

Carbonate collapse and the late Paleozoic ice age marine biodiversity crisis

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ABSTRACT

The late Paleozoic ice age (LPIA) was characterized by persistently low diversity of marine invertebrates following a second-order mass extinction. Here, we used a data set of North American (paleotropical) fossil occurrences of brachiopod, bivalve, and coral genera from the Paleobiology Database, combined with lithologic data from Macrostrat, to demonstrate that low diversity was caused by the collapse of carbonate environments during the LPIA. After dividing the data by lithology, low diversity was evident only in carbonate environments, whereas diversity within siliciclastic environments actually increased during the LPIA, after a brief decline in the Serpukhovian (late Mississippian). Diversity patterns closely matched respective changes in the volume of carbonate and siliciclastic rocks. The contrasting patterns observed in the two environments suggest that habitat loss was a direct cause of changes in diversity, because other factors, such as temperature, would have affected genera in both environments. A causal relationship is also supported by the finding that diversity remained high in carbonate refugia (carbonate beds within majority-siliciclastic formations) until the Bashkirian, postdating the onset of icehouse conditions by ~8 m.y. Our results provide a unifying, mechanistic explanation for the distinctive characteristics of the biotic impact, including its disproportionate effect on the tropical marine invertebrate fauna, prolonged recovery from extinction, low macroevolutionary rates during the recovery interval, and regional differences in its expression.

INTRODUCTION

Marine ecosystems were impacted in late Paleozoic time by the development of a cold and dynamic global climate associated with the late Paleozoic ice age (LPIA; Stanley and Powell, 2003; Montañez and Poulsen, 2013). Icehouse conditions emerged relatively suddenly in the late Mississippian (latest Viséan–early Serpukhovian; Smith and Read, 2000; Davies, 2008; Fielding and Frank, 2015) and then effectively ended ~40 m.y. later in the Early Permian (Sakmarian; Montañez et al., 2007; Montañez and Poulsen, 2013), although regional ice centers persisted through the Permian at southern high latitudes (Frank et al., 2015; see also supplementary information in the GSA Data Repository¹).

The biotic response to this climate event exhibits several distinctive characteristics that call for a unifying explanation. First, the impact was concentrated among marine invertebrates, which suffered >30% extinction at the species level in the early Serpukhovian (Stanley, 2016) and experienced ecological consequences comparable to those of the largest mass extinctions (McGhee et al., 2012, 2013). Tropical faunas were especially hard hit (Powell, 2005, 2008). In contrast, neither marine fish (Friedman and Sallan, 2012) nor terrestrial floras experienced a Serpukhovian mass extinction, even though plants underwent repeated reorganization in response to climate shifts within the LPIA (Montañez et al., 2007; DiMichele et al., 2008, 2009). Some terrestrial

clades, including insects and tetrapods, diversified strongly during the LPIA (Carroll, 1982; Labandeira, 2005; Sahney et al., 2010; Misof et al., 2014). Second, global diversity did not fully rebound from the extinction until the LPIA ended, ~40 m.y. later (Bambach et al., 2004; Alroy et al., 2008; Aberhan and Kiessling, 2012; Holland and Sclafani, 2015). After other mass extinctions, diversity was generally restored to a pre-extinction level within a few million years (Erwin, 2001; Brayard et al., 2009; Chen and Benton, 2012). Third, macroevolutionary rates were unusually low throughout the recovery interval (Stanley and Powell, 2003; Segessenman and Kammer, 2018). Fourth, the impact was regionally heterogeneous in terms of timing and ecological impact (Clapham and James, 2008; Heim, 2009; Bonelli and Patzkowsky, 2011; Badyrka et al., 2013; Balseiro, 2016). Taken together, these observations imply the existence of a persistent agent through the LPIA that disproportionately affected the tropical marine invertebrate fauna.

The fact that the biotic impact coincided so closely with the LPIA is *prima facie* evidence that they were causally connected, yet the specific mechanism remains unknown. Resolution of this issue will not only improve our understanding of this distinctive interval of time, it will also provide general context for how marine ecosystems respond to major perturbations of global climate. Here, we integrated fossil occurrence data from the Paleobiology Database (<https://paleobiodb.org/>) with lithologic data from Macrostrat (<https://macrostrat.org/>; Peters et al., 2018) to explore late Paleozoic diversity

¹GSA Data Repository item 2020038, additional information on methods, is available online at <http://www.geosociety.org/datarepository/2020/>, or on request from editing@geosociety.org. Matched Paleobiology Database, Macrostrat data, raw Macrostrat data, and r scripts are available online at the Universidad Nacional de Córdoba Data Repository, <https://rdu.unc.edu.ar/bitstream/handle/11086/12914>.

dynamics in their lithologic context. We discovered that the biotic impact of the LPIA was primarily due to a reduction in carbonate habitat area caused by global cooling. This single mechanism is able to explain the distinctive characteristics of the biotic impact of the LPIA.

METHODS

Our data consist of 30,346 fossil occurrences of North American brachiopod, mollusk, and cnidarian genera sampled from Famennian-through Changhsingian-aged units (latest Devonian–Permian) from the Paleobiology Database, which were matched by collection identification (ID) to one of 4241 North American marine lithologic units obtained from Macrostrat (available from the Universidad Nacional de Cordoba Data Repository [see footnote 1]). We limited our analyses to these three representative, well-preserved taxa to minimize the risk that combining taxa with different diversity histories would produce a spurious aggregate diversity pattern, i.e., Simpson's paradox (Simpson, 1951). Rock volume was calculated as the stratigraphic thickness of a unit within a particular time interval multiplied by the area of the Macrostrat column in which it occurred. Total rock volume included all units, whereas sampled fossiliferous rock volume included only those units that contained brachiopod, mollusk, or cnidarian occurrences. We estimated sample-standardized diversity using Fisher's alpha (Hayek and Buzas, 2010), which assumes that occurrences follow a log series distribution. This is generally true for fossil data (Koch, 1987) and specifically true for ours (correlation between expected and observed richness per occurrence class, $n = 146$, $r = 0.99$, 95% confidence interval [CI] [0.97, 0.99], $p < 0.001$). Additional details on methods are available in the Data Repository.

RESULTS

Total rock volume exhibited three cycles of expansion and contraction over late Paleozoic time, broadly coinciding with global sea-level highstands (Haq and Schutter, 2008). The cycles that occurred before and after the LPIA were driven by changes in the volume of both carbonate and siliciclastic rocks, whereas the expansion during the LPIA was driven solely by changes in siliciclastic rock volume (Fig. 1A). The LPIA was characterized by reduced carbonate rock volume, driven both by a decrease in mean thickness of carbonate units and by a latitudinal contraction of carbonate deposition (Fig. 1B). The loss of carbonate rock volume is also reflected in sampled fossiliferous rock volume (Fig. 1C), which comprises 13.8% of total volume overall (20.6% of all carbonates and 10.7% of all siliciclastics). Although the per-interval sampling intensity varies from 3.3% to 19.5% (Fig. 1D), the temporal pattern of sampled fossiliferous rock volume is correlated with total rock volume

(correlation of first differences, $n = 10$, $r = 0.79$, 95% CI [0.32, 0.95], $p = 0.006$).

While total diversity dropped during the LPIA, diversity within each environment did not necessarily mirror such a trend. Diversity within siliciclastic environments increased with the expansion of such environments, while in carbonate environments, diversity decreased as they collapsed (Fig. 2A). Sampled fossiliferous rock volume was a significant predictor of sample-standardized total diversity (regression of first differences, $n = 9$, $r^2 = 0.82$, 95% CI [0.54, 0.95], $p < 0.001$). Carbonate volume was substantially more important as a predictor of total diversity than siliciclastic volume (65% vs. 35%, respectively), which we quantitatively assessed by decomposing r^2 of the multiple regression by averaging over orderings of regressors (the lmg method of Grömping, 2006). First differences of rock volume and Fisher's alpha were also correlated for both carbonate and siliciclastic environments individually (carbonates: $n = 9$, $r = 0.73$, 95% CI [0.12, 0.94], $p = 0.027$; siliciclastics: $n = 9$, $r = 0.81$, 95% CI [0.31, 0.96], $p = 0.009$; Fig. 3). Statistically indistinguishable slopes of the regression of first differences (carbonate slope = 0.0007, 95% CI [0.0004, 0.0013]; siliciclastic slope = 0.0012, 95% CI [0.0008, 0.002]) indicate that an equivalent change in rock volume in either environment would result in the same proportional change in diversity. The outsized influence of carbonate environments on total diversity was simply because the average decline in carbonate rock volume was greater than the average gain in siliciclastic rock volume. During the LPIA, carbonates lost an average of $11.0 \times 10^3 \text{ km}^3$ (or $28.1 \times 10^3 \text{ km}^3$ without a Famennian outlier), whereas siliciclastics gained $9.3 \times 10^3 \text{ km}^3$ (or $2.0 \times 10^3 \text{ km}^3$ without a Famennian outlier). Our results further show that low carbonate diversity is not a consequence of these environments becoming disproportionately depleted of occurrences;

in fact, the proportion of occupied volume increased through the late Paleozoic (Fig. 1D). Despite our attempts to equalize interval durations, stages within the LPIA tended to be shorter (mean = 8.2 m.y.) than stages before or after the LPIA (mean = 13.2 m.y.; Fig. 1E). This would not necessarily bias the diversity patterns because diversity does not tend to accumulate at a constant rate throughout an interval (Foote, 2006), obviating the role of interval length. However, even if it did, that fact cannot explain the relative differences in diversity within carbonate and siliciclastic environments, because standardizing by interval length would affect diversity in both environments equally.

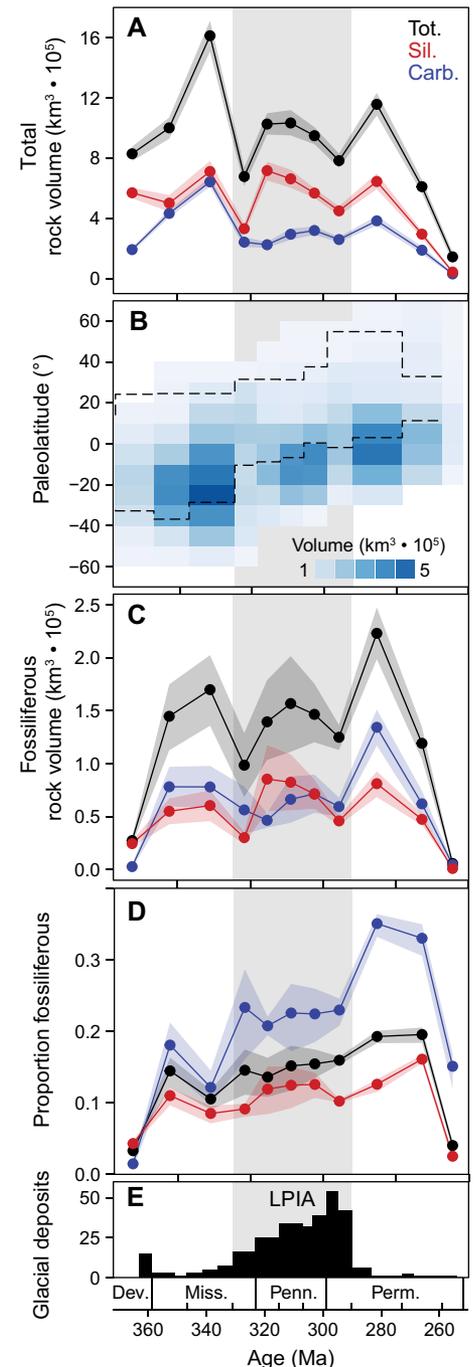


Figure 1. Trends in the volume of North American marine rocks. Late Paleozoic ice age (LPIA) extent is shown as gray shaded area. (A) Total volume of all Macrostrat (https://macrostrat.org) units: black—all lithologies; blue—carbonates; red—siliciclastics. Shaded region around each curve shows range of variation expected due to varying thickness of stratigraphic units (95% confidence intervals). (B) Paleolatitudinal distribution of total carbonate rock volume. Dashed line indicates northern and southern limits of pure carbonate units. (C) Volume of sampled fossiliferous units only. (D) Proportion of total rock volume that contains fossil occurrences of brachiopods, mollusks, and/or cnidarians (% sampled fossiliferous). (E) Frequency of glacial deposits, after Soreghan et al. (2019). Minor tick marks indicate limits of time bins used in this study (Fig. DR2 [see footnote 1]): Dev—Devonian; Miss—Mississippian; Penn—Pennsylvanian; Perm—Permian.

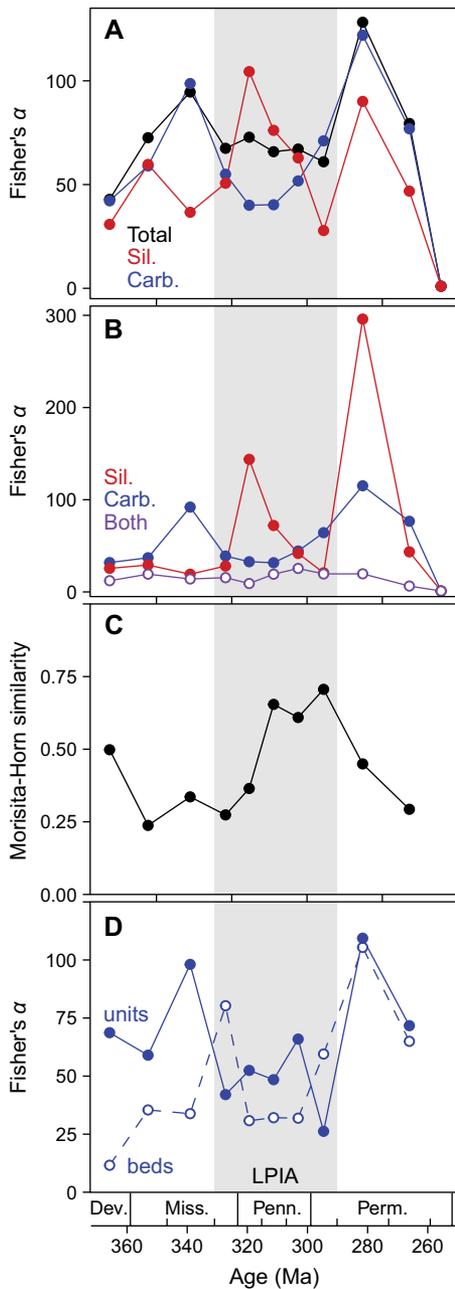


Figure 2. Trends in genus diversity from Famennian through Changhsingian stages. Late Paleozoic ice age (LPIA) extent is shown as gray shaded area. (A) Sample-standardized genus diversity in all (black), carbonate (blue), and siliciclastic (red) environments. Sum of carbonate and siliciclastic diversity may be greater than the total diversity because genera may be counted in both lithologies. Diversity loss from the Early to Middle Permian corresponds to “Olson’s extinction,” which has been documented among terrestrial vertebrates (Benton, 2012; Brocklehurst et al., 2017) but is not apparent in compilations of global marine invertebrate diversity. (B) Sample-standardized diversity by substrate affinity: blue—genera found only in carbonate environments; red—genera found only in siliciclastic environments; purple—genera found in both environments. (C) Taxonomic similarity between carbonate and siliciclastic environments, as measured by the Morisita-Horn index (Horn, 1966). (D) Sample-standardized genus diversity within carbonate units (solid line), and carbonate beds within siliciclastic units (dashed line). Dev—Devonian; Miss—Mississippian; Penn—Pennsylvanian; Perm—Permian.

kirian, ~8 m.y. after the onset of the LPIA. The pattern was reversed when the LPIA ended. Diversity rebounded first in carbonate beds within majority-siliciclastic units during the Asselian–Sakmarian, and then in majority-carbonate units during the Artinskian–Kungurian.

DISCUSSION

The collapse of carbonate environments when the LPIA began was most likely a direct effect of colder temperatures on the carbonate factory, rather than a consequence of increasing siliciclastic input caused by orogenic uplift, or reduction of shelf area due to the formation of Pangea or glacioeustatic fall. Notably, carbonates contracted latitudinally, whereas they would have contracted longitudinally if they had been primarily affected by loss of shelf area or increased siliciclastic input from the Pangean collision, which primarily affected eastern North America (Bennington, 2002). Moreover, despite glacioeustatic fall, sea level remained high in a relative sense throughout the late Paleozoic (Haq and Schutter, 2008), which in turn allowed widespread continental flooding. This is attested by the fact that large volumes of shallow-marine siliciclastic sediment were deposited until the Late Permian. Moreover, carbonate rock volume rebounded once the LPIA ended, long before Pangea began to fragment and restore shelf area lost during the initial collision.

Although temperature was the ultimate cause of diversity loss, our results indicate that the proximate cause was the loss of carbonate environments. Because temperature exerts a first-order control on both diversity (Mayhew et al., 2012) and sediment production (Cecil and Edgar, 2003), it is possible that global cool-

ing led to coordinated, but causally unrelated, changes in both rock volume and diversity. However, cooling temperatures should have impacted genera in both carbonate and siliciclastic environments that existed at the same time and at the same range of latitudes. Yet, except for a transient impact during the Serpukhovian, biodiversity within siliciclastic communities flourished during the LPIA. Further evidence that substrate was the primary agent of biotic change is shown by the fact that diversity was maintained in carbonate beds as carbonate substrates fragmented and disappeared in the late Viséan–early Serpukhovian. It is unlikely that genera living in these carbonate beds experienced a dramatically different climate than genera living in siliciclastic environments, given that the carbonate beds essentially existed contemporaneously with the siliciclastic units that contained them. Cózar et al. (2014) found that early Bashkirian carbonate beds from Morocco contain genera thought to have become extinct in the Mississippian. These carbonate beds within siliciclastic landscapes may have acted as “refugia” for taxa with an affinity for carbonate environments, as carbonate landscapes collapsed. Our results are independently supported by diversity patterns of Mississippian crinoids, which were likewise affected by the loss of carbonate substrate (Kammer and Ausich, 2006; Ausich and Kammer, 2013).

The collapse of carbonate environments documented here explains, with one mechanism, the major distinctive features of the biotic consequences of the LPIA. It explains why the extinction was mostly localized to the tropics, where nearly all extensive carbonate environments are found (Schlager, 2005), and it explains why the impact was disproportionately concentrated among marine invertebrates, which tend to have high degrees of substrate affinity (Foote, 2006; Hopkins et al., 2014). Terrestrial taxa would not have been impacted by the loss

Changes in diversity during the LPIA tended to be concentrated among substrate specialists, i.e., genera exclusively found in a single environment (Fig. 2B). Generalist taxa showed little volatility through the late Paleozoic. The changing proportions of substrate specialists and generalists caused compositional similarity between substrates to rise during the late Pennsylvanian (Fig. 2C).

We further discovered that diversity was temporarily maintained in carbonate beds after the main contraction of the carbonate landscape (Fig. 2D). Majority-carbonate units (>70% carbonate rock by volume) contracted from 54% of all units in the Viséan to just 34% in the Serpukhovian. By contrast, diversity within carbonate beds that were deposited within majority-siliciclastic units was maintained until the Bash-

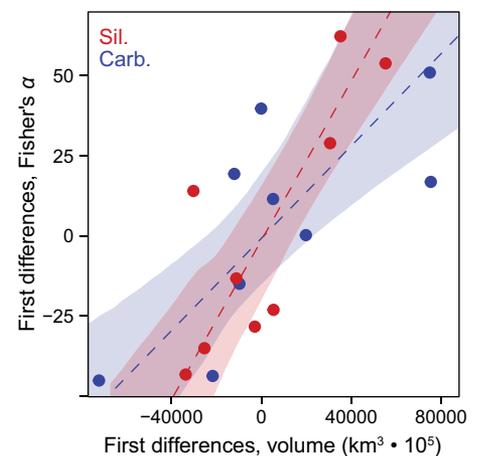


Figure 3. Correlation of first differences in rock volume and sample-standardized genus diversity, for carbonate (blue) and siliciclastic (red) environments.

of carbonate substrate, which may explain the weaker general relationship between the rock record and terrestrial biodiversity observed by Rook et al. (2013).

Our results also explain the prolonged recovery from the Serpukhovian extinction, because widespread carbonate environments did not re-establish until the LPIA ended. Although siliciclastic environments replaced much of the lost carbonate environment, taxa do not readily switch their substrate preferences to occupy new environments (Hopkins et al., 2014). The preferential loss of carbonate specialists also explains why macroevolutionary rates were at unusually low levels during the LPIA, because carbonate specialists tend to have higher macroevolutionary rates (Foote, 2006; Kiessling and Aberhan, 2007). Differential persistence of carbonate beds in different regions may explain disparities in the timing and degree of ecological impact observed in regional studies of marine invertebrates (Clapham and James, 2008; Heim, 2009; Bonelli and Patzkowsky, 2011; Badyrka et al., 2013; Balseiro, 2016).

Our results provide a case study confirmation of the importance of the rock record as a fundamental control on marine biodiversity (Peters, 2008; Hannisdal and Peters, 2011), and they provide a specific mechanism linking the two during a distinctive moment in Earth history. Although a global stratigraphic database is unavailable at this time for us to extend our analyses beyond North America, our conclusions suggest that the global severity of the biotic impact ultimately depended on the lithologic composition of global late Paleozoic rocks.

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