval is given by the black dashed line. (b) Individual effect sizes indicated by horizontal black lines; significant (2 SD) departure from mean results of the null model are given as dashed gray lines. (c) Composite range size and (d) effect size plot showing distribution of “Ordovician fauna” (i.e., genera with stratigraphic ranges beginning in the Ordovician), “*Hirnantia* fauna” (defined by Rong and Harper [1988]), and “Silurian fauna” (genera with stratigraphic ranges beginning in the Silurian). The sizes of circles are proportional to the total number of sites in which each genus is recorded.

material to address ecological questions: for example, our alpha diversity need not reflect a single community. However, we do not view this as an impediment to our results; the processes that lead to time averaging typically filter out short-term variations and high-frequency ecological variability such that fossil deposits record long-term habitat conditions (Olszewski 1999, Tomášových and Kidwell 2010). That means that our measures of alpha diversity represent larger “meta-communities,” which might be more relevant units for long-term biodiversity patterns (Hubbell 2005). Thus, time averaging actually can become an advantage when

testing macroecological hypotheses on larger temporal scales (e.g., Darroch et al. 2014).

The behavior of alpha and beta diversities over an interval of extinction

The final 1.4 million years of the Ordovician began with the onset of major global cooling, and then ended relatively abruptly with equally major global warming. Both pulses result in decreased alpha diversity relative to pre-extinction faunas. In addition, the first pulse of extinction (cooling) also greatly reduces beta diversity, whereas the second pulse (warming) increases beta

diversity. On the timescales being considered, these patterns reflect interplay between extinction, origination, and significant biogeographic shifts in the distribution of taxa (see Krug and Patzkowsky 2004, 2007, Rasmussen and Harper 2011*a, b*). Low beta diversity after the first pulse reflects the extinction of taxa typifying warm shallow-water environments: deep water taxa typifying Hirnantian faunas do not undergo pronounced range expansion so much as persevere in this interval (Fig. 7). In contrast, high beta diversity after the second pulse reflects the extinction/extirpation of this more cosmopolitan *Hirnantia* fauna, leaving behind endemic and reduced communities composed of Ordovician holdover taxa, some survivors from the *Hirnantia* fauna, and newly evolved members of the Silurian fauna (see Fig. 7*c, d*). These data indicate that different extinction mechanisms can have very different effects on beta diversity, although we will argue that the effects might not be uniform (e.g., global cooling reduces beta diversity and global warming increases it), but instead contingent upon additional factors. Although declines in gamma diversity need not require declines in both alpha and beta diversity (e.g., Raup and Sepkoski 1982, Bambach 2006), the first pulse of the extinction greatly reduces both diversity types. This becomes particularly apparent when we minimize geographic autocorrelation in our sampling and maximize the sampling intensity of individual formations. Average beta diversity among widely separated formations in the Hirnantian is much lower than those seen among widely separated formations earlier in the Ordovician (~458 to ~445.2 million years ago), suggesting that the first extinction pulse severely reduced whole faunas. (That is, 36% of the genera from the preceding Katian-2 are not sampled in the Hirnantian or in younger rocks.) Coupling low alpha diversity within Hirnantian formations with low beta diversity among the formations corroborates the idea that a general environment unable to support large numbers of different brachiopod genera prevailed in the last 1.4 million years of the Ordovician.

There are two caveats with this interpretation. First, Melchin et al. (2013) provide evidence to suggest that Hirnantian paleoenvironments were in general well oxygenated, and so the source of continuing ecological “stress” depressing alpha diversity in this stage is unclear. Despite this, other studies (e.g., Rasmussen and Harper 2011*b*) also find depressed local richness in brachiopod communities throughout the Hirnantian, suggesting that continuing perturbation was preventing rapid recovery. Second, this interval is characterized by a large proportion of Lazarus genera. Rong et al. (2006) suggest that ~30% more genera survived the first pulse of extinction than have actually been identified in the Hirnantian (see also Appendix: Fig. A16). The discovery of collective geographic refugia in the Hirnantian harboring these missing genera would necessarily revise estimates of beta diversity in this stage upwards. However, there is currently little or no evidence for

collective refugia after this pulse, suggesting instead that these taxa were geographically dispersed, rare, and characterized by low population densities (Rong et al. 2006). It is likely, therefore, that global beta diversity among brachiopod assemblages in the Hirnantian was genuinely low, and future fossil discoveries in (as yet) poorly sampled geological terranes will only reinforce this pattern.

A different scenario almost certainly applies to brachiopod faunas following the second pulse of extinction. Although gamma diversity might have been somewhat higher in the earliest Silurian (~443.8 to ~440.8 million years ago) than in the latest Ordovician, the large turnover in taxa (46% of latest Ordovician genera are not sampled from younger Silurian rocks) indicates a substantial extinction. Alpha diversity continues to remain low in the earliest Silurian (Fig. 5), but beta diversity returns to levels seen before the first extinction pulse (Fig. 6). This strongly suggests that *local* environments still were not capable of sustaining the numbers of brachiopod genera that pre-Hirnantian environments sustained. This might seem incongruent with the apparently high origination rates during the 3 million years after the second extinction pulse: 30 of the 92 Rhuddanian genera and 47 of 117 Aeronian genera are first found from those strata. However, many of these genera simply replace extinct Ordovician genera. Moreover, there seem to have been barriers to rapid dispersal, as these genera typically had very narrow geographic ranges. These barriers may have been related to sea level; several authors (Azmy et al. 1998, Zhang and Barnes 2002, Johnson 2006, Díaz-Martínez and Grahn 2007) have identified continuing eustatic sea level fluctuations in the Rhuddanian, which may have stressed brachiopod communities long after the second extinction pulse (Rasmussen and Harper 2011*b*). However, these may have also severely impacted the abilities of taxa to disperse, by reducing connectivity between epicontinental seaways and oceanic settings. Thus, the high origination rate seems to reflect local replacement of Ordovician taxa in parallel throughout the globe.

The observed patterns of alpha and gamma diversity over the two pulses of extinction are generally well supported by previous studies (e.g., Brenchley et al. 1994, Rong et al. 2006, Rasmussen and Harper 2011*a, b*), but also offer some interesting contrasts. In particular, using an independently compiled data set, Rasmussen and Harper (2011*a, b*) examined diversity metrics at both local and global scales, finding a two-phased decrease in alpha diversity at local (paleocontinental) scales over both extinction pulses, followed by swift rebound in the Rhuddanian. This recovery was faster in some paleogeographic regions (especially around Laurentia), and slower in others. At least some of these differences may be attributed to differences in the length of time bins (these authors split assemblages into the Lower, and mid-Upper Rhuddanian, while we aggregate over the entire stage); however, these con-

trasting patterns hint at strong regionalism in rates of extinction and recovery. Therefore, although we find that local environments apparently remained in general incapable of sustaining pre-extinction levels of diversity until ~10 million years after the second extinction pulse, localized paleogeographic regions likely recovered much faster.

Patterns in beta diversity between global and local scales offer sharper contrasts. Analyses performed by Rasmussen and Harper (2011b) found decreases in local-scale beta diversity (measured as the composition of species along depth gradients) after the second pulse of extinction; this is in stark contrast to our observed patterns at global scales, which show significantly high beta diversity when records are aggregated over the entire Rhuddanian. These differences likely reflect the different spatial and temporal scales of each analysis; changes in beta diversity on global scales may be governed by range size shifts, extinction/origination, and emplacement/removal of barriers to dispersal, whereas on local scales beta may be determined by niche breadth among component taxa (i.e., specialist vs. generalist), habitat availability, and community interactions.

Geographic range size shifts and beta diversity

One potential explanation for low beta diversity in the last 1.4 million years of the Ordovician is that the onset of major glaciation and marked global cooling allowed a few opportunistic “disaster taxa” (sensu Jablonski 1986b) to greatly expand their geographic ranges. However, our data suggest a more complicated explanation. The distribution of geographic range sizes among taxa in the Sandbian and Katian (458.4–445.2 million years ago) greatly resemble those of marine taxa today (see, e.g., Anderson and Marcus 1992, Willis 1922, Gaston 1996), with a typical hollow curve distribution (see Appendix: Fig. A14). However, the Hirnantian witnesses a major reduction in the variance of geographic ranges: over the last 1.4 million years of the Ordovician, we see far fewer taxa with narrow geographic ranges than we saw before. We also see fewer taxa with very broad geographic ranges in the Hirnantian (Appendix: Fig. A10), such that the first pulse of extinction dramatically altered the size–frequency structure of range size distributions, by removing both small and large-ranged taxa. The classic members of the “*Hirnantia* fauna” do not themselves benefit hugely: seven of the genera belonging to this grouping (as defined by Rong and Harper 1988) actually have *smaller* ranges in the Hirnantian than they had in Katian-2 (see Appendix: Fig. A15). Three others do expand their ranges, but none dramatically enough to deviate from null expectations. This result is surprising given the inferred constriction of tropical climate belts and expansion of cold-water biomes that occurred with the onset of Hirnantian glaciation (Melchin et al. 2013), which might be expected to allow latitudinal range

expansion in cold-adapted taxa. Instead, it appears that the geographic distribution of a general pool of brachiopod genera greatly increased following the first pulse of Ordovician extinctions ~445.2 million years ago. Rather than a few genera being found everywhere, it seems that every formation had a few genera from a common pool. In this sense, the “*Hirnantia* fauna” did not undergo range expansion, but instead became more numerous, and more common components of local assemblages.

However, we acknowledge that the expansion of geographic ranges might be greater than we have measured here, because the most commonly occurring genera in the Hirnantian are found in more formations than are commonly occurring genera before or after (see Appendix: Fig. A8). In addition, extrapolated beta diversity (sensu Chao et al. 2005) suggests that Hirnantian beta diversity was even lower relative to the older and younger intervals than we show (see Appendix: Fig. A7). However, the ranges over which genera were commonly found did not greatly increase in the Hirnantian.

“Extinction” vs. “expansion” driving changes in beta diversity

In terms of our original hypotheses (“extinction” and “expansion”) for drivers of change in beta diversity, we find no evidence for opportunity-driven expansion of geographic ranges following either the first or second pulse of extinction. After the first pulse of extinction, range sizes among the *Hirnantia* fauna remain broadly unchanged, and decrease in beta diversity is largely driven by the extinction of small-ranged endemic taxa. After the second pulse of extinction we find evidence for the opposite scenario; brachiopods from the early Silurian (~443.8–438.5 million years) show unusually *narrow* geographic ranges (Fig. 7). Thus, high beta diversity in the early Silurian is driven by the extinction of broadly distributed taxa in the second extinction pulse, and seemingly exacerbated by impediments to range expansion by surviving genera.

The findings that some Hirnantian genera appear in unusually high numbers of formations (Appendix: Fig. A8), and that extrapolated beta diversity implies a substantial pool of unsampled shared taxa (Appendix: Fig. A7), offers a case for an expansion-driven decrease in beta diversity in the Hirnantian. However, it is a weak case. The pattern across our subsampling analyses, combined with extrapolated beta diversity patterns, suggests that shared genera between two formations typically were rare in one or both of the formations. As such, this is not evidence for particular genera taking advantage of the glacial world. Instead, this re-emphasizes that available ecospace became occupied by a variety of different genera common to specific areas, rather than any one taxon that proliferated massively in the immediate aftermath of extinction. The reduction of beta diversity for the last 1.4 million

years of the Ordovician also was thus primarily extinction-driven, due to the elimination of genera with narrow geographic ranges during the first extinction pulse. We therefore conclude that changes in beta diversity over both pulses of Ordovician-Silurian extinction were overwhelmingly driven by “extinction,” as opposed to “expansion.”

Causal mechanisms of extinction and beta diversity

The two shifts in global climate over the last 1.4 million years of the Ordovician both result in low alpha and gamma diversity, but generate two very different patterns of beta diversity. We suggest that this had less to do with the “opposite” nature of the climatic changes (massive glaciation vs. global warming) than with the effects of the two changes on dispersal ability and distributions of similar environments. The onset of major glaciation ~445.2 million years ago likely facilitated the spread of genera belonging to the “*Hirnantia* fauna,” as they were already adapted to colder and deeper environments (Rong and Harper 1988, Sheehan 2001). The corresponding large drop in sea level led to a reduction in the depth and area of epicontinental seaways; this eliminated or greatly reduced taxonomic richness in brachiopod assemblages endemic to these habitats (Sheehan 2001, Finnegan et al. 2012, Rasmussen and Harper 2011*a, b*). In addition to causing the extinction of many genera (especially those with narrow geographic ranges), this also resulted in a much greater proportion of faunas sharing taxa from a particular general fauna than had existed prior to glaciation.

Global warming and major sea level rise at the end of the Hirnantian (~443.8 million years ago) provides an obvious extinction mechanism (i.e., thermal stress) for the cold-water “*Hirnantia* fauna.” In support of this, Finnegan et al. (2012) found maximum paleolatitude, a macroecological trait associated with thermal tolerance, as a strong predictor of extinction risk among brachiopod genera across the entire Ordovician-Silurian interval. However, this would have also introduced (or maintained) ecological stresses on the warm-water epicontinental brachiopod faunas, as extremely rapid environmental change can have detrimental effects on species, regardless of the direction of change. Consequently, alpha diversity took three million years to rebound to pre-extinction levels, and recovery may have been further delayed by continuing environmental change up into the Aeronian, including eustatic sea level fluctuations (Díaz-Martínez and Grahn 2007), widespread oceanic anoxia, and disruptions to primary productivity (Melchin et al. 2013). Moreover, extinction was not limited to the genera of *Hirnantia* fauna: only 15 of the 57 genera last sampled from Hirnantian rocks are from that fauna. This, coupled with the very small geographic ranges and high beta diversity in the earliest Silurian, indicates that the epicontinental sea faunas remained fragmented and unable to quickly disperse for

some time. Thus, it might be that surviving genera did not prosper so much as simply persevere for some time after both extinction pulses. Indeed, given that it seems to have taken ~3 million years for Silurian faunas to truly rebound from the second pulse of extinction, it is possible there simply was not time between pulses for the *Hirnantia* fauna to rebound.

These contrasting models for changing beta diversity over pulses of Ordovician-Silurian extinction therefore suggest that changes in the spatial fabric of global biodiversity were largely controlled by the emplacement and removal of barriers to dispersal, in combination with vicariance.

The effects of sampling strategies on perceptions of alpha, beta, and gamma over time

Our results provide an additional emphasis to the need to standardize sampling in diversity studies of all sorts. Standardizing sampling over time should attempt to account for different levels of biogeographical autocorrelation in our samples from different time intervals. This might seem like an issue affecting only paleontological data. After all, paleontologists can only sample faunas from available strata, and although paleontologists do target particular intervals of time and particular geographic regions when they can (e.g., Sheehan 1977), they also heavily sample easily available strata from any interval (Raup 1972, 1976). This is very apparent in our data: global patterns of beta diversity might easily be lost because of incredibly intense sampling of North American formations from the Sandbian–Katian (458.4–445.2 million years ago) with similar faunas due to biogeographic autocorrelation (e.g., Soininen et al. 2007). The contrasting patterns in beta diversity from raw (Fig. 3) and subsampled (Fig. 6) analyses illustrate this point; the paleogeographic reconstructions (Fig. 2) and distributions of commonly sampled taxa (Appendix: Fig. A8) indicate that the substantial decrease in Rhuddanian beta diversity recorded by the raw data is likely the result of intense sampling of a relatively small biogeographic area. After correcting for spatial autocorrelation (i.e., only using formation centroids 500+ km apart) the pattern reverses, revealing instead a significant increase in beta diversity over the second pulse of extinction, and with it a much better match with the range size data (i.e., the removal of larger-ranged members of the *Hirnantia* fauna, and consequently a decrease in mean range size and increase in faunal provinciality).

In theory, modern ecologists can sample without the limitations of what geological processes have left us. However, much relevant data for current conservation issues was collected years and even decades ago with different biases (e.g., proximity to research stations, and other factors). This might leave large ecological databases with similar spatial biases that will require similar treatments.

Implications for the current biodiversity crisis

The Ordovician-Silurian extinction has been used by previous workers as an analogue for present-day global change (in particular the second pulse, which coincided with an interval of rapid global warming and high-latitude deglaciation); consequently our data here are relevant to the current biodiversity crisis, and can be used as a basis for predictive biogeographic models. First, our data illustrate that taxa with narrow geographic ranges are extremely vulnerable and at high risk of extinction, and emphasize the importance of conservation efforts aimed at protecting narrow-ranging and endemic species. Second, our results indicate that, if climate change is prolonged (or doubled dipped, as in this case), disaster and opportunistic taxa are unlikely to be able to take advantage of potential empty niche space, and subsequently expand their distributions. In other words, even if speciation rates increase in parallel with extinction, such that newly evolved taxa take advantage of empty niche space, this is not likely to translate into taxa that have broad geographic ranges and less vulnerability to extinction. Third, our results illustrate that pulses of extinction with different causal mechanisms can have opposite effects on patterns of beta diversity, which likely reflects sea level change and the changing abilities of taxa to disperse. Specifically, we find that beta diversity following the second pulse remains high and geographic range sizes remain small until late in the subsequent rebound. This illustrates that, at least on longer timescales, with global warming and rising sea level we might not necessarily expect decreases in beta diversity with increased ability of marine organisms to disperse. This will be particularly true if sea level continues to fluctuate. As a corollary, we suggest that (at least on the larger temporal and spatial scales analyzed here) decrease in alpha diversity may be a more sensitive indicator of ecological crisis when mass extinction coincides with deglaciation and sea level rise. These results further predict that within local assemblages, overall alpha diversity will remain low, while distinct differences in taxa will remain between regions.

CONCLUSION

Our patterns of alpha, beta, and gamma diversity indicate dramatic restructuring in the spatial organization of brachiopod communities in response to Ordovician and Silurian extinction, which coincide with major changes in climate and the distributions of basic habitats. In the context of our original questions, we find that: (1) alpha and beta diversity can respond differently to extinction; (2) alpha and beta diversity can respond in markedly different fashion to pulses of extinction with different causal mechanisms; (3) changes in beta diversity associated with extinction are typically accompanied by changes in geographic range size; (4) changing beta diversity and range size (at least over the Ordovician-Silurian event) was driven by the extinction

of taxa with statistically small and large ranges, rather than dramatic range expansion/contraction in opportunistic and “disaster” taxa that survive into the aftermath; and finally, (5) analysis of biogeographic patterns and beta diversity in the fossil record may be heavily affected by sampling intensity over time, and in space (necessitating a series of distance- and sample-based corrections). These findings illustrate that the fossil record can be a powerful source of historical spatial data, and is well suited to addressing questions surrounding the assembly of biotas on longer temporal scales than are typically afforded by neontological and ecological data. This study also demonstrates that the fossil record of mass extinction can (and should) be exploited in order to help build predictive models for current and future biodiversity loss (see also Hull and Darroch 2013). Lastly, this study reinforces the profound role played by global- and regional-scale processes, in this case mass extinction events, in sculpting spatial patterns in biogeography.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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