



Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition

Scott D. Evans^{a,1}, Chenyi Tu^b, Adriana Rizzo^b, Rachel L. Surprenant^b, Phillip C. Boan^b, Heather McCandless^b, Nathan Marshall^b, Shuhai Xiao^a, and Mary L. Droser^b

Edited by Donald Canfield, Syddansk Universitet, Odense M., Denmark; received May 2, 2022; accepted October 1, 2022

The Ediacara Biota—the oldest communities of complex, macroscopic fossils—consists of three temporally distinct assemblages: the Avalon (ca. 575–560 Ma), White Sea (ca. 560–550 Ma), and Nama (ca. 550–539 Ma). Generic diversity varies among assemblages, with a notable decline at the transition from White Sea to Nama. Preservation and sampling biases, biotic replacement, and environmental perturbation have been proposed as potential mechanisms for this drop in diversity. Here, we compile a global database of the Ediacara Biota, specifically targeting taphonomic and paleoecological characters, to test these hypotheses. Major ecological shifts in feeding mode, life habit, and tiering level accompany an increase in generic richness between the Avalon and White Sea assemblages. We find that ~80% of White Sea taxa are absent from the Nama interval, comparable to loss during Phanerozoic mass extinctions. The paleolatitudes, depositional environments, and preservational modes that characterize the White Sea assemblage are well represented in the Nama, indicating that this decline is not the result of sampling bias. Counter to expectations of the biotic replacement model, there are minimal ecological differences between these two assemblages. However, taxa that disappear exhibit a variety of morphological and behavioral characters consistent with an environmentally driven extinction event. The preferential survival of taxa with high surface area relative to volume may suggest that this was related to reduced global oceanic oxygen availability. Thus, our data support a link between Ediacaran biotic turnover and environmental change, similar to other major mass extinctions in the geologic record.

biodiversity | Ediacara Biota | environmental change | extinction | oxygen

Soft-bodied fossils of the Ediacara Biota comprise the oldest communities of macroscopic organisms, including animals, and are critical for understanding the advent and diversification of complex life (1, 2). However, equally important are the dynamics that lead to the disappearance of such animals (3–6). Two major drops in diversity of the Ediacara Biota have been recognized, an initial decrease between the White Sea and Nama assemblages and a second across the Ediacaran–Cambrian boundary (Fig. 1 and ref. (5)). Although these events may be related, they are separated by more than 10 My and vary in magnitude and taxa impacted. The exceptional conditions required to preserve the Ediacara Biota also leave uncertainty around potential taphonomic biases that may contribute to such patterns. Diversity crises shaped the course of evolution in the Phanerozoic. Thus, a comprehensive understanding of each of these Ediacaran events is critical to determine the fate of Earth's early animals.

Similar mechanisms have been proposed for losses of diversity during both the White Sea–Nama and Ediacaran–Cambrian transitions. One suggestion is that taxa did not go extinct but instead are not preserved in subsequent intervals (the “Cheshire cat” model of ref. (3)). Biases may include differences in the paleolatitudes and paleoenvironments sampled as well as variable taphonomic windows preserving fossils from each assemblage (7). Alternatively, these events may represent true extinctions triggered by either biotic or abiotic factors or some combination thereof (3, 5). The biotic replacement model, generally attributing the demise of the Ediacara Biota to competition with more advanced “Cambrian-style” metazoans, focuses on the impact of bioturbators as indicated by increases in trace fossil diversity (e.g., ref. (8)). Such ecosystem engineers are proposed to have fundamentally changed carbon packaging and fluid transport in the latest Ediacaran (3, 4, 8–10). Alternatively, the catastrophic extinction model posits that a major environmental perturbation led to the rapid loss of a variety of Ediacara taxa (3, 5) supported by geochemical data for environmental conditions, such as changes in oxygen availability (e.g., ref. (11)).

Here, we use a holistic approach, combining the distribution, taphonomy, and ecology of constituent taxa, to investigate changes in the Ediacara Biota through compilation of global occurrence data. Specifically, we test for potential sampling biases in the form of

Significance

Mass extinctions are well recognized as significant steps in the evolutionary trajectory of life on this planet. Here, we document the oldest known extinction of animals and test for potential causes. Our results indicate that, like younger diversity crises, this event was caused by major shifts in environmental conditions. Particularly, we find support for decreased global oxygen availability as the mechanism responsible for this extinction. This suggests that abiotic controls have had significant impacts on diversity patterns throughout the more than 570-My history of animals on this planet.

Author affiliations: ^aDepartment of Geosciences, Virginia Tech, Blacksburg, VA 24061; and ^bDepartment of Earth and Planetary Sciences, University of California, Riverside, CA 92521

Author contributions: S.D.E. and M.L.D. designed research; S.D.E., C.T., A.R., R.L.S., P.C.B., H.M., N.M., S.X., and M.L.D. performed research; S.D.E., C.T., A.R., R.L.S., P.C.B., H.M., N.M., and M.L.D. contributed new reagents/analytic tools; S.D.E., C.T., A.R., R.L.S., P.C.B., H.M., N.M., S.X., and M.L.D. analyzed data; and S.D.E. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2022 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

¹To whom correspondence may be addressed. Email: scotte23@vt.edu.

This article contains supporting information online at <http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2207475119/-DCSupplemental>.

Published November 7, 2022.

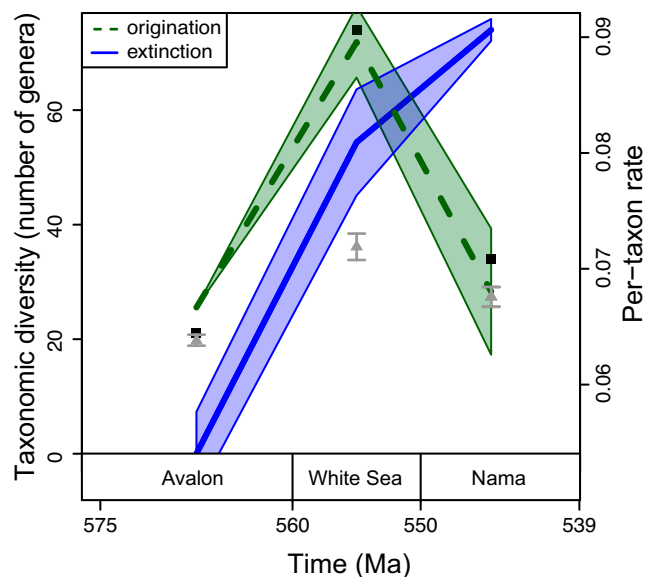


Fig. 1. Raw generic diversity (black squares), bootstrapped diversity (gray triangles), bootstrapped (42) per taxon extinction rate (solid blue), and origination rate (dashed green). Error bars represent 1 SD. For bootstrapping analysis, database occurrences were randomly subsampled to 50 occurrences.

major differences in the paleolatitudes, facies associations, or preservational modes that could account for apparent changes in taxonomic composition. Based on the lack of correlation between these factors, we then investigate paleoecological trends through the Ediacaran under the assumption that, as with other diversity crises in the fossil record (12), patterns of selectivity across these intervals should reflect the factors responsible for such change. Analysis was conducted by comparing differences between the three assemblages—necessarily representing time-averaged groups of organisms on the order of millions to tens of millions of years—as in previous studies (e.g., refs. (3, 5, 13)). However, we also examined patterns of change involving taxa that survived and went extinct at the end of the White Sea assemblage to investigate changes on relatively shorter geologic timescales.

Results

We find support for a significant drop in diversity between the White Sea and Nama assemblages, consistent with previous reports (5, 6, 13). Specifically, of the 70 genera identified from the White Sea interval, only 14 are recognized in the Nama assemblage, indicating the (geologically) rapid loss of ~80% of constituent organisms. The transition between these assemblages involved both elevated extinction and decreased origination rates (Fig. 1).

Sampling Biases: Paleogeography, Paleoenvironments, and Preservation. Using recent continental reconstructions (14), we find that changes in paleogeographic distribution do not match diversity trends (Fig. 2A, *SI Appendix*, Fig. S1, and (7)). Localities containing fossils attributed to the White Sea assemblage occur preferentially at low latitudes ($\leq 30^\circ\text{N}$ or S). Those containing the Avalon and Nama assemblages are more broadly distributed; however, Nama localities are similarly concentrated at low latitudes. Controversy exists regarding the mechanisms behind plate motion and, thus, the exact continental configurations during the Proterozoic (e.g., refs. (14, 15)). However, given the distribution of localities associated with each assemblage over multiple paleocontinents, these changes do not appear to impact our results and

would likely only increase the latitudinal heterogeneity of both the White Sea and Nama assemblages.

While the Avalon assemblage occupies comparatively deep depositional environments, both the White Sea and Nama assemblages are characterized by relatively shallow paleoenvironments, primarily attributed to the inner and middle shelf (Fig. 2B). There is a consistent increase in the No. of distinct taphonomic modes in successively younger assemblages (Fig. 2C). Importantly, preservation in siliciclastic sediments as casts and molds accounts for the highest diversity of White Sea taxa and is well represented in the fossil record of both the Avalon and Nama assemblages.

Paleoecology. We find significant differences in the feeding mode, life habit, ecological tier, and maximum body size between the Avalon and White Sea assemblages (Table 1). These changes, at least in part, reflect the advent and diversification of mobile taxa that fed directly on organic mats in the White Sea assemblage (e.g., *Dickinsonia* and *Kimberella* (1, 2)). Such taxa occupy the lowest ecological tier and typically reach smaller maximum sizes compared with the large, upright, sessile fronds that dominated the Avalon assemblage (Fig. 3). In contrast, there are no significant paleoecological difference between the White Sea and Nama assemblages except with respect to surface area relative to volume (Table 1 and Fig. 3). These trends hold irrespective of controversies over inferred feeding modes (e.g., whether rangeomorphs are interpreted as osmotrophs or suspension feeders; *SI Appendix*, Table S1). Taxa that survived the White Sea–Nama transition preferentially exhibit morphologies that maximize surface area relative to volume, as previously recognized (13); reached higher ecological tiers; and attained greater maximum sizes. While there are uncertainties associated with these interpretations (e.g., whether erniettomorphs are considered to exhibit high surface area relative to volume), various treatment confirms the preferential survival of taxa that maximize cell contact with seawater (*SI Appendix*, Table S2).

Discussion

Global occurrence data for the Ediacara macrobiota systematically demonstrate that changes in diversity cannot be attributed to sampling biases, consistent with previous suggestions (6, 7, 9, 16). Specifically, the paleolatitudes, paleoenvironments, and preservational modes characteristic of the White Sea assemblage are well represented at Nama-aged fossil localities. Variable sampling and reporting make the integration of abundance data into a global database, such as the one constructed here, difficult (although see refs. (17, 18) for comparisons of a few key localities). However, at classic localities in both South Australia and Russia, occurrence data indicate that fossils of the White Sea assemblage are found throughout stratigraphic packages several 10's to more than 100 m in thickness (19, 20), potentially representing a period of more than 4 My (21). Less than 20% of such taxa have been recognized in the variety of fossil-rich deposits younger than ~550 Ma. Thus, the decline in diversity between these assemblages is indicative of an extinction event, with the percentage of genera lost comparable to that experienced by marine invertebrates during the “Big 5” Phanerozoic mass extinctions (22, 23).

Biotic Replacement versus Environmental Catastrophe during the White Sea–Nama Transition. Patterns of selectivity during periods of biotic turnover reflect the underlying causes of such change (e.g., ref. (12)). The paleoecological data compiled here provide the opportunity to test for such trends. Despite clear differences between the Avalon and subsequent

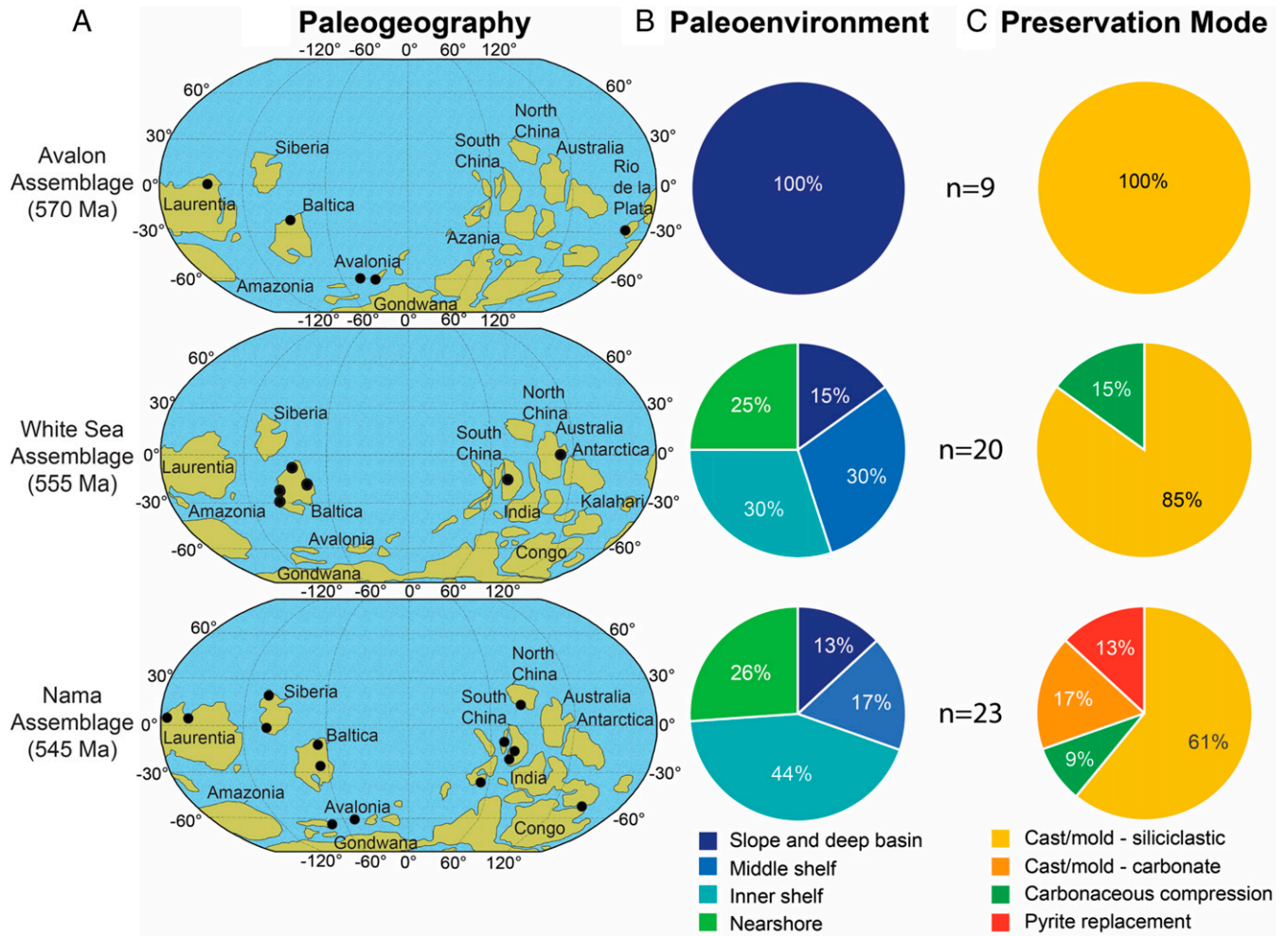


Fig. 2. Paleogeographic distribution of fossil localities (A) within the three assemblages of the Ediacara Biota based on continental configurations by Merdith et al. (14) and pie charts with the distribution of paleoenvironments (B) and modes of preservation (C) sampled for each assemblage, with “n” referring to the No. of formations/facies sampled in each time bin. See *SI Appendix, Fig. S1* for locality labels.

assemblages, we find no statistically significant distinctions in life mode, feeding habit, tiering, or body size when comparing taxa from the White Sea and Nama intervals (Table 1 and Fig. 3). Biotic replacement by ecosystem engineers is proposed to have preferentially impacted sessile, suspension feeding organisms reliant on specific nutrient supply pathways (3, 8, 10). If such changes were responsible for the loss of White Sea taxa, we would expect to see shifts in the ecologies of Ediacaran organisms that

Table 1. Epps-Singleton *P* values comparing the Avalon (A), White Sea (WS), and Nama (N) assemblages as well as all WS assemblage taxa to those that went extinct (Ext) and those that survived (Sur) into the latest Ediacaran

	A-WS	WS-N	WS-Ext	WS-Sur
Feeding mode	<<0.001	0.33	0.95	0.22
Life habit	<<0.001	0.06	0.92	0.05
Ecological tier	0.002 (–)	0.24	0.59	0.004 (+)
Max body size (mm)	<<0.001 (–)	0.08	0.53	0.006 (+)
Min body size (mm)	0.16	0.14	0.73	0.08
SA/V	<<0.001 (–)	0.006 (+)	0.71	<<0.001 (+)

Bold indicates statistical significance ($P < 0.05$). Signs in parentheses indicate the direction of significant change for size-based variables (e.g., negative change in ecological tier indicates that taxa from the Avalon assemblage occupy higher ecological tiers than those from the White Sea).

persisted into the Nama interval. Instead, our data indicate that all feeding modes and life habits were subject to similar levels of extinction during this event, inconsistent with expectations of the biotic-replacement hypothesis.

Additional evidence suggests that ecosystem engineers were unlikely to have caused the drop in diversity leading to the Nama assemblage. Evidence for such behavior is recorded by trace fossils, and previous studies document the evolution of burrowing activities through the late Ediacaran (4, 8–10). The White Sea interval is characterized by simple horizontal trails (e.g., refs. (9, 24)), which would have had limited impacts on Ediacaran ecosystems. Increased activity and complexity of ecosystem engineers are not observed until the time of the already depauperate Nama assemblage (8, 10), postdating the White Sea–Nama transition. Darroch et al. (5) convincingly argue that biotic replacement is a geologically slow process, requiring temporal overlap between ultimately successful organisms and those they drive to extinction. Thus, although potentially relevant for the demise of the Ediacara Biota more than 10 My later, such activity is unlikely to have been responsible for the event that led to the loss of most of the White Sea assemblage.

Ubiquitous organic mats characteristic of this period were integral to the Ediacara Biota, especially mobile mat feeding organisms that diversified in the White Sea assemblage (e.g., ref. (2)). The decline of mats in the Paleozoic is directly tied to the proliferation of efficient bioturbating animals in the

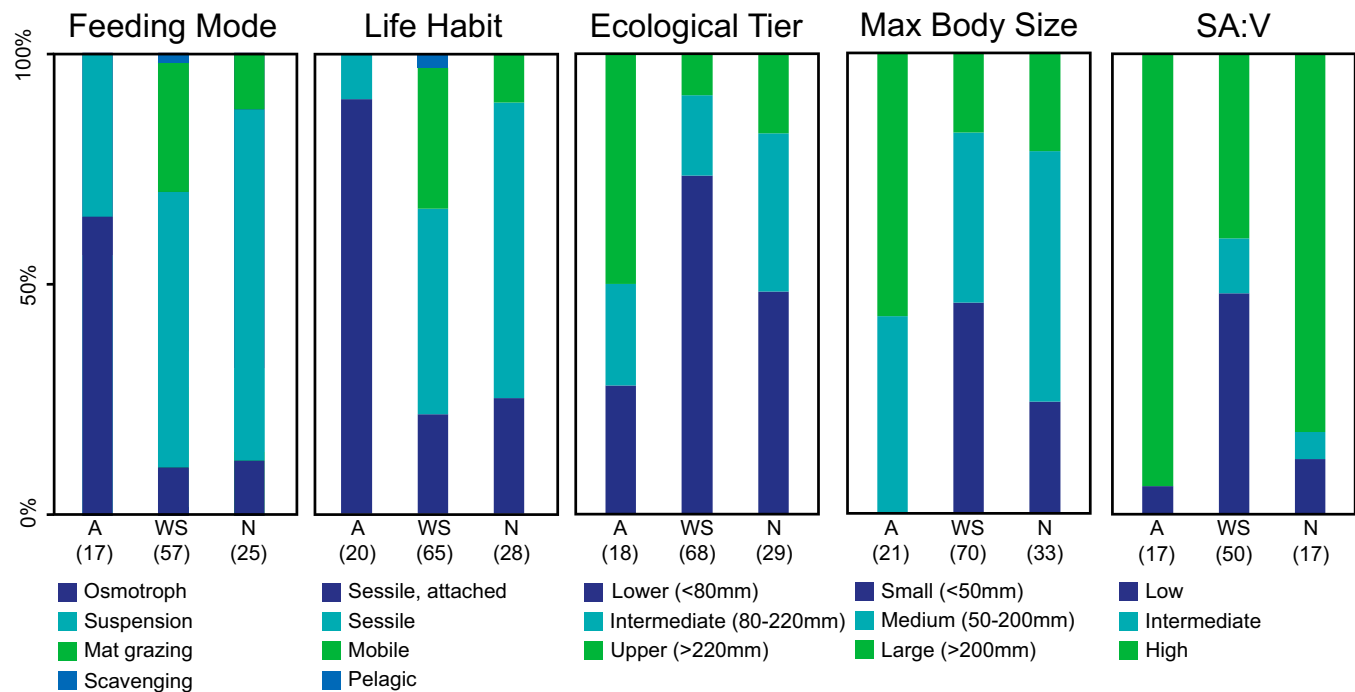


Fig. 3. Stacked bar histograms for the Avalon (A), White Sea (WS), and Nama (N) assemblages for various ecological metrics, including surface area relative to volume (SA:V). Values in parentheses indicate the total No. of taxa for which a given metric was assigned.

late Ediacaran and into the Cambrian (9, 25). Thus, another possible explanation for the demise of the White Sea assemblage is the loss of such habitats, for which they were specifically adapted. Although there is evidence for a decrease in the total proportion of taxa that fed directly on mats in the Nama assemblage (Fig. 3), this does not represent a statistically significant decline (Table 1). Furthermore, such taxa were not preferentially impacted during the White Sea–Nama extinction. Sedimentological evidence suggests that shallow marine environments characterized by organic mats were present during the Nama assemblage (4, 26) and likely continued into the early Cambrian (9, 27). Thus, these habitats were still available long after this event.

The only significant change identified here between the White Sea and Nama assemblages is an increase in taxa whose morphologies exhibit clear adaptations to maximize surface area relative to volume. Uncertainty regarding the reconstructions of certain morphogroups may impact the significance of these trends (*SI Appendix, Table S2*). However, high surface area to volume ratios are positively correlated with survivorship of this extinction, regardless of how such taxa are classified. By maximizing the relative proportions of cells in direct contact with seawater, high-surface-area taxa would have been comparatively better adapted to survive in low-oxygen environments (e.g., refs. (13, 28)). This group is dominated by large, upright frondose organisms (e.g., *Arborea*, *Charnia*, *Rangia*, and *Swartpuntia*), which likely contributed to the preferential survival of taxa reaching greater ecological tiers and maximum body size.

The link between biodiversity crises and environmental change is well established (e.g., refs. (29, 30)). The ultimate causes of mass extinctions include major drivers, such as bolide impacts, eruption of large igneous provinces, and/or tectonic shifts, which produce major changes in redox state, temperature, and/or oceanic pH, leading to diversity decline (e.g., refs. (18, 30)). While our data do not provide direct information on the ultimate driver of this event, the broad range of paleoecologies impacted across the White Sea–Nama extinction is

consistent with the predicted effects of a catastrophic environmental perturbation. The preferential survivorship of taxa whose morphologies suggest tolerance of low-oxygen conditions may indicate that anoxia was the proximal factor responsible for this decline in diversity. This is congruent with previously proposed links between decreased global oxygen availability and a drop in diversity between the White Sea and Nama assemblages (13) and the hypothesis that major mass extinctions in early animals are directly linked to fluctuations in global redox conditions (31). Recent identification of a potentially global carbon isotope excursion at ~550 Ma (21) further supports a major environmental shift during this transition, potentially related to fluctuating redox conditions. While uncertainty of timing and difficulties estimating background extinction rates during the Ediacaran leaves characterization as a true “mass extinction” equivocal (22), this nevertheless represents the earliest extinction in the fossil record of macroscopic animals.

The Nama Assemblage and the Ediacaran–Cambrian Transition.

Our data do not directly address what happened to the Ediacara Biota following the White Sea–Nama extinction event. Previous studies demonstrate that, in addition to low overall species richness, Nama-aged communities can be characterized by high dominance and relatively simple ecological interactions compared with the rest of the Ediacara Biota, especially the White Sea assemblage (2, 32, 33). Comparison of the No. of paleocontinents and paleoenvironments in which representatives from each assemblage are found may support preferred survivorship of taxa with broader paleogeographic distributions and environmental tolerance across the White Sea–Nama extinction (*SI Appendix, Table S3*). This is consistent with the Nama assemblage representing generalist taxa that survived a major environmental perturbation, a common pattern observed in the Phanerozoic (34), and/or stressed conditions during the latest Ediacaran (5, 16, 33). The latter may be supported by geochemical evidence for fluctuating redox conditions during

the last 10 My of the Proterozoic (11, 35, 36). Additional stress during the Nama assemblage may further be attributed to increases in ecosystem engineering discussed above.

Most taxa from the Nama interval did not survive into the Cambrian, although there are a few exceptions (e.g., ref. (37)). Within the Ediacara Biota, candidate sponges, ctenophores, cnidarians, and bilaterians have all been proposed (1, 2, 38). Thus, despite the extinction of specific genera, these clades must have persisted into the Phanerozoic. It is possible that other characters—in addition to high cell contact with seawater—allowed certain metazoans to preferentially survive redox stress during the latest Ediacaran (e.g., ref. (11)). For example, trace fossil evidence suggests that the White Sea bilaterian *Ikaria* was able to target preferentially oxygenated habitats (39, 40). These taxa may have proliferated during this interval, eventually surviving the Ediacaran–Cambrian transition, as suggested by increased trace fossil diversity and complexity coincident with the appearance of skeletonized forms and the depauperate Nama assemblage (4, 8, 10). However, such patterns and whether latest Ediacara soft-bodied taxa were replaced by these more-complex metazoans (4, 9), impacted by additional environmental perturbation near the Ediacaran–Cambrian boundary (11, 41), or some combination thereof (8, 10) require further evaluation.

Materials and Methods

We compiled a database of Ediacaran fossil occurrences from the available literature (Dataset S1). Because we are primarily interested in the fate of

soft-bodied Ediacaran animals, we excluded microfossils, algae, biomineralized taxa, and trace fossils (see *SI Appendix* for detailed information on what was included and data standardization). A unique entry was created for each fossil occurrence, including information regarding the locality, stratigraphy, lithology, preservational mode, and interpreted depositional setting. We also recorded the life habit, feeding mode, tiering level, body size (maximum and minimum), and relative surface area to volume of taxa based on previously published interpretations when available. Origination and extinction rates were calculated following established protocols (42). Recent continental reconstructions (14) were used to map paleogeographic locations (Fig. 2A). We used the Epps-Singleton two-sample test to evaluate the null hypothesis that assemblages represent random samples of the same distribution, with $P < 0.05$ indicating significantly different distributions. This test was chosen based on applicability for both continuous (e.g., body size) and ordinal (e.g., feeding mode) variables (43). We determine whether the mean and 95% CIs for significant changes in ecological tier, size, and surface area relative to volume increased or decreased between assemblages. To investigate potential patterns related to changes at the end of the White Sea assemblage, we also compared this entire group with taxa that survived into the Nama assemblage, as well as those that went extinct. All statistical analysis was conducted using the freely available PAST software (<https://www.nhm.uio.no/english/research/infrastructure/past/>).

Data, Materials, and Software Availability. All data are included in the manuscript and/or supporting information.

ACKNOWLEDGMENTS. This work was supported by an Agouron Geobiology Fellowship (S.D.E.), a NASA Exobiology grant (80NSSC19K0472 to S.D.E. and M.L.D.), and an NSF grant (EAR 2021207 to S.X.).

1. S. Xiao, M. Laflamme, On the eve of animal radiation: Phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol. Evol.* **24**, 31–40 (2009).
2. M. L. Droser, J. G. Gehling, The advent of animals: The view from the Ediacaran. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 4865–4870 (2015).
3. M. Laflamme, S. A. Darroch, S. M. Tweed, K. J. Peterson, D. H. Erwin, The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat? *Gondwana Res.* **23**, 558–573 (2013).
4. A. V. Kolesnikov, V. V. Marusin, K. E. Nagovitsin, A. V. Maslov, D. V. Grazhdankin, Ediacaran biota in the aftermath of the Kotlinian Crisis: Asha Group of the South Urals. *Precambrian Res.* **263**, 59–78 (2015).
5. S. A. F. Darroch, E. F. Smith, M. Laflamme, D. H. Erwin, Ediacaran extinction and Cambrian explosion. *Trends Ecol. Evol.* **33**, 653–663 (2018).
6. A. D. Muscente *et al.*, Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. *Nat. Commun.* **10**, 911 (2019).
7. C. E. Boddy, E. G. Mitchell, A. Merdith, A. G. Liu, Palaeolatitudinal distribution of the Ediacaran macrobiota. *J. Geol. Soc. London* **179**, 10.1144/jgs2021-030 (2022).
8. A. T. Cribb *et al.*, Increase in metazoan ecosystem engineering prior to the Ediacaran–Cambrian boundary in the Nama Group, Namibia. *R. Soc. Open Sci.* **6**, 190548 (2019).
9. L. A. Buatois, G. M. Narbonne, M. G. Mangano, N. B. Carmona, P. Myrow, Ediacaran matground ecology persisted into the earliest Cambrian. *Nat. Commun.* **5**, 3544 (2014).
10. S. A. Darroch *et al.*, The trace fossil record of the Nama Group, Namibia: Exploring the terminal Ediacaran roots of the Cambrian explosion. *Earth Sci. Rev.* **212**, 103435 (2021).
11. F. Zhang *et al.*, Extensive marine anoxia during the terminal Ediacaran Period. *Sci. Adv.* **4**, ean8983 (2018).
12. D. Jablonski, Mass extinctions and macroevolution. *Paleobiology* **31**, 192–210 (2004).
13. S. D. Evans, C. W. Diamond, M. L. Droser, T. W. Lyons, Dynamic oxygen and coupled biological and ecological innovation during the second wave of the Ediacara Biota. *Emerg. Top. Life Sci.* **2**, 223–233 (2018).
14. A. S. Merdith *et al.*, Extending full-plate tectonic models into deep time: Linking the Neoproterozoic and the Phanerozoic. *Earth Sci. Rev.* **214**, 103477 (2021).
15. B. Robert, M. Greff-Lefftz, J. Besse, True polar wander: A key indicator for plate configuration and mantle convection during the late Neoproterozoic. *Geochim. Geophys. Geosyst.* **19**, 3478–3495 (2018).
16. T. H. Boag, S. A. Darroch, M. Laflamme, Ediacaran distributions in space and time: Testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* **42**, 574–594 (2016).
17. M. E. Clapham, G. M. Narbonne, J. G. Gehling, Paleoeology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology* **29**, 527–544 (2003).
18. S. H. Vaziri, M. R. Majidifard, S. A. Darroch, S. A. M. Laflamme, Ediacaran diversity and paleoecology from central Iran. *J. Paleontol.* **95**, 236–251 (2021).
19. D. Grazhdankin, Patterns of evolution of the Ediacaran soft-bodied biota. *J. Paleontol.* **88**, 269–283 (2014).
20. L. G. Tarhan, M. L. Droser, J. G. Gehling, Depositional and preservational environments of the Ediacara Member, Rawnsley Quartzite (South Australia): Assessment of paleoenvironmental proxies and the timing of ‘ferruginization’. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **434**, 4–13 (2015).
21. C. Yang *et al.*, The tempo of Ediacaran evolution. *Sci. Adv.* **7**, eabi9643 (2021).
22. D. M. Raup, J. J. Sepkoski Jr., Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503 (1982).
23. D. P. G. Bond, S. E. Grasby, On the causes of mass extinctions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **478**, 3–29 (2017).
24. S. Jensen, The proterozoic and earliest cambrian trace fossil record; patterns, problems and perspectives. *Integr. Comp. Biol.* **43**, 219–228 (2003).
25. L. G. Tarhan, The early Paleozoic development of turbation–Evolutionary and geobiological consequences. *Earth Sci. Rev.* **178**, 177–207 (2018).
26. E. H. Bouougri, H. Porada, Siliciclastic biolaminites indicative of widespread microbial mats in the Neoproterozoic Nama Group of Namibia. *J. Afr. Earth Sci.* **48**, 38–48 (2007).
27. W. Zheng *et al.*, Microbially induced sedimentary structures from the Xinji Formation (Cambrian Series 2), Western Henan, North China. *Geol. J.* **56**, 5363–5373 (2021).
28. J. L. Payne *et al.*, The evolutionary consequences of oxygenic photosynthesis: A body size perspective. *Photosynth. Res.* **107**, 37–57 (2011).
29. D. H. Erwin, Climate as a driver of evolutionary change. *Curr. Biol.* **19**, R575–R583 (2009).
30. B. Hannisdal, S. E. Peters, Phanerozoic Earth system evolution and marine biodiversity. *Science* **334**, 1121–1124 (2011).
31. R. G. Stockey, A. Pohl, A. Ridgwell, S. Finnegan, E. A. Sperling, Decreasing Phanerozoic extinction intensity as a consequence of Earth surface oxygenation and metazoan ecophysiology. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2101900118 (2021).
32. S. A. Darroch *et al.*, Biotic replacement and mass extinction of the Ediacara biota. *Proc. Biol. Sci.* **282**, 20151003 (2015).
33. S. A. F. Darroch, M. Laflamme, P. J. Wagner, High ecological complexity in benthic Ediacaran communities. *Nat. Ecol. Evol.* **2**, 1541–1547 (2018b).
34. D. Jablonski, “Extinctions in the fossil record” in *Extinction Rates*, J. H. Lawton, R. M. May, Eds. (Oxford University Press, 1995), pp. 25–44.
35. F. Bowyer, R. A. Wood, S. W. Poulton, Controls on the evolution of Ediacaran metazoan ecosystems: A redox perspective. *Geobiology* **15**, 516–551 (2017).
36. W. Shi *et al.*, Decoupled oxygenation of the Ediacaran ocean and atmosphere during the rise of early animals. *Earth Planet. Sci. Lett.* **591**, 117619 (2022).
37. S. Jensen, J. G. Gehling, M. L. Droser, Ediacara-type fossils in Cambrian sediments. *Nature* **393**, 567–569 (1998).
38. D. H. Erwin *et al.*, The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097 (2011).
39. J. G. Gehling, M. L. Droser, Ediacaran scavenging as a prelude to predation. *Emerg. Top. Life Sci.* **2**, 213–222 (2018).
40. S. D. Evans, I. V. Hughes, J. G. Gehling, M. L. Droser, Discovery of the oldest bilaterian from the Ediacaran of South Australia. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 7845–7850 (2020).
41. E. B. Hodgins *et al.*, A link between rift-related volcanism and end-Ediacaran extinction? Integrated chemostratigraphy, biostratigraphy, and U-Pb geochronology from Sonora, Mexico. *Geology* **49**, 115–119 (2021).
42. M. Foote, Origination and extinction components of taxonomic diversity: General problems. *Paleobiology* **26**, 74–102 (2000).
43. S. J. Goerg, J. Kaiser, Nonparametric testing of distributions—The Epps-Singleton two-sample test using the empirical characteristic function. *Stata J.* **9**, 454–465 (2009).