<RRH>*Ediacaran–Cambrian rock and fossil records*

<LRH>D. C. Segessenman and S. E. Peters

Transgression–regression cycles drive correlations in Ediacaran–Cambrian rock and fossil records

Daniel C. Segessenman[1] and Shanan E. Peters[2]

[1]Department of Geoscience, University of Wisconsin–Madison, Madison, Wisconsin 53706, U.S.A. Present address: Atmospheric, Oceanic, and Earth Sciences Department, George Mason University, Fairfax, Virginia 22030, U.S.A.

[2] Department of Geoscience, University of Wisconsin–Madison, Madison, Wisconsin 53706, U.S.A.; Email: peters@geology.wisc.edu

Non-technical Summary.—Ediacaran-age sedimentary rocks (635–538.8 million years ago) contain the oldest animal fossils that are visible to the naked eye. Several explanations have been suggested for the origins of animals in the Ediacaran, their disappearance at the end of the Ediacaran, and the following Cambrian explosion of animals (538.8–485.4 million years ago). For this study, we examined Ediacaran–Cambrian evolutionary patterns and how fossils (data from the Paleobiology Database) are related to the amount of sedimentary rock (data from Macrostrat) from the same time. Amounts of Cambrian rock increase to more than five times the

amount of rock in the Ediacaran. The number of fossils increases in an equally dramatic manner from the Ediacaran to the Cambrian, and there are strong positive correlations between the amount of rock and the number of fossils. It is well known that in the Cambrian, sea level rose, leading to the flooding of the North American continent. This relative rise in sea level would have increased the amount of rock deposited on the continent. Cambrian flooding of the continent would have also provided a wider variety of shallow-marine environments for Cambrian animals to expand into, providing at least a partial explanation for the dramatic increase in the number and physical diversity of Cambrian fossils. A smaller flooding event during the Ediacaran may have enabled early fossil animals to develop evolutionary traits for shallow-marine environments that allowed them to rapidly evolve during the larger flooding in the Cambrian. The results of this study demonstrate that relative sea-level rise and associated continental-scale flooding known to influence the amount of rock may have played a role in shaping evolutionary patterns of Earth’s earliest animals.

Abstract.—Strata of the Ediacaran Period (635–538.8 Ma) yield the oldest known fossils of complex, macroscopic organisms in the geologic record. These “Ediacaran-type” macrofossils (known as the Ediacaran biota) first appear in mid-Ediacaran strata, experience an apparent decline through the terminal Ediacaran, and directly precede the Cambrian (538.8–485.4 Ma) radiation of animals. Existing hypotheses for the origin and demise of the Ediacaran biota include: changing oceanic redox states, biotic replacement by succeeding Cambrian-type fauna, and mass extinction driven by environmental change. Few studies frame trends in Ediacaran and Cambrian macroevolution from the perspective of the sedimentary rock record, despite well-documented Phanerozoic covariation of macroevolutionary patterns and sedimentary rock quantity. Here we present a quantitative analysis of North American Ediacaran–Cambrian rock and fossil records from Macrostrat and the Paleobiology Database. Marine sedimentary rock quantity increases nearly monotonically and by more than a factor of five from the latest Ediacaran to the late Cambrian. Ediacaran–Cambrian fossil quantities exhibit a comparable trajectory and have strong ($r_s > 0.8$) positive correlations with marine sedimentary area and volume flux at multiple temporal resolutions. Even so, Ediacaran fossil quantities are dramatically reduced in comparison to the Cambrian when normalized by the quantity of preserved marine rock. Although aspects of these results are consistent with the expectations of a simple fossil preservation–induced sampling bias, together they suggest that transgression–regression and a large expansion of marine shelf environments coincided with the diversification of animals during a dramatic transition that is starkly evident in both the sedimentary rock and fossil records.

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Corresponding author:

Daniel C. Segessenman; Email: dsegesse@gmu.edu

<H1>**Introduction**

The oldest complex macrofossils are found globally in sedimentary rocks of Ediacaran age (Sprigg 1947; Glaessner 1959; Knoll and Carroll 1999; Xiao and Laflamme 2009; Xiao and Narbonne 2020). These distinctive, phylogenetically enigmatic fossils, often referred to as "Ediacaran-type macrofossils" or the "Ediacaran biota," include taxa that are recognized as the oldest known metazoans (Droser and Gehling 2015; Bobrovskiy et al. 2018a; Muscente et al. 2019; Wood et al. 2019; Evans et al. 2020; Dunn et al. 2021; Shore et al. 2021) and taxa now recognized as non-metazoan (e.g., *Beltanelliformis*; Bobrovskiy et al. 2018b). Since the Ediacaran's addition to the Geologic Time Scale (Knoll et al. 2006), significant advancements have been made in correlating its fossil-bearing stratigraphy, resulting in a general global division between a pre-Gaskiers (Pu et al., 2016) lower Ediacaran sequence typically dominated by microfossil assemblages (but not limited to them; e.g., Liu and Tindal, 2021; Yang et al., 2022) and an upper Ediacaran post-Gaskiers sequence that bears the Ediacaran biota (e.g., Rooney et al. 2020; Xiao and Narbonne 2020; Yang et al. 2021). The Ediacaran biota typically disappears by the Ediacaran/Cambrian transition (particularly in North America) and gives way to the distinctive faunal assemblages of the early Cambrian (Darroch et al. 2018; Muscente et al. 2019; Bowyer et al. 2022). There are many hypotheses concerning the appearance and disappearance of the Ediacaran biota, including changing redox (oxic/anoxic) states in Ediacaran oceans (Sperling et al. 2016; Zhang et al. 2019), preservational biases caused by unique Ediacaran taphonomy or lack of outcrop (Seilacher 1984; Laflamme et al. 2013; Gehling et al. 2019; Cuthill 2022), and environmental catastrophe or biotic replacement–driven mass extinction (Darroch et al. 2018; Tarhan et al. 2018; Zhang et al. 2021). All of these proposed hypotheses invoke mechanisms known to exert controls on macroevolutionary trends observed from marine metazoan fossils in the Phanerozoic (Valentine 1969; Raup and Sepkoski 1982; Stanley 2007; Erwin 2008; Alroy 2010; Hannisdal and Peters 2011; Aberhan and Kiessling 2012; and many others). However, few studies have examined the relationship between preserved rock quantity and macroevolution during the Ediacaran and across the Ediacaran/Cambrian transition.

Correlation of macroevolutionary patterns and sedimentary rock volume in deep time is a well-documented phenomenon (Newell 1959; Raup 1972, 1976; Sepkoski et al. 1981; Peters and Foote 2001, 2002; Smith 2001, 2007; Smith et al. 2001; Peters 2005, 2006; Smith and McGowan 2007; McGowan and Smith 2008; Heim and Peters 2011; Peters et al. 2013; Rook et al. 2013; Dunhill et al. 2014; Benton 2015; Benson et al., 2021). Sloss sequences linked to expansion and contraction of marine shelf area have also long been recognized in Phanerozoic strata as a second-order (~10^7 yr) control on the continental distribution of sedimentary rocks (e.g., Sloss 1963; Mackenzie and Pigott 1981; Haq et al. 1987; Miller et al. 2005; Haq and Schutter 2008; Meyers and Peters 2011; Peters and Heim 2011b; Nance et al., 2014; Husson and Peters 2018). A matter of continuing debate is whether or not the correlation between rock and fossil records in deep time is indicative of preservation bias distorting patterns observed in the fossil record, or whether it is instead a signal of geologic process that acted as a "common cause" mechanism, driving both patterns of biological diversity and preserved rock quantity (Crampton et al. 2003; Peters 2008; Peters and Heim 2011a; Peters et al. 2013, 2022; Holland 2017; Husson and Peters 2018; Nawrot et al. 2018). A Sloss sequence–like signal ("Mackenzie" sequence) coinciding with an increase in the number of rock units containing Ediacaran macrofossils has been observed in a macrostratigraphic analysis of a new compilation for the Ediacaran System in North America (Segessenman and Peters 2023). A more detailed analysis examining relationships between the rock and fossil records in this new compilation is warranted to provide new perspective on the relationship between macroevolutionary trends and sedimentary patterns during the Ediacaran/Cambrian transition. Here we present a quantitative analysis of intersecting rock and fossil datasets from the data platforms of Macrostrat (https://macrostrat.org; Peters et al.

2018; Segessenman and Peters 2023) and the Paleobiology Database (PBDB; https://paleobiodb.org).

<H1>**Methods**

Boundary ages, thicknesses, and lithologies of 546 revised Ediacaran (Segessenman and Peters 2023) and 2063 Cambrian (Peters et al. 2018) Macrostrat rock units (https://macrostrat.org) were matched (by location and rock unit name) to 412 Ediacaran and 16,133 Cambrian North American fossil occurrences from the PBDB (https://paleobiodb.org), accessed using the PBDB application programming interface (Peters and McClennen 2016). Rock unit age models and characteristics were compiled and established as part of previous studies (Peters et al. 2018; Segessenman and Peters 2023: p. 401). The rock unit age models were not adjusted for this study; instead, only the maximum and minimum ages of PBDB fossil occurrences were modified to reflect the constraints of the stratigraphic age models. Fossil occurrences are a fundamental unit in the PBDB and are defined as an instance of a particular organism at a particular location in time and space. PBDB fossil occurrences that did not have an exact matching unit name in the Macrostrat dataset were assigned to the Macrostrat unit that was geographically nearest and temporally overlapping and that shared a lithology with the collection-listed lithology. A total of 1088 Ediacaran and Cambrian PBDB occurrences that did not have any taxonomic information or that had a match distance (between PBDB occurrence coordinates and Macrostrat column centroids) greater than 300 km and no direct Macrostrat unit name match were removed from the dataset. An additional 20 PBDB occurrences with low-resolution age assignments such as “Neoproterozoic” (e.g., *Grypania spiralis*) were also removed. Ichnofossil occurrences were not removed but were restricted to calculations of fossil occupancy in the rock record; that is, a rock unit would be counted as "occupied" by fossils if it contained at least one fossil (including ichnofossil) occurrence. With the aforementioned approach, 403 Ediacaran and 15,034 Cambrian fossil occurrences were matched to 40 Ediacaran and 322 Cambrian Macrostrat rock units at the stratigraphic levels of member, formation, or group. Raw tables of Macrostrat units matched to PBDB occurrences and the R scripts used to generate figures/tables for this study can be found in the Supplementary Material (Supplement S1—Code). A table of Macrostrat unit_id's, stratigraphic names, counts of PBDB occurrences matched to each stratigraphic name, and modeled unit bounding ages is available in Supplementary Table S1. In addition, a table of PBDB fossil occurrences, their PBDB assigned stratigraphies/ages, and the Macrostrat matched stratigraphies/ages is available in Supplementary Table S2.

For each fossil occurrence, the PBDB reported minimum and maximum ages were used, unless the occurrence ages exceeded the modeled boundary ages of the containing rock unit (for further descriptions of Macrostrat boundary age models, see Peters et al. 2018; Segessenman and Peters 2023). For example, an Ediacaran PBDB occurrence with a minimum age of 538.8 Ma and a maximum age of 635 Ma (most Ediacaran PBDB entries have these assigned ages) matched to a rock unit with an upper boundary age of 550 Ma and a lower boundary age of 580 Ma would be given a new, narrower age range of 580–550 Ma. In this way, PBDB occurrence minimum and maximum ages were bound to their matched rock units' bounding ages within Macrostrat's continuous time age model. The number of genera were derived from the number of occurrences by counting the number of unique genus names among occurrences for each time interval. Rock units with sedimentary lithologies and a thickness of zero (no available published thickness estimate) were given a median thickness calculated from thicknesses of the 10 most proximal (within 250 km), temporally overlapping rock units with sedimentary lithologies. This resulted in simulated thicknesses (median of all simulated thicknesses was ~358 m) for 151 Cambrian age units, which comprises ~7% of all North American Cambrian rock units. All calculations of rock and fossil quantities were made with 1 Myr time steps (consistent with a "continuous" age model construction), except for correlations between rock and fossil quantities, which were computed with 1, 5, and 10 Myr bins. The 10 Myr bins are the primary focus of our correlation analysis, as that time span is the resolution most appropriate for second-order scale influences (10^7 yr) and for the resolution of geochronologic constraints in the Ediacaran and early Cambrian.

Once all relevant Ediacaran–Cambrian rock unit and fossil occurrence characteristics were matched by formation name and/or spatiotemporal overlap, aggregate metrics were computed. Metrics used to describe the PBDB fossil dataset include counts of fossil occurrences; genus richness; and Shannon *H* indices for diversity, occurrences among lithologies, and occurrences among locations (Shannon 1948). Fossil occurrence locations were identified using the PBDB "states" field, which records the state or province in which the occurrence is located. Shannon *H* values (Shannon-Wiener Index) were generated for each 1 Myr time step (635–485 Ma) for both occurrences among genera and occurrences among geographic locations using the *diversity* function from the R package vegan (Oksanen et al. 2022). Metrics used to describe the Macrostrat marine sedimentary rock datasets include counts of rock units, preserved area (km^2), volume flux (km^3/Myr), median rock unit thickness (m), and median unit duration (Myr). Bootstrap resampling ("block" sampling method with a 7 Myr moving window) was used to generate 2σ confidence intervals for the number of fossil occurrences, genera, counts of sedimentary units (with and without occurrences), median rock unit thickness, and median rock unit duration.

Counts of occupied rock (rocks that contain at least one occurrence), Spearman rank correlation coefficients of time-series first differences, and Spearman rank correlation coefficients (r_s) of raw rock and fossil metrics were calculated to describe the intersection of the rock and fossil datasets. Correlation calculations for the Ediacaran dataset were temporally limited to 585 Ma and younger due to a lack of fossil data pre–585 Ma. Sedimentary rock lithologies were grouped into two general categories for this study: siliciclastics and carbonates. Macrostrat rock units include lithology as a relative percentage (e.g., 70% limestone, 15% sandstone, 15% shale) and general depositional environment (e.g., marine, nonmarine). Only marine sedimentary rock proportions that fit within the two general lithologic categories were included in calculations and time series for this study. To facilitate more direct comparison of rock quantities from the mesostrat Ediacaran dataset and the “whole-crust” Cambrian Macrostrat dataset, Ediacaran mesostrat column areas were scaled by a factor of 1.85; the justification for this is that the two compilations used different methods to determine column geographic footprints, which leads to a scalar offset in the area estimate for the same body of rock (for scalar calculation and discussion, see Segessenman and Peters 2023: p. 405).

<H1>**Results**

<H2>*Trends in Ediacaran–Cambrian Rock and Fossil Records*

Maps of rock and fossil locations were plotted to show the geographic distribution of marine sedimentary rock–bearing stratigraphic columns and fossil collections (a set of PBDB occurrences that are colocated geographically and temporally) across North America grouped by subdivisions of Ediacaran and Cambrian time (Fig. 1). Fossil collections are generally more widespread at times with increased marine sedimentary rock (represented by number of columns) and are less widespread at times with decreased marine sedimentary rock (Fig. 1). An animation of rock and fossil locations on North America in 5 Myr bins is available as Supplementary Figure S1. Note that Macrostrat columns include subsurface data, and therefore sedimentary rock is generally much more widespread than fossil collections, which are restricted primarily to outcrop belts.

Starting at ca. 585 Ma, the number of fossil occurrences and genera increase to a late Ediacaran maximum, chiefly due to Mistaken Point collections, (ca. 565 Ma; >130 occurrences) then sharply decrease and plateau until the Ediacaran/Cambrian transition (Fig. 2A). Fossil occurrences remain (locally) decreased across the Ediacaran/Cambrian boundary, but monotonically increase through the early and mid-Cambrian to a maximum (>3200 occurrences) after ca. 515 Ma (Fig. 2A). The maximum number of occurrences and genera are both an order of magnitude greater in the Cambrian than in the Ediacaran, with trends in the number of genera generally following that of occurrences (Fig. 2A). Increasing numbers of occurrences and genera coincide with increasing marine sedimentary unit counts, area, and volume flux in the Ediacaran and Cambrian (Fig. 2A–D). Rock–fossil fluctuations broadly correspond to the Mackenzie and Sauk Sloss sequences, apart from three deviations: (1) the ca. 570 Ma increase in the number of occurrences and genera does not coincide with an increase in sedimentary unit counts, rock area, or volume flux; (2) an Ediacaran volume flux increase to a period maximum (ca. 550 Ma) coincides with a decrease and local plateau in the number of fossil occurrences and genera; and (3) late Cambrian fossil occurrences/genera experience little change during a period maximum in rock area and significantly decreased volume flux (Fig. 2A–D).

The proportion of occupied marine sedimentary rock area (area of rock units that contain at least one occurrence, including ichnofossils) remains at or below 20%, and unit counts remain at or below 10% after 580 Ma in the Ediacaran (Fig. 2E). Occurrence occupancy falls to nearly 5% by the latest Ediacaran before increasing through the early and mid-Cambrian to a local maximum of nearly 25% (ca. 515 Ma), despite the fact that much of the Cambrian rock record is in the subsurface of North America. The occupied proportion of volume flux fluctuates greatly during the Ediacaran because of greater sensitivity to overall lower preserved rock volume and fossil occurrences. For example, the large pulse to nearly 60% of volume occupancy is due to a small number of late Ediacaran occurrences in thick, undivided stratigraphic sections in the SE United States (Segessenman and Peters 2023; Fig. 1E). Cambrian proportions of occupied sedimentary volume fluctuate to a much lesser degree due to a greater quantity of preserved rock and better geochronologic constraints (Fig. 2E). These results highlight that the character of the sedimentary record changes dramatically across the Ediacaran/Cambrian boundary, providing a strong physical justification for the position of the system and the Proterozoic/Phanerozoic eon boundary. Additionally, the quantified rock and fossil records exhibit parallel changes that broadly correspond to the Mackenzie and Sauk Sloss sequences.

<H2>*Character of Fossil-bearing Ediacaran–Cambrian Rock Units*

Median thickness and duration of sedimentary rock units differ between occupied units and all sedimentary rock units during the Ediacaran (Fig. 3A,B). The median thickness of all sedimentary rock units is relatively high in the early Ediacaran (due to a relatively low number of columns with thick, undivided sections), declines after ca. 590 Ma to a mid- to late Ediacaran plateau, and decreases continuously after the Ediacaran/Cambrian transition (Fig. 3A). The median thickness of occupied sedimentary units fluctuates dramatically during the mid- to late Ediacaran, reaching highs greater than all sedimentary units at ca. 575–550 Ma before a local maximum during the Ediacaran/Cambrian transition (Fig. 3A). By ca. 530 Ma, the median thickness of occupied sedimentary units fluctuates much less and remains consistent with all sedimentary units as it generally decreases through the remainder of the Cambrian (Fig. 3A). The significant increases of occupied unit thickness at ca. 575–550 Ma are likely due to few geochronologic constraints and low total preserved sediment volume that results in thicker, undivided stratigraphic sections (Fig. 3A). However, the increase in median thickness at the Ediacaran/Cambrian transition may also be due to regression marking the end of the Mackenzie sequence, which would have left only the thickest and most continuous stratigraphic sections on the continental margins.

Median durations of all sedimentary units (black line) follow a similar trend to that of unit median thicknesses (Fig. 3B). Median duration is relatively high during the early Ediacaran; decreases to a plateau starting at ca. 585 Ma, except for an increase from 567 to 563 Ma; increases more significantly during the Ediacaran/Cambrian transition; and decreases for most of the Cambrian (Fig. 3B). The median durations of all sedimentary units and occupied sedimentary units are noticeably elevated during the Ediacaran/Cambrian transition, a departure from the median thickness (Fig. 3A,B). The median duration of occupied units from the mid- to late Ediacaran follows a similar trend to that of all sedimentary units, although it is lower relative to total sedimentary units, except during the Ediacaran/Cambrian transition (Fig. 3B). The Ediacaran/Cambrian transition increase in the median duration of occupied units is most likely due to very few fossil occurrences reported within the few thick, continuous sections of rock that span this boundary (Fig. 3B). In a similar manner to that of the median thickness, marine regression may have contributed to the median duration increase observed in all sedimentary units during the Ediacaran/Cambrian transition through the reduction of shorter-duration, more-proximal stratigraphic sections (Fig. 3A,B).

The lithologies yielding fossil occurrences exhibit distinct differences between the Ediacaran and Cambrian (Fig. 3C). The comparatively rare Ediacaran occurrences are almost exclusively reported from siliciclastic lithologies in contrast to early Cambrian occurrences, which are dominantly from carbonates (Fig. 3C). Interestingly, Ediacaran occurrences are reported primarily from siliciclastic lithologies, despite increased proportions of carbonate at the same time (ca. 577–555 Ma; Figs. 2C,D, and 3C). At ca. 515 Ma, there is a rapid increase in the proportion of Cambrian fossil occurrences reported from fine-grain sedimentary rocks (Fig. 3C), although fossils reported from carbonate lithologies dominate the majority of the Cambrian rock record (Fig. 2C,D). Overall, these results are consistent with known differences in the preservation of Ediacaran (largely preserved in microbial mat–influenced siliciclastics) and Cambrian (large increase in calcifiers) taxa that generally mirror changes in the nature of Ediacaran–Cambrian sedimentary units.

<H2>*Ediacaran–Cambrian Macroevolutionary Trends*

Fossil occurrences and unique genera were normalized by counts of sedimentary units, preserved rock area, and volume flux for the Ediacaran and Cambrian (Fig. 4). Even when the decreased sedimentary rock quantity in the Ediacaran is accounted for, the numbers of occurrences and unique genera in the Cambrian rapidly surpasses those of the Ediacaran (Fig. 4). The late Ediacaran maximum in fossil occurrences and genera from ca. 570 to 555 Ma (Fig. 2A) remains the most significant increase in the Ediacaran when normalized by rock quantities (Fig. 4). Increases in normalized occurrences and genera during the Cambrian are present but muted (Fig. 4) when compared with the raw values (Fig. 2A). However, two intervals appear to be significant from this perspective: (1) the increase of normalized occurrences and genera from ca. 520 to 505 Ma and (2) the volume flux–normalized increase of occurrences and genera during the latest

Cambrian after ca. 497 Ma (Fig. 4). The sharp increase in occurrences and genera from ca. 515 to 505 Ma is because of sampling from the Stephen Formation (includes the Burgess Shale), which makes up ~10% of Cambrian occurrences in this study's dataset (Fig. 4). The volume flux–normalized increase of occurrences and genera after ca. 497 Ma can be attributed to the decreased volume at the end of the Cambrian coinciding with little change in the number of occurrences and genera (Figs. 2A,D, and 4).

The Shannon *H* index of generic diversity was calculated for each 1 Myr time step through the Ediacaran and Cambrian to summarize the distribution of occurrences among genera (Fig. 5A,B). Shannon *H*-values were also calculated to summarize the distribution of occurrences among locations to highlight periods of potentially uneven locality sampling (Fig. 5C). After the initial Ediacaran increase in the number of genera at ca. 585 Ma, generic Shannon *H* index values fluctuate, but remain close to a value of 3.5 until the latest Ediacaran (Fig. 5B). Cambrian Shannon *H* index values continually increase after the Ediacaran/Cambrian transition to a maximum of 6 by the latest Cambrian, indicating increasing generic diversity and "evenness" of occurrence frequency across genera (Fig. 5B). These results are interesting, because the ca. 570–555 Ma high in the number of occurrences and genera (Fig. 2A) does not stand out except for a minor pulse at 565 Ma (Fig. 5B). Furthermore, the Shannon *H* index calculated for the frequency of occurrences across location names during this same interval (ca. 570–555 Ma), exhibits a decrease that indicates a greater number of genera are reported from a less diverse pool of locations (Fig 5C). For this particular time period, the dominant source of occurrences (and therefore a source of sampling bias) is the Conception Group of Newfoundland (includes the Mistaken Point Fm.). This phenomenon is also present in the Cambrian record from ca. 515 to 505 Ma, the same interval in which samples from the Stephen Formation/Burgess Shale impact the normalized occurrence and genus curves (Figs. 4, 5C). Except for the aforementioned deviations and the Ediacaran/Cambrian transition, the overall diversity and evenness of sampling locations increases through the Ediacaran and Cambrian (Fig. 5C).

<H2>*Correlations of Rock and Fossil Record*

Spearman rank-order correlation coefficients (r_s) and respective p-values for various metrics describing the rock and fossil records were calculated using 1, 5, and 10 Myr bins (Table 1). To calculate these correlations, the *surrogateCor* function from the astrochron package in R was used (Meyers 2014). The *surrogateCor* function was designed to calculate correlations and estimate the statistical significance of those correlations using the method of Ebisuzaki (1997), in which time series are derived from stratigraphic successions. Correlations within a 95% or 90% confidence interval (p-value < 0.05 or 0.1, respectively) were considered (green and yellow shaded cells in Table 1, respectively). There is a very strong positive correlation between the number of occurrences and genera at all temporal resolutions (r_s = 0.986, 0.951, 0.973; Table 1), making the two metrics largely interchangeable. The numbers of occurrences and genera are also both positively correlated with sedimentary area, although the number of genera exhibits a stronger positive correlation at the 5 and 10 Myr temporal resolutions (r_s = 0.851, 0.891 and 0.856, 0.955, respectively; Table 1). A similar result is obtained when comparing occurrence and genus counts with the median unit thickness and carbonate flux. In all other cases, occurrences and genera have similar correlations or occurrences have slightly stronger correlations than genera (Table 1). Spearman correlation coefficients for the first differences of rock and fossil metrics were also calculated using 1, 5, and 10 Myr bins. The 10 Myr resolution first differences for number of sedimentary marine units, median unit thickness, total area, siliciclastic area (although only for occurrences), total volume flux, and carbonate volume flux had significant correlations (strong to moderate) with fossil metrics. The 5 Myr resolution first differences had less consistently significant correlations (moderate to weak), and 1 Myr resolution first differences had almost no significant correlations (Supplementary Table S3).

A strong negative correlation is present between the number of genera/occurrences and the median duration and thickness of marine sedimentary units, possibly indicating that the presence of fossils leads to a greater potential for temporal subdivision of rock units into thinner intervals. Carbonate volume flux has a positive correlation with the number of fossil occurrences and genera at all resolutions, although only at the 90% confidence level (Table 1). There is no statistically significant correlation between the number of genera or fossil occurrences and the area of carbonates, except at the 10 Myr resolution for the number of fossil occurrences (Table 1). Correlations between sedimentary rock quantities and the fossil record were also calculated separately for the Ediacaran (post–585 Ma) and Cambrian periods (Supplementary Tables S4, S5). Post–585 Ma Ediacaran rock–fossil correlations are rarely statistically significant, due primarily to fewer data points and/or greater uncertainties in Ediacaran rock and fossil ages (Supplementary Table S4). Cambrian rock–fossil correlations show similar but weaker correlations to those of the combined Ediacaran–Cambrian rock–fossil records, with the notable exception of stronger correlations between fossil quantities and carbonate area/volume (Supplementary Table S5).

<H1>**Discussion**

Geochronologic and biostratigraphic controls are less resolved in the Ediacaran and early Cambrian than in much of the rest of the Phanerozoic. Although studies providing and refining taxonomy, biostratigraphy, chemostratigraphy, and radioisotopic dates from the Ediacaran system have increased in frequency globally since its formal addition to the Geologic Time Scale in 2006 (Knoll et al. 2006), it remains a formidable challenge to correlate Ediacaran sections regionally and globally. The age models used in this study for the Ediacaran and Cambrian systems of North America (for full description, see methods section of Segessenman and Peters 2023: pp. 401–403) were compiled with the intention of reflecting current published interpretations; a "state of the Ediacaran–Cambrian of North America." We do not assert that our compilation and age models are without error, but that we have characterized the aggregate understanding of these systems in a stratigraphically self-consistent way, such that the overarching temporal trends will likely endure, even when new discoveries and analyses require the age models to be revised, expanding and/or compressing the stratigraphically grounded temporal patterns documented here. We present correlation results at the 1, 5, and 10 Myr resolutions, but the following discussion focuses primarily on the 10 Myr resolution results, as that is the resolution that is likely to be most reflective of the age model's precision.

There are strong positive correlations between raw time series of occurrences, diversity, and sedimentary rock quantities for the mid- to late Ediacaran and Cambrian (Table 1), but first differences are moderately to weakly correlated. The lack of strong significant correlation between first differences in rock and fossil metrics suggests that sampling bias is not a primary driver of the strong correlations that are evident in the raw metrics. This stands in contrast to the situation for most of the remaining Phanerozoic, where first differences in rock quantity and fossil occurrences/diversity are more strongly correlated (Crampton et al. 2003; Peters and Heim 2011a; Peters et al. 2013), but the long-term trends in each diverge toward the Recent, with diversity continuing to increase and shallow-marine rock quantity remaining steady or even declining (Benson et al. 2021; Peters et al. 2022). The Ediacaran–Cambrian (635–485.4 Ma), by contrast, exhibits a significant decrease in rock quantity with increasing age (Fig. 2C,D), a pattern that is generally predicted by all models of erosion-dominated sedimentary rock cycling (Peters and Husson 2017). In the case of the Ediacaran–Cambrian, though, it is apparent that the large decrease in sedimentary rock quantity with increasing age primarily reflects the signature of an increase in the depositional area of marine sediments throughout the late Ediacaran and Cambrian. This led to the progressive deposition of an increasingly expansive, relatively thin veneer (at least across the North American continental interior) of Cambrian marine sediment over area-limited Ediacaran sediments and a much wider area of exposed heterogeneous Precambrian igneous and metamorphic basement rocks (Peters and Gaines 2012). Regardless of whether these basement rocks were exhumed during Snowball Earth glaciations (Keller et al. 2019; McDannell and Keller 2022) or during a more protracted, multistaged tectonic uplift history (e.g., Flowers et al. 2020; Sturrock et al. 2021), it is clear that the Great Unconformity in North America is defined in large part by a shift from net continental denudation to net burial by Cambrian and younger sedimentary cover. This Phanerozoic cover has survived to the present day largely intact, although some unknown amount of Cambrian sediment has been lost from the Canadian Shield, thereby reducing the apparent increase in shelf area implied by the surviving record. Focused erosion sometime between the Ediacaran and Cambrian of a type not repeated in the later Phanerozoic seems unlikely to be driving the temporal trajectory of sedimentary rock quantity during this interval (Peak et al. 2023). Instead, continental-scale transgressive–regressive cycles are the probable drivers of observed trends in Ediacaran–Cambrian sedimentary rock quantities. Thus, the primary signal in the surviving sedimentary rock record is one of environmental change and real shifts in the extent of epicontinental marine sedimentation, not postdepositional modification of some markedly different environmental history.

Preserved sedimentary volume flux on continents is primarily controlled by accommodation and sediment supply (Miall 2016). Evidence suggests that Laurentia, which constitutes the bulk of North America, had ample sediment supply during the Ediacaran but was generally accommodation limited due to an apparent lack of continental basins and limited continental flooding. Changes in accommodation would then have been driven primarily by local tectonics (such as that of Ediacaran–Cambrian Laurentian margin rifting; Macdonald et al. 2023) and/or fluctuations in base level (as observed in "Western Laurentia" from Segessenman and Peters [2023]), either due to continental margin subsidence, global sea-level rise, or both. In light of this, an increase in preserved rock volume flux, and a more minor area increase, with a high proportion of carbonates after ca. 580 Ma, is interpreted as an increase in accommodation driven by base-level rise on the Laurentian margin. An increase in Ediacaran fossil occurrences and genera coincides with the post–580 Ma sedimentary volume flux increase and its subsequent decrease at the Ediacaran/Cambrian transition (Figs. 1–5; Table 1). Similarly, the dramatic radiation of organisms in the Cambrian is matched by an equally dramatic increase in the volume and area of sedimentary rock preserved on Laurentia, although the increase in Cambrian sedimentary volume cannot entirely explain the Cambrian's increased fossil occurrences and generic richness (Figs. 1, 2A–D).

Though correlation does not necessitate causation, it can be assumed that second-order (10^7 yr) changes in sedimentary area and volume flux are strongly influenced by changes in accommodation and are not influenced by changes in the number of fossil occurrences or genera. Preserved sedimentary volume can, however, influence the overall abundance of fossils and is subject to common cause mechanisms that can drive parallel changes in both the rock record and biological communities. Transgression, driven by subsidence and/or global sea-level rise, would have increased potential habitable ecospace, which in turn would create more potential environments in which organisms may be preserved (Fig. 1). This does not necessarily mean that the probability of preservation in a given environment increased, but it does imply that the number of organisms that could be preserved and recovered as fossils in North America increased. Although, the probability of preservation would have increased in the Cambrian due to the rapid diversification of calcifiers, which may have been enabled by (but not necessarily driven by; see Gilbert et al. 2022) increased availability of carbonate-dominated shallow-marine environments (Knoll 2003; Fig. 3C). The combined effects of taphonomic change and ecospace expansion may help to explain the rapid, dramatic Cambrian increases in biodiversity, even when normalized to rock quantity (Fig. 4).

An increasing number of sedimentary units, particularly during the Cambrian, may represent increasing environmental heterogeneity and ecological opportunity (influencing macroevolution and taphonomy) as shallow-marine shelf habitat space expanded, potentially driving generic richness as well as an increase in the total number of organisms inhabiting an increasingly broad and heterogeneous shelf. Increasing environmental heterogeneity is also indicated by an observed increase in regional differences of faunal compositions coincident with the Cambrian radiation (Na et al. 2022). This relationship may be evidenced by a stronger correlation between genera and preserved sedimentary area (0.955) than the number of occurrences and preserved sedimentary area (0.891), as well as by the fact that genera exhibit a strong correlation with the number of sedimentary units (Table 1). Regression at the end of the Ediacaran would have had the opposite effect and is evidenced by decreased sedimentary area and volume flux (Fig. 2C,D), an increase in the median duration of sedimentary units (Fig. 3B), and the presence of a globally occurring (though likely diachronous) sequence boundary across the Ediacaran/Cambrian transition (Shahkarami et al. 2020; Bowyer et al. 2022).

In addition to the stark changes in rock quantity and biodiversity discussed above, there is an equally dramatic shift in the overall character of metazoans from the Ediacaran to the Cambrian (Butterfield 2009; Darroch et al. 2018; Zhuravlev and Wood 2018; Bowyer et al. 2022). Although faunal compositions of the Ediacaran are clearly distinct from those of the Cambrian (Erwin 2021), morphologies and behaviors thought to originate in the Cambrian have been documented in late Ediacaran strata (Bengtson and Zhao 1992; Gehling and Droser 2018; Cai et al. 2019; Wood et al. 2019; Tarhan et al. 2020; Darroch et al. 2021). However, Cambrian communities include an increasing number of calcifiers and taxa with larger maximum body sizes, and there are increased traces of more metabolically demanding behaviors such as complex feeding/burrowing patterns, increased motility, and increased predator–prey interactions (Schiffbauer et al. 2016; Zhuravlev and Wood 2020; Zhang and Shu 2021). Alongside significant environmental change discussed previously, two other major factors are cited as key drivers of Ediacaran–Cambrian metazoan macroevolution: (1) increasing atmospheric pO_2 buildup that may have enabled the development of taxa with larger body sizes and more metabolically demanding behaviors (Och and Shields-Zhou 2012; Lenton et al. 2014; Chen et al. 2015; He et al. 2019; Cole et al. 2020; Jiang et al. 2022) and (2) significant geochemical change in shallow-marine environments, such as increased dissolved Ca^{2+} concentrations and availability of biolimiting nutrients that may have enabled increased prevalence of calcifying taxa (Brennan et al. 2004; Peters and Gaines 2012; Wang et al. 2018; Li et al. 2020; Cherry et al. 2022; Weldeghebriel et al. 2022).

Atmospheric pO_2 buildup through geologic time on Earth is directly related to increased burial of organic carbon (Berner 1982), a process influenced by continental flooding shifting deposition from short-lived oceanic crust to long-lived continental reservoirs. Similarly, flooding of Laurentia during a time in which its surface geology may have largely consisted of exposed crystalline basement following Cryogenian glaciation has been cited as a potential source of increased biolimiting nutrients and Ca^{2+} concentrations in shallow-marine settings during the Cambrian. Cambrian continental flooding is an influential factor that, given the unique geologic and paleobiological contexts of the Ediacaran–Cambrian Earth, may have served as a driver of a "perfect storm" that enabled the Cambrian explosion of life, where minor flooding in the Ediacaran enabled metazoan biologic innovations that then truly "exploded" during the Cambrian Sauk transgression. Ultimately, the geologic process(es) driving the observed flooding signatures in the Ediacaran and Cambrian are matters of ongoing research, although mantle dynamics (Zou et al. 2023), rift-related continental margin subsidence, and the locus of subduction globally (Macdonald et al. 2023; Tasistro-Hart and Macdonald 2023) have been cited as potential drivers.

The extent to which the results presented here are representative of global trends in Ediacaran–Cambrian macroevolution and macrostratigraphy has not been directly examined due to Macrostrat's current North American focus. However, it is recognized that early Ediacaran rock and fossil records are better preserved on other continents (e.g., China; Cunningham et al. 2017; Yang et al. 2022), and that fossiliferous latest Ediacaran to Ediacaran/Cambrian transition strata are more common on other continents (e.g., White Sea and Nama assemblages; Waggoner 2003). Decreased rock volume at the latest Ediacaran on North America is consistent with regressive systems tracts identified at the Ediacaran/Cambrian transition globally (Bowyer et al.

2022). However, the general lack of terminal Ediacaran biota fossils in North America could indicate that Laurentia's taxa were harder hit in an end-Ediacaran extinction event, that environmental conditions were particularly poor for preservation, that fossil-bearing strata have been eroded, or a combination of these. Early Ediacaran sections do exist on North America, but they are rarer and largely un-fossiliferous. This may be a result of conditions unfavorable to fossil preservation combined with low rock preservation but could also indicate that the Ediacaran biota did not originally develop in Laurentia, but arrived later. Despite these differences from global Ediacaran strata, our results are generally consistent with a mid- to late Ediacaran appearance of the Ediacaran biota, an apparent late Ediacaran diversity maximum, and, albeit earlier than global sections, an end-Ediacaran decline (Xiao and Narbonne 2020; Evans et al. 2022). In addition, our results, when combined with earlier Ediacaran fossils such as those of the Lantian or Weng'an biotas (Cunningham et al. 2017; Yang et al. 2022) and latest Ediacaran assemblages such as those of the White Sea or Nama (Waggoner 2003), suggest a more protracted radiation of metazoans through the Ediacaran and a "less explosive" (but still greater magnitude and comparatively rapid) Cambrian radiation (Wood et al. 2019; Servais et al. 2023) that broadly mirrors patterns of continental transgression and regression recognized globally (Sloss 1963; Sears and Price 2003; Avigad et al. 2005; Lorentzen et al. 2018).

We do not suggest that a mid-Ediacaran transgression (Mackenzie sequence) drove the origins of metazoans, that terminal Ediacaran regression functioned as a primary driver of Ediacaran-type fauna extinction, or that the radiation of life in the Cambrian was solely due to a coincident expansion of habitable shallow-shelf ecospace. Fossil occurrences and genera normalized to rock quantities indicate that sedimentary rock volume alone cannot explain all patterns in the fossil record (Fig. 4). Rather, the results presented herein provide new perspectives on transgression–regression cycles as strong environmental correlates of the appearance and diversification of the Ediacaran biota in the mid-Ediacaran, their apparent decline at the terminal Ediacaran, and the transition to (and rapid expansion of) Cambrian-type fauna during the Sauk transgression. Our results do not preclude any existing hypotheses driving evolution during the Ediacaran and Cambrian; instead, they demonstrate the influence of transgressive–regressive cycles in the observed sedimentary record at the dawn of animal life and provide a rock record–based framework within which to interpret and test existing hypotheses of macroevolutionary drivers. Expansion of the Macrostrat database to other continents and continued growth of the PBDB will enable further assessment of how the rock and fossil records covary at the dawn of animal life and the subsequent Cambrian explosion.

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Data Availability Statement. All supplementary data files for this study, including R scripts for analyses, an animation of fossil and stratigraphic column locations through time, tables of rock units matched to fossil occurrences, tables of fossil occurrence assigned ages, and correlations for Ediacaran and Cambrian rock and fossil quantities as separate time periods are available from the Dryad Digital Depository: https://doi.org/10.5061/dryad.xwdbrv1k9.

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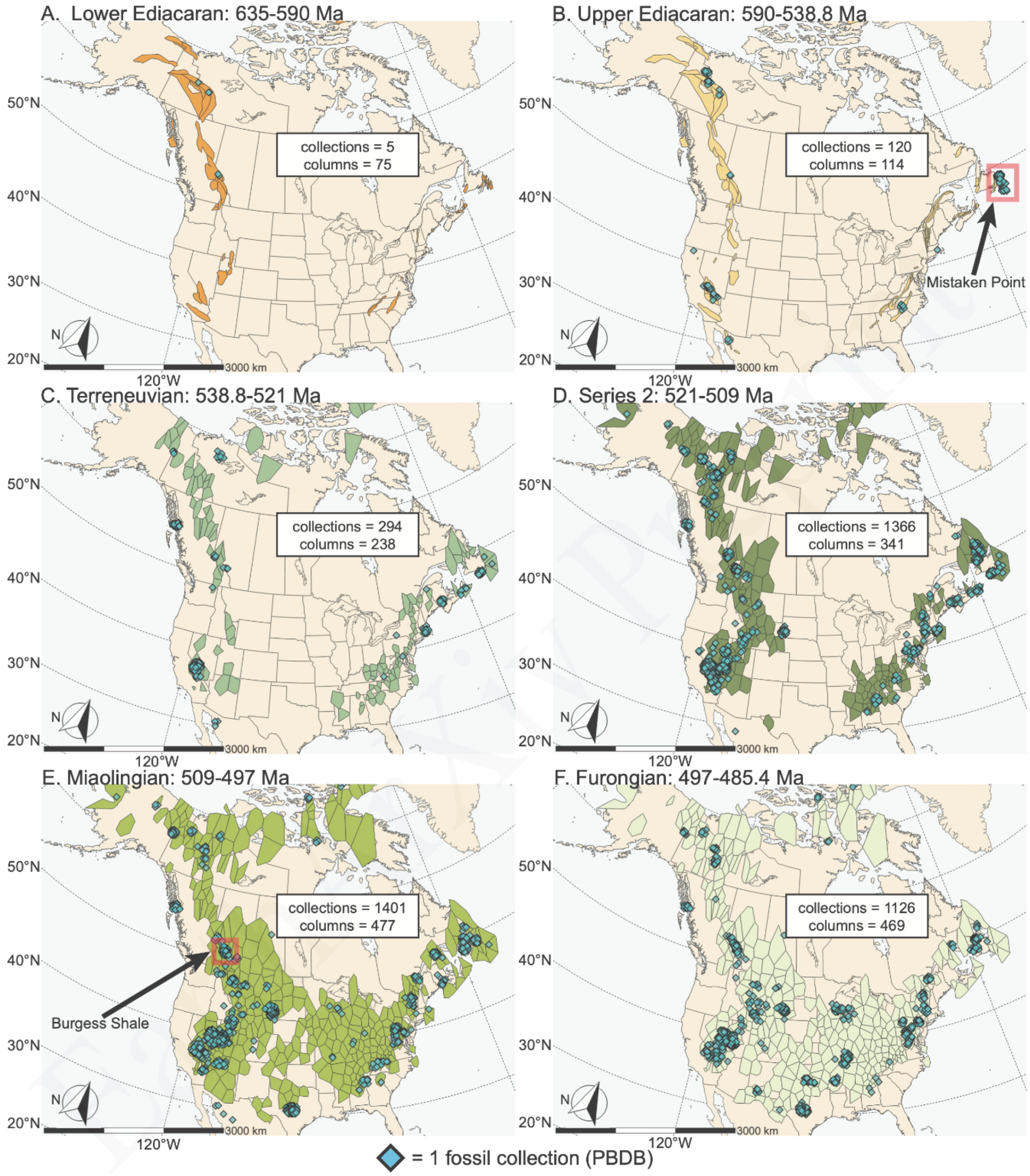
Table 1. Spearman rank correlation coefficients, ρ (r_s), and associated p-values calculated between Ediacaran–Cambrian sedimentary rock and fossil quantities in 1, 5, and 10 Myr bins. Green cells represent correlation coefficients with corresponding p-values in the 95% confidence interval ($p < 0.05$), and yellow cells represent the 90% confidence interval ($p < 0.1$). Bold values are Spearman's rho (ρ) rank correlation coefficients. "No. of sed. marine units" is the number of sedimentary marine units.

Correlations with no. of occurrences	1 Myr bins ρ (r_s)	1 Myr bins p-value	5 Myr bins ρ (r_s)	5 Myr bins p-value	10 Myr bins ρ (r_s)	10 Myr bins p-value
No. of genera	**0.986**	0.01	**0.951**	0.01	**0.973**	0.01
No. of sed. marine units	**0.89**	0.01	**0.87**	0.011	**0.927**	0.01
Median unit duration	**−0.812**	0.01	**−0.874**	0.01	**−0.882**	0.01
Median unit thickness	**−0.788**	0.01	**−0.809**	0.045	**−0.887**	0.024
Area (total)	**0.886**	0.01	**0.851**	0.01	**0.891**	0.024
Area (siliciclastic)	**0.934**	0.01	**0.919**	0.01	**0.909**	0.013
Area (carbonate)	**0.593**	0.15	**0.612**	0.192	**0.700**	0.097
Flux (total)	**0.799**	0.01	**0.862**	0.01	**0.891**	0.015
Flux (siliciclastic)	**0.72**	0.01	**0.838**	0.012	**0.873**	0.011
Flux (carbonate)	**0.662**	**0.1**	**0.751**	0.095	**0.809**	0.068

Correlations with no. of genera	1 Myr bins ρ (r_s)	1 Myr bins p-value	5 Myr bins ρ (r_s)	5 Myr bins p-value	10 Myr bins ρ (r_s)	10 Myr bins p-value
—	—	—	—	—	—	—
No. of sed. marine units	**0.885**	0.01	**0.886**	0.01	**0.927**	0.01
Median unit duration	**−0.841**	0.01	**−0.889**	0.01	**−0.873**	0.01
Median unit thickness	**−0.813**	0.012	**−0.825**	0.038	**−0.933**	0.018
Area (total)	**0.873**	0.01	**0.856**	0.014	**0.955**	0.01
Area (siliciclastic)	**0.922**	0.01	**0.891**	0.01	**0.909**	0.019
Area (carbonate)	**0.625**	0.15	**0.617**	0.18	**0.682**	0.126
Flux (total)	**0.831**	0.01	**0.882**	0.01	**0.864**	0.033
Flux (siliciclastic)	**0.736**	0.01	**0.853**	0.01	**0.845**	0.026
Flux (carbonate)	**0.69**	0.094	**0.753**	0.084	**0.818**	0.06

Figure 1. Maps of North America with sediment-bearing column areas from Macrostrat (colored polygons) and fossil collection locations from the Paleobiology Database (PBDB; blue diamonds). Fossil collection locations have been randomly offset by a factor of 0.5%. Total numbers of columns and fossil collections are shown on each map. A, Lower Ediacaran (635–590 Ma); B, upper Ediacaran (590–538.8 Ma); C, Terreneuvian (538.8–521 Ma); D, Series 2 (521–509 Ma); E, Miaolingian (509–497 Ma); F, Furongian (497–485.4 Ma). Lower Ediacaran and upper Ediacaran informal divisions based on initial rise in preserved sediment area and volume. Cambrian epoch timings based on Cohen et al. (2013; updated v2022/10).


A. Lower Ediacaran: 635-590 Ma
collections = 5
columns = 75
B. Upper Ediacaran: 590-538.8 Ma
collections = 120
columns = 114
Mistaken Point
C. Terreneuvian: 538.8-521 Ma
collections = 294
columns = 238
D. Series 2: 521-509 Ma
collections = 1366
columns = 341
E. Miaolingian: 509-497 Ma
collections = 1401
columns = 477
Burgess Shale
F. Furongian: 497-485.4 Ma
collections = 1126
columns = 469
50°N
40°N
30°N
20°N
120°W
3000 km
N
= 1 fossil collection (PBDB)

904

905

906

Figure 2. Time series of rock and fossil metrics from the Ediacaran and Cambrian with Mackenzie and Sauk Sloss sequences and the Ediacaran/Cambrian transition highlighted. A, Log-scale plot of the number of occurrences and genera with bootstrap resampling–generated confidence intervals (2σ); B, log-scale plot of the total number of sedimentary rock units and the number of rock units that contain at least one fossil occurrence with bootstrap resampling–generated confidence intervals (2σ); C, stacked area plot of preserved marine sedimentary rock area (km^2) divided into clastic (grain size–based) and carbonate categories; D, stacked area plot of calculated marine sedimentary volume flux (km^3/Myr); and E, proportion of fossil-occupied sedimentary units (black), area (blue), and volume flux (red). Note that pre–580 Ma occurrences include fossil data from thicker, undivided stratigraphic sections with few geochronologic constraints.

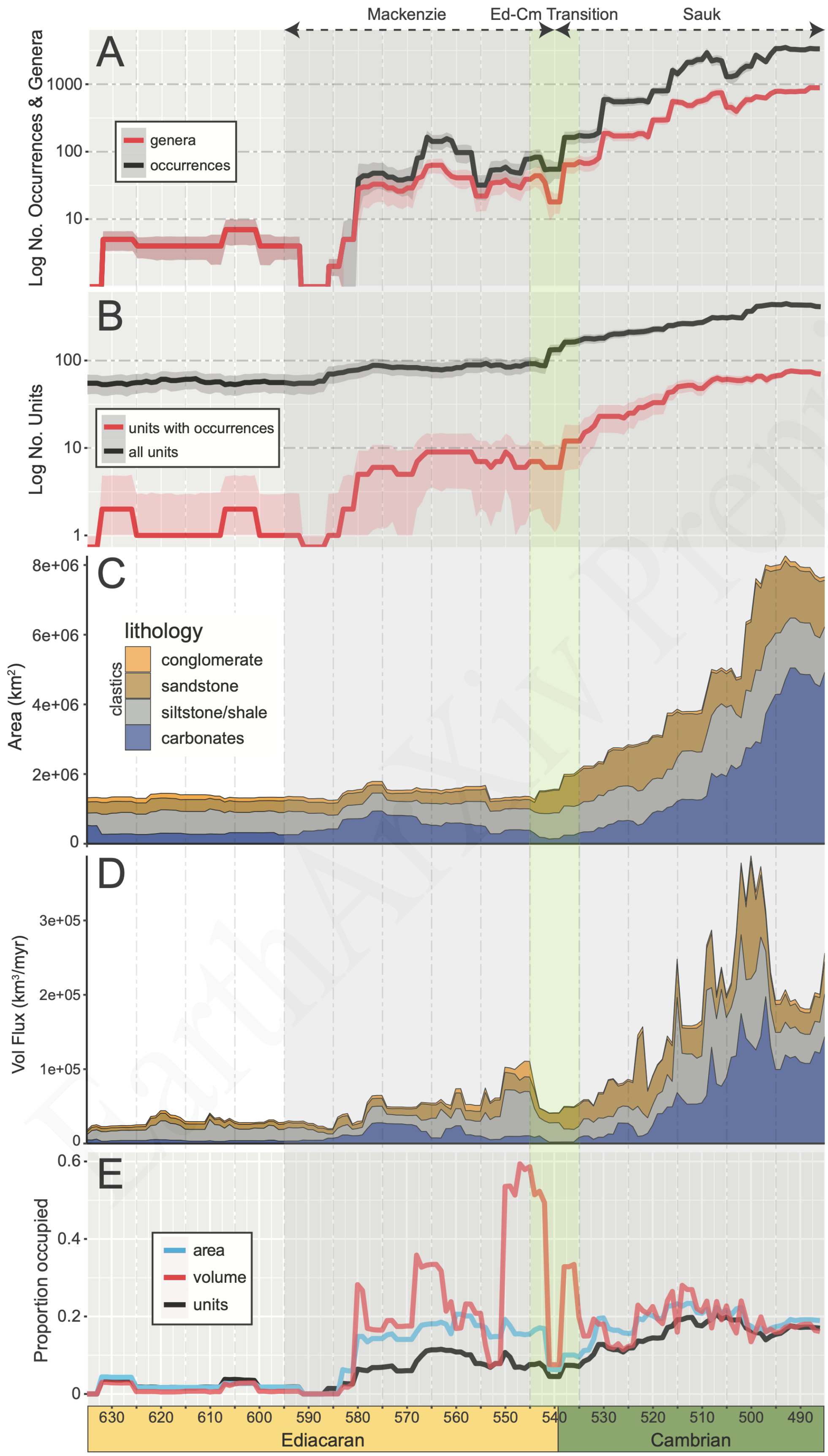

Mackenzie
Ed-Cm Transition
Sauk
A
Log No. Occurrences & Genera
1000
100
10
genera
occurrences
B
Log No. Units
100
10
1
units with occurrences
all units
C
Area (km²)
8e+06
6e+06
4e+06
2e+06
0
lithology
clastics
conglomerate
sandstone
siltstone/shale
carbonates
D
Vol Flux (km³/myr)
3e+05
2e+05
1e+05
0
E
Proportion occupied
0.6
0.4
0.2
0
area
volume
units
630 620 610 600 590 580 570 560 550 540 530 520 510 500 490
Ediacaran
Cambrian

Figure 3. Time series of median thickness and duration of sedimentary rocks and the number of occurrences reported from clastic and carbonate lithologies with Mackenzie and Sauk Sloss sequences and the Ediacaran/Cambrian transition highlighted. A, Median thickness (m) of all sedimentary units (black) with bootstrap resampling–generated confidence interval (2σ) and only sedimentary units that are occupied (contain at least one occurrence; red); B, median duration (Myr) of all sedimentary units (black) with bootstrap resampling–generated confidence interval (2σ) and only sedimentary units that are occupied (red); and C, stacked area of occurrence counts by Paleobiology Database (PBDB) reported lithology. A single occurrence can have multiple lithologies and therefore can be counted within multiple lithologic categories for one time interval.

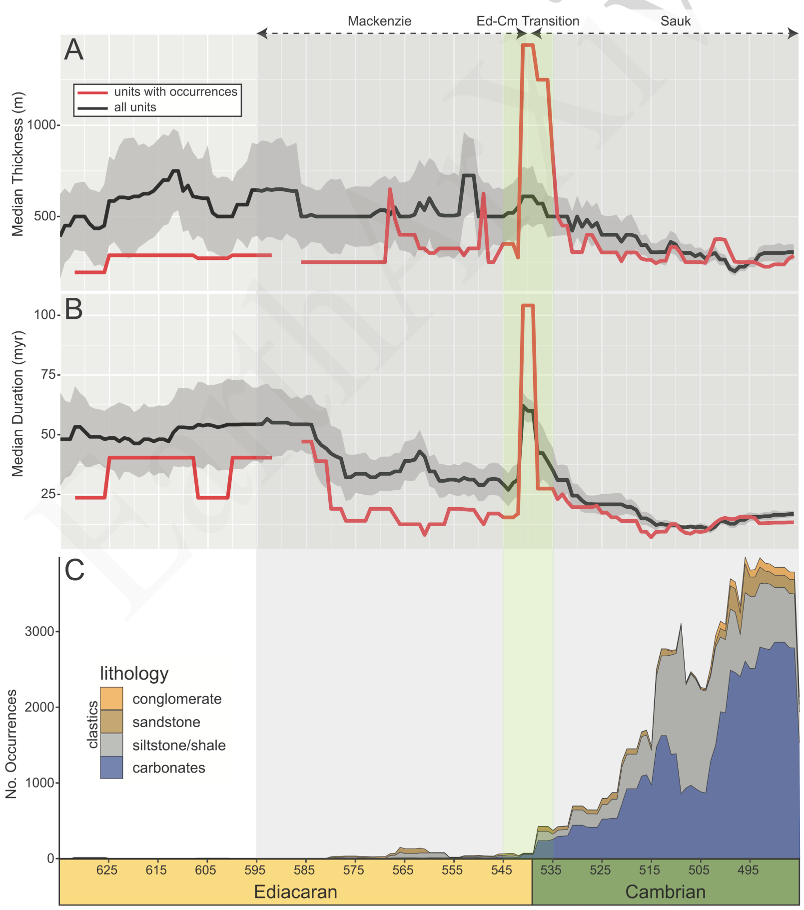


Figure 4. Time series of occurrence and genus counts normalized by sedimentary rock units (occurrences/rock unit), rock area (occurrences/10,000 km^2), and volume flux (occurrences/1000 km^3/Myr) with Mackenzie and Sauk Sloss sequences and the Ediacaran/Cambrian transition highlighted. A, Counts of occurrences normalized to sedimentary rock quantities; and B, counts of genera normalized to sedimentary rock quantities. See text for discussion.

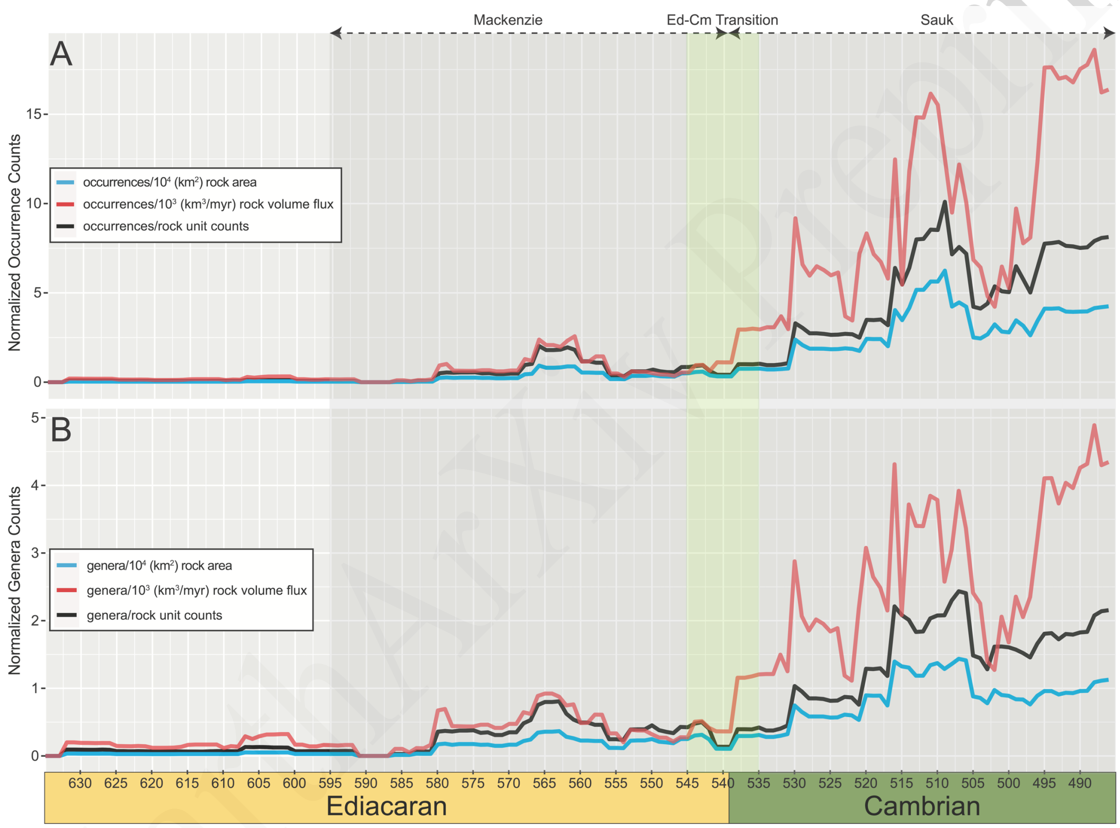
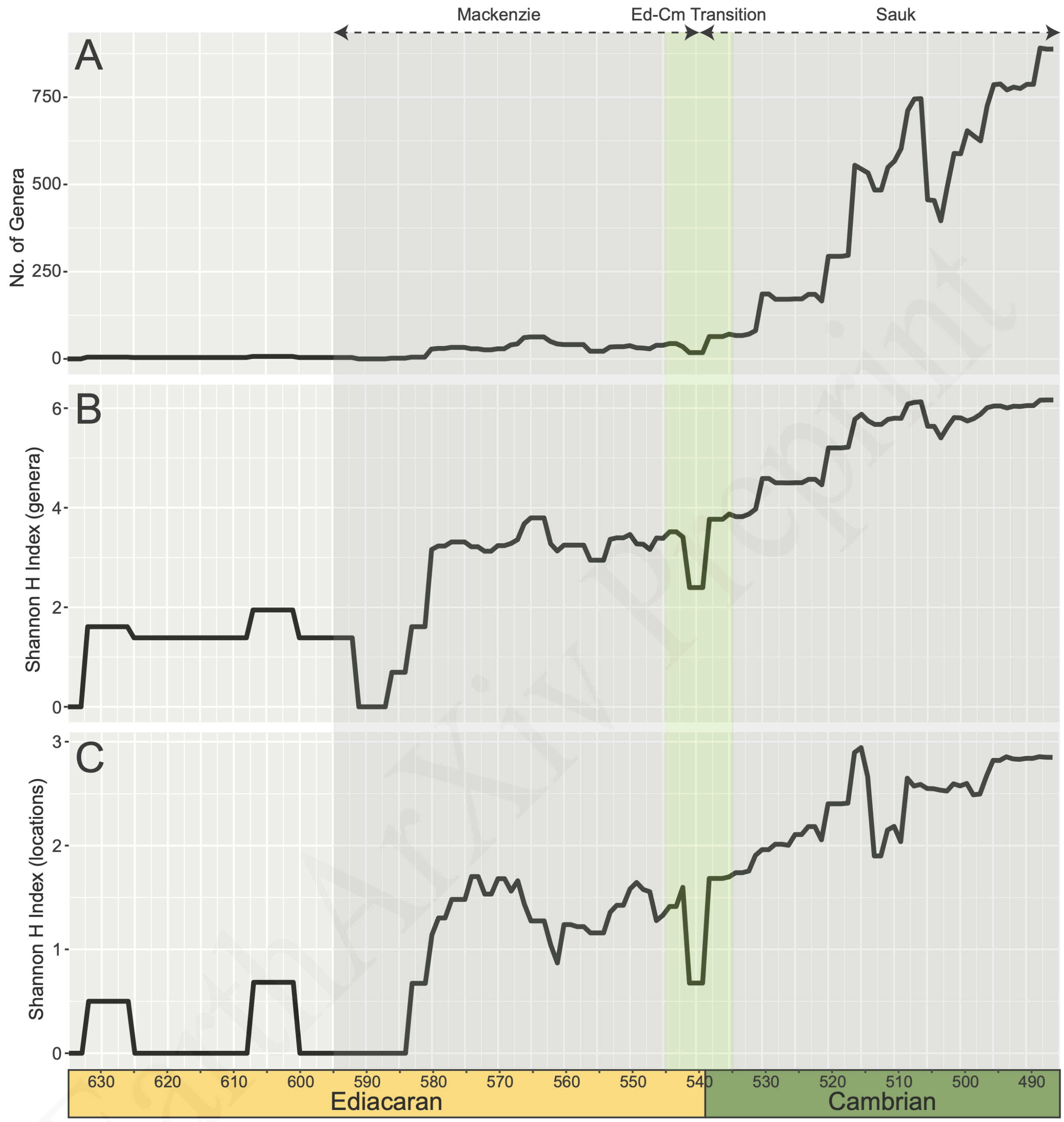


Figure 5. Time series of raw genus counts and the Shannon *H* indices of unique genus names and their reported locations (“states” field in the Paleobiology Database [PBDB]) with Mackenzie and Sauk Sloss sequences and the Ediacaran/Cambrian transition highlighted. A, Raw genus counts; B, Shannon *H* index of unique genera names and their occurrence frequencies; and C, Shannon *H* index of unique state names and their occurrence frequencies. Decreases in Shannon *H* indices from ca. 565–555 Ma and ca. 515–505 Ma represent intervals in which sampling is dominated by collections at specific localities (Mistaken Point Fm., Newfoundland, Canada, and Stephen Fm., British Columbia, Canada, respectively).


Mackenzie
Ed-Cm Transition
Sauk
A
B
C
No. of Genera
Shannon H Index (genera)
Shannon H Index (locations)
0
250
500
750
2
4
6
1
3
630
620
610
600
590
580
570
560
550
540
530
520
510
500
490
Ediacaran
Cambrian

953