

Climate Change and Mass Extinction Risk in an Endemic-Rich Late Devonian Fauna

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Abstract

The fossil record can illuminate factors that contribute to extinction risk during times of global environmental disturbance; for example, inferred thermal tolerance is an important predictor of extinction during several mass extinctions that corresponded with climate change^{1,2}. Additionally, members of geographically isolated biotas may face higher risk because they have less opportunity to migrate to suitable climate refugia during environmental disturbances. Here, we investigate how these two types of risk intersect in the well-preserved brachiopod fauna of the Appalachian Foreland Basin during the two pulses of the Frasnian-Famennian mass extinction (Late Devonian, ~372 Ma^{3,4}). The selectivity of extinction supports climate change (cooling) as the primary kill mechanism in this fauna, with warm-adapted taxa going extinct preferentially. Overall, the extinction was mild relative to other regions, despite the many endemic species. However, taxa that were vulnerable to climate change went extinct more rapidly, during the first extinction pulse, such that the second pulse was insignificant. These results suggest that vulnerable taxa in geographically isolated biotas face heightened extinction risk at the initiation of environmental stress, but that other regions may “catch up” if environmental stress repeats or intensifies.

Main Text

Survival through major climatic fluctuations may depend on a species' ability to migrate to climate refugia⁵, but many species face climatic, environmental, and geographic barriers to migration. Inability to migrate may be particularly acute in the modern world, as climate change coincides with land-use changes and habitat fragmentation. The fossil record is increasingly used to evaluate potential extinction risk factors during mass extinctions, and it has the potential to illuminate how different types of risk interact⁶. To this end, we document the fate of a semi-isolated regional fauna during the Frasnian-Famennian mass extinction in the Late Devonian. Two pulses of extinction were separated by about 800,000 years (the “Kellwasser Events”), with the second pulse viewed as more severe^{3,4}. Both pulses are associated with global cooling, the expansion of low-oxygen conditions in marine environments, and carbon cycle disruption⁷⁻¹⁰.

Combined with low speciation rates¹¹, these pulses of extinction drove a decline in global standing diversity in the oceans and considerable ecological change¹². Despite a general increase in cosmopolitanism at this time¹¹, extensive new fossil collecting and revised stratigraphic correlations indicate that the pre-extinction brachiopod fauna in the Appalachian Foreland Basin^{13,14} consisted mostly of endemic species (75%), in accordance with previous observations that this fauna was distinct from similar-aged assemblages from central and western North America¹⁵. The Appalachian Basin was partially isolated from other North American marine basins by land barriers and by differences in habitat: the Appalachian seaway received high siliciclastic sediment input from the nearby Acadian Mountains, and substrate is a major control on brachiopod distributions. In addition, fauna in epicontinental seas may have faced added climatic barriers to migration¹⁶.

To examine the pacing and selectivity of the extinction, we intensively collected rhynchonelliform brachiopods from numerous stratigraphic sections along a shallow-to-deep habitat transect in Pennsylvania and New York (Fig. 1A). Brachiopods were abundant in the Devonian, and their calcitic shells preserved readily. The primary dataset consists of 7,933 specimens from 94 bulk samples from the Wiscoy Formation (prior to the first extinction pulse) and 7,095 specimens from 97 bulk samples from the Canaseraga Formation (between the two pulses and immediately after the second pulse). We also collected many thousands of additional fossils that were not counted but were used to verify stratigraphic ranges and identify victims and survivors.

The first pulse of extinction was substantial, with 55% of species extirpated (Fig. 2A), but the second pulse was negligible, with only one member of the original Wiscoy fauna dying out (*Cyrtospirifer chemungensis*). Following the first pulse of extinction, there was an influx of new species, and one of these immigrants also died out in the second pulse (*Spinatrypa planosulcata*, Fig. 2A). The last occurrences of the victims of the first pulse were spread out over the upper several meters of the Wiscoy Formation (Fig. 2A), which we attribute to the Signor-Lipps effect and facies effects¹⁷ (for comparison, the highest Wiscoy occurrences of survivor species were also spread out over several meters).

At one or more localities, *Spinatrypa hystrix* and *Schizophoria amanaensis* last occurred above the Pipe Creek Formation (the dark shale unit associated with the first extinction pulse) but within the $\delta^{13}\text{C}_{\text{org}}$ excursion that marks the Earth-system disturbance associated with the extinction (e.g., *S. hystrix* in Fig. 2A). These species could be considered survivors that perished soon after the first pulse of extinction for unrelated reasons (e.g., if the extinction kill mechanism only operated during deposition of the Pipe Creek), or they could be considered victims (e.g., if the kill mechanism operated throughout the biogeochemical disturbance); this complexity was revealed by sampling multiple stratigraphic sections along a paleodepth-transect¹⁷. Therefore, we ran the analyses twice, counting these species both as victims and as survivors, with the same result (Table 1).

Given the temporal coincidence of global cooling and the demise of tropical taxa, climate change has been suggested frequently as a proximal kill mechanism^{18–20}. Ocean anoxia is also frequently invoked as a kill mechanism, in addition to several other potential factors^{9,21–25}. To evaluate the importance of cooling and anoxia as kill mechanisms in this basin, we evaluated extinction selectivity of brachiopods during the first extinction pulse using exact logistic regression²⁶. Sensitivity to climate change is often assessed in fossil species using paleolatitudinal range; in this case, species were scored as being more warm-adapted if they extended from the Appalachian Basin to lower latitudes (Table S3). We also assessed sensitivity to cooling based on paleolatitudinal distribution at the order level (Fig. 2B), as differential sensitivity at this level has been discussed previously^{27,28}.

Species living in shallow water are less likely to be exposed to low-oxygen conditions, as oxygen readily mixes into shallower water, and anoxia is postulated to spread across the shelf from deeper habitats. We thus used onshore-offshore habitat preference as a predictor of exposure to anoxia¹. Habitat preference

was measured using non-metric multidimensional scaling (NMDS)^{29–31} of the 94 bulk fossil samples from the Wiscoy Formation, which immediately precedes the first extinction pulse, taken along a transect that encompassed all habitats in which brachiopods were common (Fig 1A). Position on the first NMDS axis was strongly related to onshore-offshore position, as indicated by (1) samples from more offshore paleoenvironments (the informal “Muddy Member”) plotting to the left of samples from more onshore paleoenvironments (the informal “Sandy Member”), and (2) samples from more western (distal) localities plotting to the left of samples from more eastern locations within the same member (Fig. 3A). Position on NMDS axis 2 was related to the abundance of *Ambocoelia gregaria*, which occurs in great abundance in certain environments and has been described as an opportunistic species²⁹ (Fig. 3).

In univariate tests, both metrics related to temperature tolerance were significantly related to extinction in the first extinction pulse (Fig. S1; Table S5), with warm-adapted taxa more likely to go extinct. In fact, all species that extended into lower latitudes perished, as did most species belonging to tropically affiliated orders Atrypida, Strophomenida, and Orthida (Fig. 2). No other variable was significant in univariate tests, including onshore-offshore habitat preference (Fig. S1; Table S5). For the exact logistic regression, we combined our two metrics related to temperature tolerance into a composite metric, although using just one or the other produced the same results. The regression indicated, again, that only temperature tolerance predicted extinction versus survival (Table 1), supporting climate change as an important primary kill mechanism. Mean species body size and mean local relative abundance were also used as predictors^{32–34} but were not significant (Table 1).

Just as extinction selectivity provided no support to anoxia as a proximal kill mechanism, geochemical analysis of our stratigraphic sections also suggests that anoxia did not penetrate shallow-water habitats. Although prior trace metal studies indicated intermittent periods of anoxia in more offshore habitats in western New York where macrofossils are rare^{7,35}, analyses of the Pipe Creek Formation in our field area indicate at most dysoxia that decreased in intensity shoreward (Fig. 1B). Similarly, the presence of trace and body fossils indicate dysoxia¹³, similar to other dark shales in the region³⁶. Critically, the Pipe Creek Formation corresponds with a transgression in which all facies would have shifted upslope, and there is no evidence that oxygen levels did not continue to increase shoreward at this time, with brachiopod species tracking their preferred habitats³⁷. These results do not rule out a role for anoxia in other regions, nor a secondary role this region.

Given that few species went extinct in the second pulse, we did not test for selectivity. However, cooling as a proximal kill mechanism is consistent with the fact that one of the only losses was *Spinatrypa planosulcata*, which migrated in after the first pulse of extinction and belongs to a tropically affiliated order (Fig. 2B).

Thus, in the Appalachian Basin, we find that (1) selectivity supports climate change as the major proximal kill mechanism, and (2) almost all brachiopod species losses occurred during the first pulse of extinction, such that the extinction can scarcely be described as having two pulses. All members of the tropical orders Atrypida and Strophomenida that were present in the Wiscoy Formation were eliminated in

the first extinction pulse, with one atrypid migrating in afterward (Fig. 2A). This highly selective first pulse of extinction drove a notable change in the taxonomic composition of the fauna towards dominance by productids, spirifers, and rhynchonellids (Fig. 2A).

In fact, patterns of extinction in the Appalachian Basin were quite unusual – for example, numerous strophomenids and atrypids survived the first extinction pulse in the central and western United States, despite a larger overall proportion of species dying out^{15,38}. The major change in taxonomic composition of the brachiopod fauna did not occur elsewhere until the second extinction pulse, which was large and devastating (e.g., only 4 of 35 New Mexico species are known to survive the second pulse^{27,39}). Diversity also declined during both extinction pulses in shallow marine basins in Europe, with the lowest diversity reached after the second pulse of extinction^{40–42}. Across much of Europe and Southern China, major losses of atrypid and strophomenid brachiopods occurred during the second extinction pulse and recovery communities were dominated by eurythermal and cosmopolitan species^{43–46}.

Numerous factors contribute to a species' extinction risk⁶, with thermal tolerance important in many mass extinctions associated with climate change^{1,2}. Despite the large number of endemic species, extinction risk was not higher in the Appalachian Basin than in other regions – in fact, overall extinction magnitudes were lower than in other parts of North America^{15,38,39}. Rather, the species that were vulnerable to climate change were eliminated in the first pulse of climate change, with the surviving fauna persisting relatively untroubled through the second pulse. In other words, in this biogeographic setting, the “low-hanging fruit” were eliminated in the first pulse, such that the second pulse was almost non-existent. In contrast, in other parts of the world, members of warm-adapted clades (e.g., atrypids, strophomenids) survived the first pulse but succumbed to the second. It is worth noting that current global paleontological databases lack the temporal resolution to examine extinction patterns at this level of detail, highlighting the continued usefulness of detailed local and regional studies. It is also worth emphasizing that larger geographic ranges did not buffer against extirpation in this fauna⁴⁷ – species whose ranges extended to other basins actually had higher extinction risk, presumably because (in this particular fauna) these were the species that were adapted to warmer climates.

These results suggest that multiple sources of extinction risk should continue to be evaluated for modern organisms, including both species-level traits and biogeographic context. However, the interaction among these sources of risk may depend critically on the time scale of observation and of environmental disruption. In the endemic-rich, semi-isolated fauna studied here, extinctions were concentrated at the onset of environmental disturbance, whereas elsewhere, substantial extinction extended throughout both disturbances. If environmental disruption and climate change are temporal persistent and/or recurrent, peak extinction intensity may occur non-synchronously in different geographic settings as vulnerable species are progressively eliminated in different biogeographic settings. These results also suggest that, at the global level, extinction can be mitigated by limiting the persistence and recurrence of adverse conditions.

Methods

Samples

The positions of the first and second extinction pulses were established by biostratigraphy¹⁴ and carbon isotope stratigraphy (Fig. 2A). The Wiscoy Formation immediately precedes the Pipe Creek Formation, which is temporally equivalent to the first extinction pulse (Fig. 2A). The second extinction pulse corresponds to a thinner shale bed in the upper Canaseraga Formation (Fig. 2A). 94 bulk fossil samples were collected from the Wiscoy Formation from 17 localities representing measured stratigraphic sections as well as smaller outcrops (Fig. 1A, Table S1)¹⁴. These samples contained 7,933 rhynchonelliform brachiopod fossils from 26 species, with at least 30 individuals per sample. All samples represent a single bed or a few adjacent beds of similar paleoenvironment. Identifications were based on several sources that have illustrated the brachiopod fauna^{13,48–50}. To avoid double-counting of individuals, parts and counterparts of fragmented rock samples were compared, and only brachiopods with at least half a valve visible were counted.

Chonetid brachiopods were excluded because they were small, sometimes not well preserved, and difficult to identify to the species level. Species with very low total abundance across Wiscoy samples (<10 specimens) were also excluded from analysis. Including these taxa would only strengthen the results, as the excluded taxa survived the extinction and belonged to orders that occur at high latitudes. We could only include species in the regression analyses that occurred in our Wiscoy Formation samples, and several species reported in the literature did not occur in our samples. Had we been able to include these species, it would likewise have strengthened the results, as they all survived the extinction and all had non-tropical affinities according to our metrics (e.g., *Praewaagenoconcha speciosa*, *P. lachrymosa*).

We divided the Wiscoy into two informal units that represent different paleoenvironments (Figs. 2A, S1). At the DAN and BCP sections (Fig. 1A), the “Sandy Member” consists of hummocky- or swaley-bedded, very fine sandstones with interbedded mudstones, indicative of storm reworking and interpreted as deposited just above mean storm weather wave base. To the southeast at CAM and TGB (Fig. 1), the “Sandy Member” has less mudstone and more amalgamated, swaley-bedded sandstone; the paleoenvironment is interpreted as above storm-weather wave base but below fair-weather wave base¹³. Farther east (location TF), grain size increases into coarser sands, plant material is more abundant, and paleoenvironment is interpreted to have been above fair-weather wave base. The “Muddy Member” consists mostly of mudstone with some interbeds of silt or very fine sand, deposited at or below mean storm-weather wave base.

Data Analysis

Analyses were conducted using R Statistical Software version 4.0.1 and the Calibrate, Plotrix, logistf, and Vegan Packages. Species’ habitat preferences within the Wiscoy Formation were evaluated using non-metric multidimensional scaling (NMDS)^{29,30,51} based on species’ proportional abundances within

samples using Bray-Curtis similarity in three dimensions (stress = 0.1245). To separate the effects of onshore-offshore habitat from the effects of opportunistic species blooms for purposes of the regression analysis, the NMDS results were rotated slightly in Figure 3, which can be justified since the orientation of the point cloud in the original NMDS is based on statistical properties of the data instead of biological properties²⁹. The rotation had no effects on the results; the original NMDS is shown in Figure S2.

A number of species in the Wiscoy also occur in western and central North America, which were at slightly lower latitudes than the Appalachian Basin in the Late Devonian. These species were identified by comparison with taxonomic works^{27,49} and museum collections. In a few cases, our assignments differ slightly from those of other studies⁴⁷ due to differences in taxonomic treatment (e.g., our splitting Wiscoy *Spinatrypa* into two species). We also inferred temperature tolerance at the order level, given previous reports of strong tropical preference of some orders²⁷. Mid- to high-latitude records of brachiopods are relatively sparse during the Frasnian, so we used paleolatitudinal distribution during the Early-Middle Devonian, combining occurrences from the northern and southern hemispheres (Table S3). After excluding orders not represented in the regression analysis, the occurrences were combined into 10° bins, and the “preferred paleolatitude” for each order was calculated as the weighted average of the proportional abundances in these bins (Fig. 2B). Each species within the same taxonomic order was given the same value. For the regression analysis, these two metrics of temperature tolerance were combined by converting each to z-scores and summing the two values for each species.

Body size measurements were obtained for at least 20 individuals of each species, or for all available specimens if fewer than 20 were present, and the geometric mean of length and width was calculated. The third potential body size measurement could not be obtained from some moldic fossils and was excluded. Abundance was calculated as the log of the mean proportional abundance for each species. Other measures of abundance (e.g., number of samples in which a species occurs) were highly correlated with this measure.

To test each parameter for importance towards species extinction, an exact logistic regression was run for all possible model combinations of predictor variables (Table 1). Firth’s method was chosen due to the separation within our data and small sample size of species²⁶. Analyses were run twice to account for the possibility of *S. hystrix* and *S. amanaensis* as both victims and survivors of the first extinction pulse (Table 1).

Trace metals

Trace metal proxies have been used previously to assess oxygen levels during the extinction pulses in New York, primarily in offshore sections^{7,8,35}. We extended these studies to more onshore settings for the first extinction pulse using XRF and ICP analyses to detect trace metal concentrations. For comparability with previous studies, we focused on Mo concentrations. Mo values between 2-30 ppm are considered dysoxic, intermittently anoxic or euxinic between 30-100 ppm, and permanently anoxic greater than 100 ppm⁵².

Declarations

Data Availability

The fossil data that support this study are available in the Paleobiology Database (PBDB) at <https://paleobiodb.org/> with the identifiers [accession numbers to be inserted here]. The authors declare that all other data supporting the findings of this study are available within the paper and its supplementary information files.

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Author contributions:

JQP and AMB contributed data, performed analyses, wrote the text, and created figures. SKB, JAB, and MTH contributed data, comments, and revisions.

Competing Interest Declaration:

The authors declare that they have no conflict of interest.

Materials and Correspondence:

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Tables

Table 1. Exact logistic regression results of variables predicting the likelihood of extinction of brachiopod species (see Methods). A. Analyses run with *Spinatrypa hystrix* and *Schizophoria amanaensis* as victims. Odds ratio = 9.621, p-value = 0.047. B. Analyses run with *Spinatrypa hystrix* and *Schizophoria amanaensis* as survivors. Odds ratio = 16.154, p-value = 0.003.

1. Parameter	Thermal Tolerance (Composite Metric)	Body Size	Mean Depth	% Abundance
<i>Odds Ratio</i>	0.11	0.99	4.04	0.39
<i>p-value</i>	0.0002	0.9893	0.2449	0.5838
<i>Confidence Interval</i>	(-7.26, -0.78)	(-0.49, 0.23)	(-0.97, 6.63)	(-6.06, 4.86)

2. Parameter	Thermal Tolerance (Composite Metric)	Body Size	Mean Depth	% Abundance
<i>Odds Ratio</i>	0.30	0.97	2.21	0.26
<i>p-value</i>	0.0101	0.6770	0.4222	0.1638
<i>Confidence Interval</i>	(-2.94, -0.24)	(-0.21, 0.12)	(-1.26, 2.93)	(-3.89, 0.52)

Figures

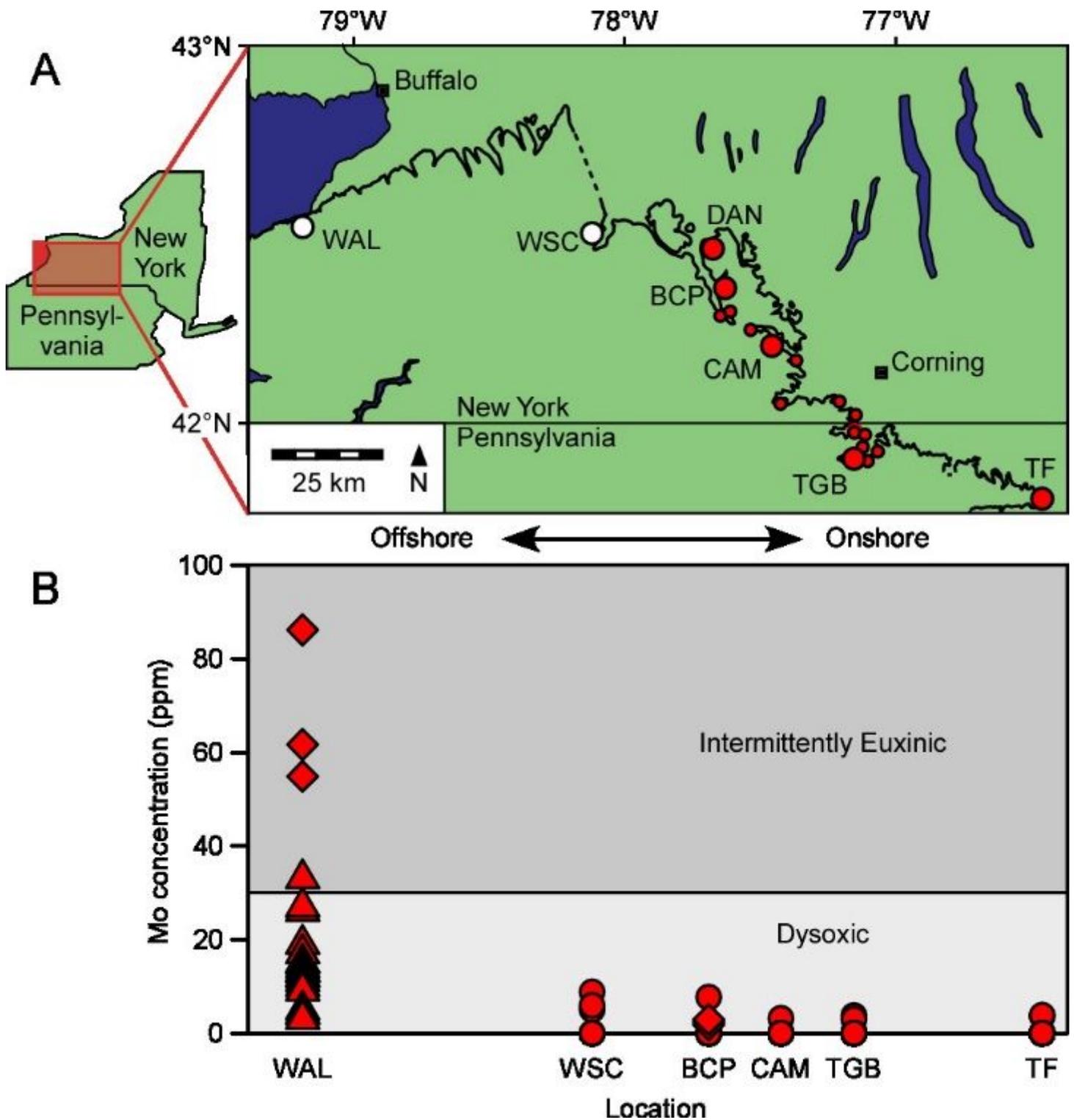


Figure 1

Locations and paleoenvironmental proxy data. A. Map of study area (modified from 14). Large red circles represent measured stratigraphic sections from which numerous samples were collected, and small red circles represent additional sampling localities (see Table S1 for coordinates). White circles represent sections sampled only for geochemistry due to rarity of macrofossils. B. Mo concentrations from the Pipe Creek Formation as a proxy for oxygen level during the first extinction pulse. In the onshore localities examined here (WSC-TF), Mo concentrations were below the detection limit in some samples. The

“Dysoxic” and “Intermittently Euxinic” fields follow ref. 53 and 54. Sources of data: circles = this study; diamonds = ref. 35; triangles = ref. 7. See Table S2 for data. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

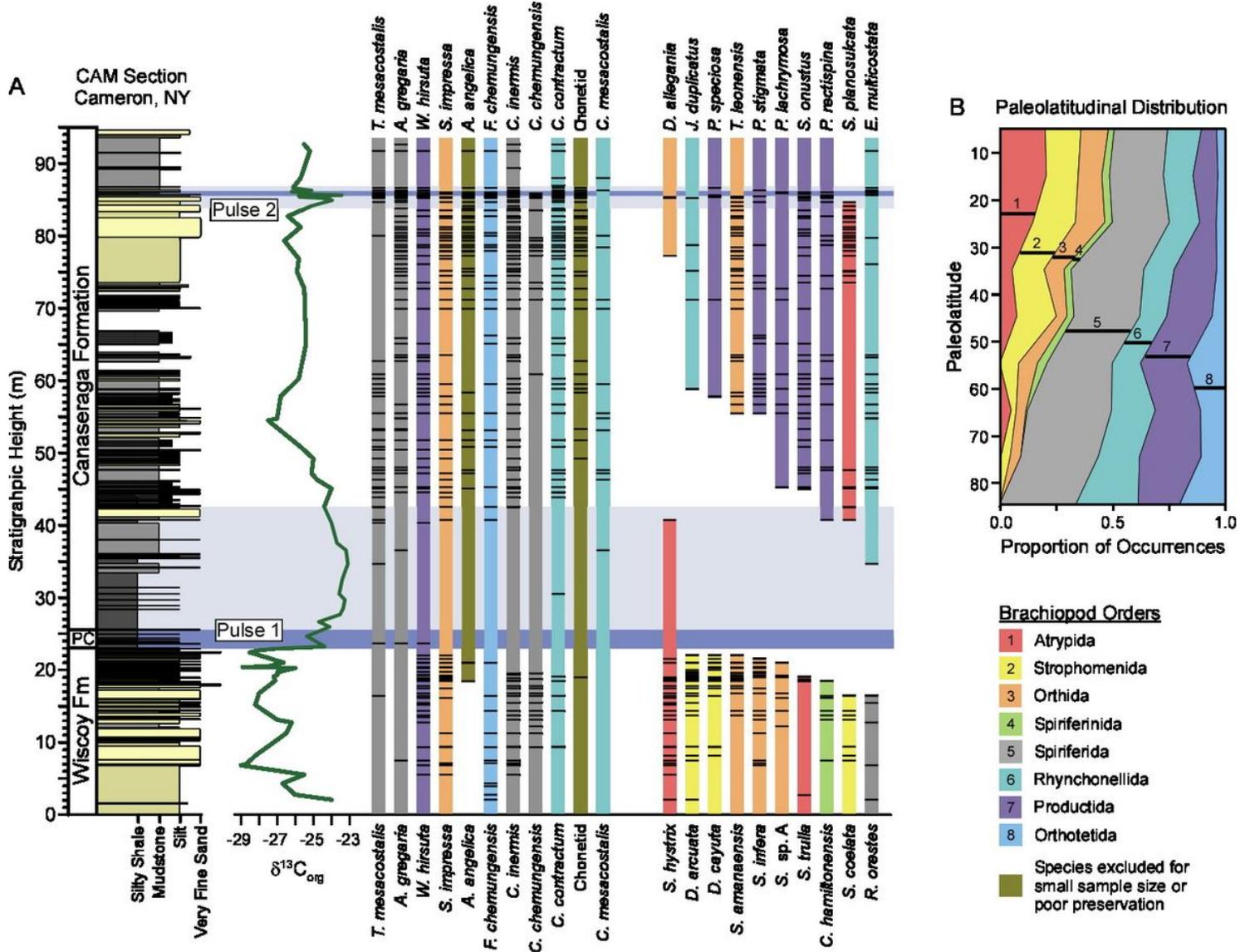


Figure 2

Stratigraphic and paleolatitudinal distributions of brachiopods. A. Stratigraphic section through the two extinction pulses (“Pulse 1” and “Pulse 2”) at location CAM showing $\delta^{13}C_{org}$ excursions and brachiopod species occurrences (horizontal black dashes). Not all species are present at this section. Colored vertical bars mark the total known stratigraphic ranges of species and are extended to the base or top of the section for species known to occur lower or higher based on data from other localities. Color indicates taxonomic order for each species. Full species names are given in Table S4. B. Paleolatitudinal

distribution for brachiopod orders during the Devonian, showing only orders included in the regression analysis. Black lines indicate the weighted averages of the paleolatitudinal distributions of the orders.

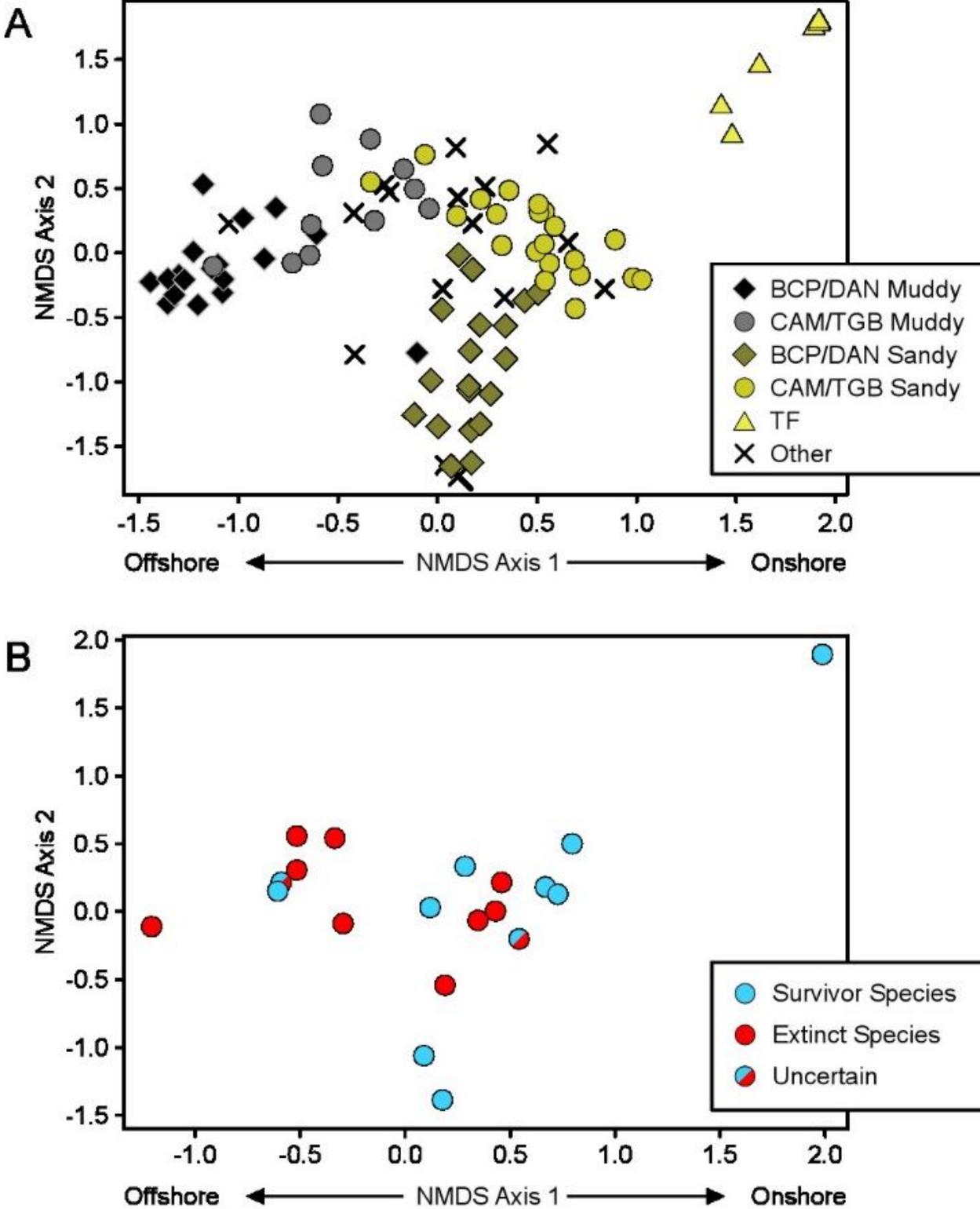


Figure 3

NMDS ordination of the brachiopod fauna from the Wiscoy Formation, which immediately precedes the first extinction pulse. A. Samples labeled by locality and informal stratigraphic unit (offshore “Muddy Member” or onshore “Sandy Member”). Samples that plot at the negative end of NMDS Axis 2 contain a

high abundance of *Ambocoelia gregaria*, which has been described as an opportunistic species that does not fall cleanly along onshore-offshore gradients in ordinations²⁹. B. Species labeled as victims or survivors of the first extinction pulse.

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