

PALEONTOLOGY

Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—The role of bioturbation and bioerosion

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The Cambrian explosion (CE) and the great Ordovician biodiversification event (GOBE) are the two most important radiations in Paleozoic oceans. We quantify the role of bioturbation and bioerosion in ecospace utilization and ecosystem engineering using information from 1367 stratigraphic units. An increase in all diversity metrics is demonstrated for the Ediacaran-Cambrian transition, followed by a decrease in most values during the middle to late Cambrian, and by a more modest increase during the Ordovician. A marked increase in ichnodiversity and ichnodisparity of bioturbation is shown during the CE and of bioerosion during the GOBE. Innovations took place first in offshore settings and later expanded into marginal-marine, nearshore, deep-water, and carbonate environments. This study highlights the importance of the CE, despite its Ediacaran roots. Differences in infaunalization in offshore and shelf paleoenvironments favor the hypothesis of early Cambrian wedge-shaped oxygen minimum zones instead of a horizontally stratified ocean.

INTRODUCTION

The Cambrian explosion (CE) and the great Ordovician biodiversification event (GOBE) (1, 2) have been traditionally considered as discrete episodes, but more recently, an alternative has been advanced that these were phases of a long-term metazoan radiation spanning the Ediacaran and early Paleozoic (3). The CE was signaled by the appearance of most of the body plans in the fossil record, whereas the GOBE was characterized by a global three- to fourfold increase in the number of marine animal families and genera (1, 2). Ecospace analysis has shown marked increases in ecological modes of life as a result of both evolutionary radiations (4), although functional diversity was certainly limited in early Paleozoic oceans compared with that of modern seas (5).

Bioturbation—the biogenic reworking of sediment—is now regarded as a major force in macroevolution, playing a substantial role in geobiologic feedbacks and geochemical cycles, but the extent of its importance during the CE and GOBE is still controversial (6–9). The impact of bioturbation is highly dependent on the abundance, mobility, and size of the bioturbators (10). As a result, functional diversity instead of taxonomic diversity plays a major role in biogeochemical cycling. Bioerosion—the corrosion and abrasion of hard substrates—plays a key role in carbonate ecosystem health (e.g., in coral reefs), predation pressure, ocean acidification, and global warming, but its ecological and evolutionary impact in deep time has rarely been addressed (11).

The objectives of this paper are as follows: (i) to reconstruct ichnodiversity and ichnodisparity trajectories and patterns of ecospace utilization and ecosystem engineering along the marine depositional profile during the CE and the GOBE, (ii) to assess in which environ-

ments evolutionary innovations in bioturbation and bioerosion originated and determine the patterns of environmental expansion, and (iii) to use this information to test competing hypotheses surrounding the timing and extent of ocean oxygenation. To quantify the role of bioturbation and bioerosion during the CE and the GOBE, we constructed a global dataset (table S1 and S2 and figs. S1 to S7) of trace fossil occurrences in marginal-marine to fully marine environments from a survey of 1367 Ediacaran-Ordovician stratigraphic units. Of these, the presence of trace fossils was confirmed in 639 units. Ichnotaxonomic determinations were critically assessed on a case-by-case basis, and various metrics were considered to evaluate ecospace utilization and ecosystem engineering (see Materials and Methods). Seven paleoenvironmental subdivisions along the depositional profile were considered. Because trace fossils are typically preserved in situ and display a close link with environmental factors, and given that facies analysis has become an increasingly refined technique, it is possible to provide a more detailed characterization of facies constraints for trace fossils than for body fossils, allowing greater paleoenvironmental resolution in comparison with previous macroevolutionary studies. This more refined facies resolution allows better integration with geochemical proxies, providing independent constraints to evaluate contrasting scenarios of marine oxygenation. We performed statistical tests to evaluate potential correlations between any of the diversity metrics and the total number of lithostratigraphic units (see Materials and Methods). This is a robust dataset that shows that the trace fossil record is essentially continuous across a wide variety of depositional environments.

RESULTS

Our data show that the increase in global ichnodiversity and ichnodisparity at the Ediacaran-Terreneuvian transition (i.e., Precambrian-Cambrian transition) was accompanied by a marked increase in the numbers of modes of life and styles of ecosystem engineering (Figs. 1 to 3 and figs. S1 to S7). If all environments are considered together, most metrics show a decrease during the Miaolingian (i.e., middle Cambrian), reaching minimum values during the Furongian

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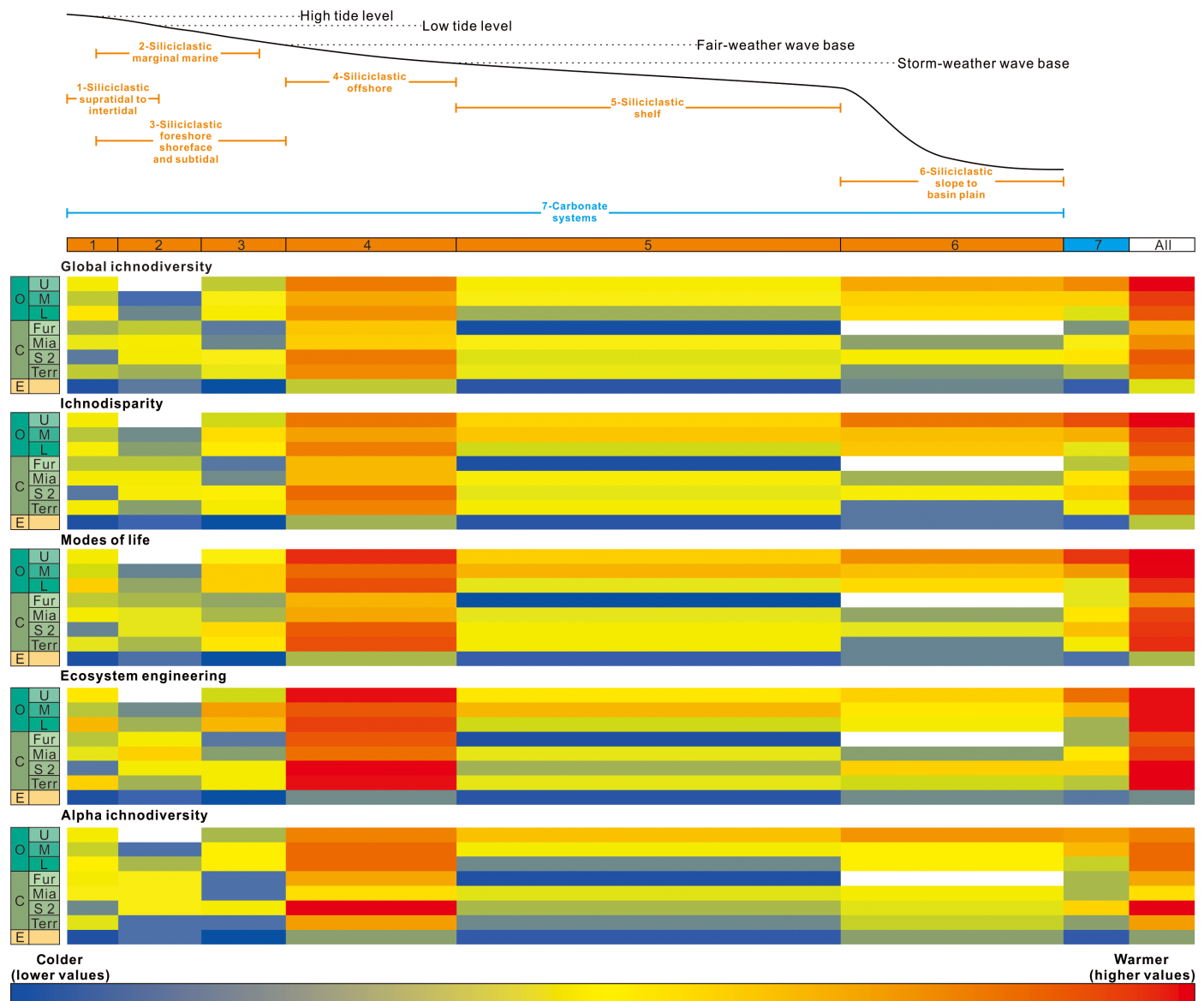


Fig. 1. Heatmap of metrics used in this study. Modes of life (ML), ecosystem engineering (EE), global ichnodiversity (GI), maximum alpha ichnodiversity (AI), and ichnodiversity (Id) along the depositional profile during the Ediacaran-Ordovician. Values from coldest to warmest in each metric are as follows: ML, 2 to 35; EE, 1 to 23; GI, 1 to 110; AI, 1 to 40; and Id, 1 to 49.

(i.e., late Cambrian), then followed by a more modest increase during the Ordovician (Fig. 2). Of the 135 potential modes of life, only 10 were occupied by the end of the Ediacaran. In contrast, 31 and 35 modes of life are documented for the Terreneuvian and Late Ordovician, respectively. Of the 140 potential combinations for mechanisms of substrate penetration and sediment modification, 6 were present during the Ediacaran, 23 during the Terreneuvian, and 22 during the Late Ordovician.

Data analysis from the different environmental and chronostratigraphic bins indicates that ecospace colonization was diachronic (Fig. 1). The most marked changes were associated with Terreneuvian siliciclastic offshore settings, which were characterized by a marked increase not only in numbers of modes of life and styles of ecosystem engineering but also of ichnodiversity, global ichnodiversity,

and maximum alpha ichnodiversity (fig. S4). Notably, the numbers of modes of life and styles of ecosystem engineering remained relatively stable during the rest of the Cambrian and through the Ordovician. However, global and maximum alpha ichnodiversities show a marked increase during Cambrian Epoch 2. In particular, data from siliciclastic offshore environments show the establishment of infaunal communities with a well-developed tiering structure since the early Cambrian. These communities were characterized by niche partitioning in semi-infaunal, shallow, intermediate, and deep tiers, with bioturbators redistributing sediment particles through essentially the same interactions identified in modern shallow-marine settings (12).

The trace fossil record of siliciclastic marginal-marine environments shows an increase in all metrics during the Ediacaran-Terreneuvian

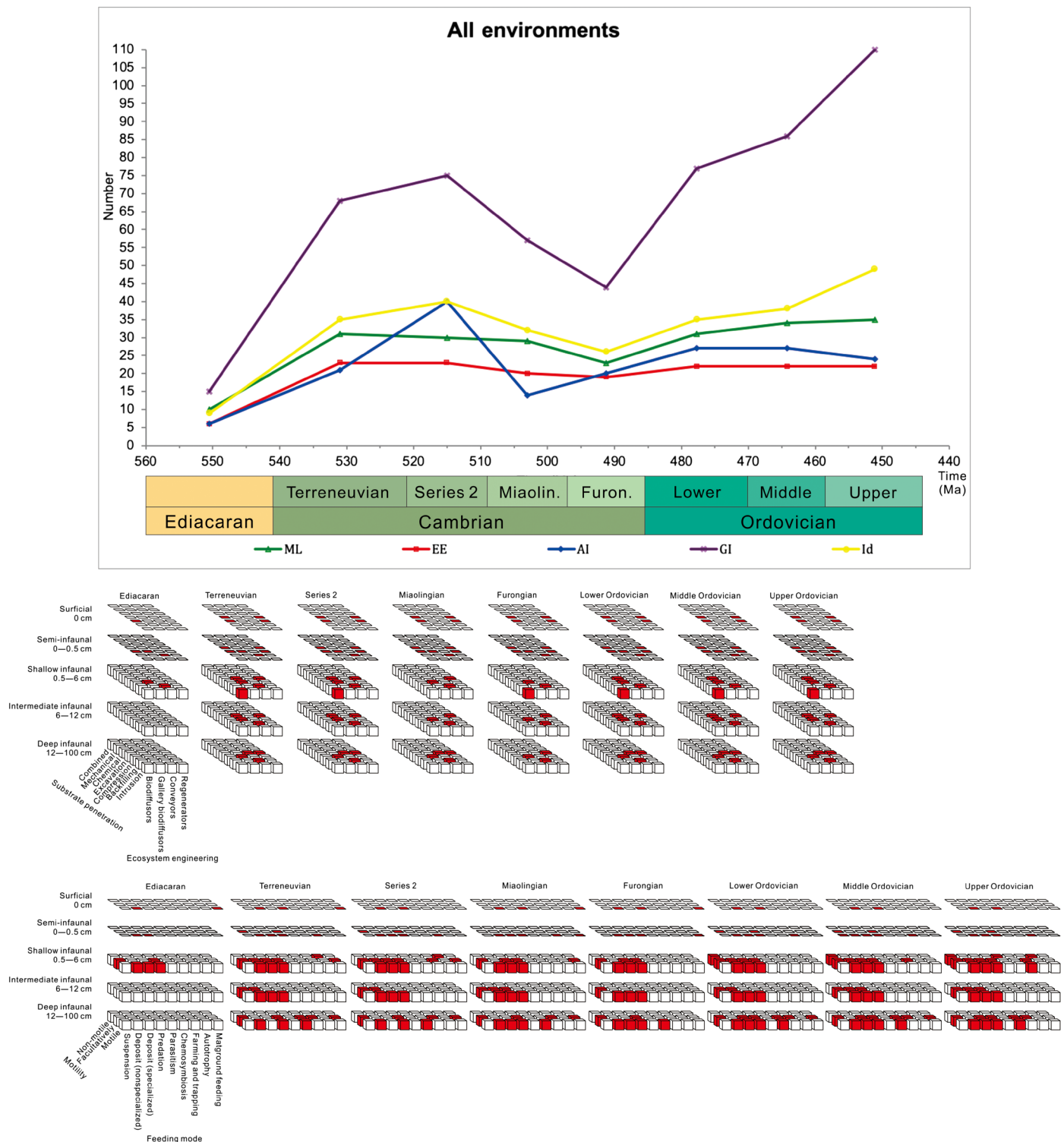


Fig. 2. Plot of changes in modes of life (ML), ecosystem engineering (EE), maximum alpha ichnodiversity (AI), global ichnodiversity (GI), and ichnodispersity (Id) in all environments. Counts are plotted at the middle of the series intervals.

transition with a step-wise increase during the rest of the studied interval (fig. S1). Overall ecospace utilization in marginal-marine environments remained less exploited than in fully marine environments. For example, the numbers of modes of life identified in

brackish-water, marginal-marine settings for the Late Ordovician was lower than those obtained for shallow-marine offshore settings in the Terreneuvian. Although there was a rapid increase in the number of styles of ecosystem engineering in marginal-marine

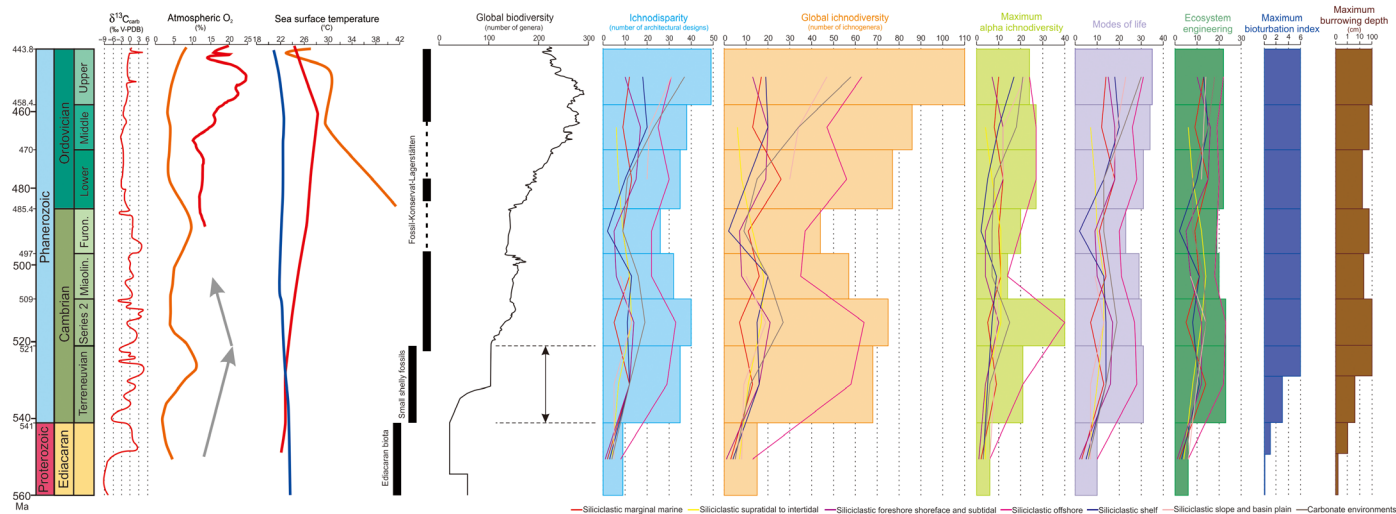


Fig. 3. Summary of metrics used in this study and potential correlations with other parameters. Modes of life (ML), ecosystem engineering (EE), global ichnodiversity (GI), maximum alpha ichnodiversity (AI), and ichnodisparity (Id) during the Ediacaran-Ordovician. Boxes represent all environments combined. Black dashed lines and arrows highlights the approximately 20-Ma difference between early Cambrian diversification based on trace fossils and body fossils. Carbon isotope curve is a composite from Narbonne *et al.* (34) (Ediacaran), Peng *et al.* (35) (Cambrian), and Edwards (24) (Ordovician). Atmospheric oxygen level from Edwards (24) (red) and Krause *et al.* (36) (orange). Gray arrows indicate global ocean oxygenation (24) and following deoxygenation (36). Sea surface temperature from Mills *et al.* (37) (red and blue, updated GEOCARBSULF and COPSE models) and Trotter *et al.* (38) (orange). Small shelly fossils and Ediacaran biota from Erwin and Valentine (1). Generic diversity curves for Ediacaran body fossils after Darroch *et al.* (39) and for Cambrian-Ordovician body fossils after Fan *et al.* (40). The peak in maximum alpha ichnodiversity in Cambrian Series 2 is most likely a monographic effect. Maximum bioturbation index and burrowing depth based on Mángano and Buatois (6) and own data.

environments during the Terreneuvian, no further changes are apparent during the rest of the Cambrian and all through the Ordovician.

In siliciclastic supratidal to intertidal settings, the main increase in all metrics took place during the Terreneuvian to Cambrian Epoch 2 (fig. S2). A drop in all metrics was apparent during the Ordovician. Siliciclastic foreshore, shoreface, and subtidal sandy settings show a very low number in all metrics through all the Ediacaran (fig. S3). A constant increase in the numbers of modes of life and styles of ecosystem engineering is evident during the whole Terreneuvian. Notably, a drop in all metrics is apparent in these nearshore settings during the Miaolingian-Furongian, with a recovery during the Ordovician. However, statistical analysis may suggest that this drop could be related to a relative lack of studies for this particular interval (table S3).

In siliciclastic shelf environments, all metrics show a marked increase in the Terreneuvian, but all values other than maximum alpha ichnodiversity show a drop during Cambrian Epoch 2 (fig. S5). After a recovery during the Miaolingian, all values drop markedly in the Furongian. Increases in all values are recorded throughout the Ordovician, although a drop in the number of styles of ecosystem engineering and modes of life is apparent during the Late Ordovician.

Siliciclastic slope and basin-plain environments show an increase in all metrics during the Terreneuvian and Cambrian Epoch 2 followed by a drop in the Miaolingian (fig. S6). No data are available for Furongian deep-water settings, and a sustained increase in essentially all metrics took place during the Ordovician. Overall, ecospace utilization in deep-marine environments lagged behind that of shallow-water settings, although significant correlations between ichnologic parameters and the total number of lithostratigraphic units (table S3) prevent establishing a well-supported pattern.

Carbonate settings show a pattern that markedly departs from that of siliciclastic settings, although there are significant correlations between diversity metrics and sampling proxies (table S3). First, an increase in modes of life, styles of ecosystem engineering, ichnodisparity, global ichnodiversity, and maximum alpha ichnodiversity took place during the Terreneuvian (fig. S7). A subsequent increase in all these metrics took place during the Middle Ordovician, with a notable further increase in the number of modes of life, global ichnodiversity, and ichnodisparity during the Late Ordovician. Although the overall pattern may have been affected by sampling intensity (table S3), there is a notable consistency with studies on the basis of body fossils.

DISCUSSION

Our analysis underscores the importance of the CE and the GOBE not only as times of ichnodiversity increase but also of substantial changes in ecospace utilization in concert with increased modes of ecosystem engineering in marine environments (Figs. 2 and 3). No decoupling between maximum alpha and global ichnodiversity is evident; the two essentially follow identical trajectories most of the time. In turn, global ichnodiversity and ichnodisparity follow similar trajectories for bioturbation structures during the CE, but not for the GOBE when the increase in ichnodiversity was not followed by an equally important increase in ichnodisparity (11). In contrast, the GOBE was characterized by an increase in both global ichnodiversity and ichnodisparity of bioerosion structures, revealing major evolutionary innovations in hardground communities (11). Our study highlights the uniqueness and importance of the CE, despite the fact that its roots were present in the Ediacaran (13).

A comparison between trace- and body-fossil diversity shows times of coincidental increases, as well as macroevolutionary lags

between both metrics (Fig. 3). The most marked increase in ichnodiversity and ichnodisparity took place during the early part of the Terreneuvian (i.e., Fortunian), followed by another increase during Epoch 2 (6, 11). Although these two-phase increases are also seen in diversity of body fossils at the genus level (Fig. 3), the CE of body fossils has been historically attributed to the later diversity increase of Epoch 2. Therefore, the most important increase in ichnodiversity and ichnodisparity in the history of the biosphere occurred approximately 20 million years (Ma) earlier than the explosion in body fossils (6, 11). Some of the novel types of bioturbation structures include penetrative feeding traces, sediment bulldozers, and farming burrows in the Fortunian, followed by deep domiciles of infaunal suspension feeders in Stage 2 (6). This pattern suggests the presence in shallow-marine environments of a soft-bodied benthos that is not captured by the body-fossil record, most notably euarthropods, priapulids, nematodes, polychaetes, and, most likely, also enteropneusts and phoronids (14). These bioturbators may have been instrumental in creating niches that were subsequently occupied by the younger Cambrian faunas. During the middle and late Cambrian (i.e., Miaolingian and Furongian), a general plateau is reached by body-fossil diversity at all taxonomic levels, whereas a drop is seen in trace fossil diversity (Fig. 3). The subsequent increase in diversity associated with the GOBE is apparent for both body and trace fossils (Figs. 2 and 3).

Our analysis provides additional support to the hypothesis that the infaunal ecospace was markedly underutilized during the Ediacaran. Mid and deep tiers remained vacant along the depositional profile in both siliciclastic and carbonate settings, including stable fully marine settings below fair-weather wave base. Occupation of these deeper tiers started during the Terreneuvian and continued at an accelerated rate during the Cambrian Epoch 2. Comparison with ecospace analysis on the basis of body fossils suggests similar trends (4). The Ediacaran-Terreneuvian time span was characterized by the overrepresentation of a wide variety of feeding styles that are here broadly included in the category of matground feeding. The latter include not only mat grazing but also undermat mining, mat scratching, and mat digestion (table S1). These styles were particularly common during the Fortunian. Other feeding strategies, such as specialized and nonspecialized deposit feeding, suspension feeding, and predation, became progressively more important during the rest of the Cambrian and the Ordovician. The drop in global ichnodiversity, ichnodisparity, modes of life, and styles of ecosystem engineering during the Furongian was coincident with a mass extinction event and may reflect the expansion of anoxic water onto marine platforms (15). In addition, the fact that the trend of continuous increase in all ichnologic parameters was interrupted and reversed during the Miaolingian-Furongian suggests that the CE and GOBE were discrete events for the benthos. Notably, the picture for the plankton is remarkably different, with a major radiation taking place in the Furongian, suggesting a link between these two evolutionary radiations (2).

Segregation of data into environmental and chronostratigraphic bins allows discrimination of facies and temporal controls, yielding insights into the pace of evolutionary innovations along the depositional profile (Fig. 1). Our analysis indicates that major evolutionary innovations took place first in marine siliciclastic environments below the fair-weather wave base but above storm wave base (i.e., offshore), and only later expanded into shallower, marginal-marine, and near-shore settings, as well as to below storm wave base (i.e., shelf, slope, and basin plain) and carbonate environments.

The sustained increase in all metrics in all siliciclastic nearshore settings during the later part of the Terreneuvian (Stage 2) and the Cambrian Epoch 2 essentially reflects the appearance of densely packed infaunal communities of suspension feeders that were able to penetrate deeply into sandy sediment under agitated waters due to the activity of waves and currents (6). The extensive construction of deep-tier dwelling burrows may have had marked impacts in shoreface, sandflat, and subtidal sandbar complexes through increased bioirrigation, translocation of material, mucus secretion, promotion of microbial growth, and deepening of the redox discontinuity surface (6).

The marked increase in all metrics of animal-substrate interactions in siliciclastic offshore settings was coincident with an inferred rise of ocean oxygenation (16, 17) and the appearance of the sediment mixed layer (7) during the early Cambrian, further emphasizing the impact of bioturbation during the CE. Ichnologic evidence from Namibia indicates that an increase in trace fossil complexity and ecosystem engineering took place in siliciclastic offshore settings by the end of the terminal Ediacaran (13, 14, 18). However, this increase cannot be confirmed with our global analysis because when the Ediacaran is split into Vendian and Nama assemblages (19), there are significant correlations between these parameters and the total number of lithostratigraphic units (table S3).

Reconstructing redox conditions during the early Cambrian has been controversial, with interpretations on the basis of geochemical proxies ranging from anoxic to fully oxygenated conditions (16). The fact that almost all ichnologic metrics show an increase in offshore (i.e., above storm wave base) and nearshore (i.e., above fair-weather wave base) settings, but a drop in shelf environments (i.e., below storm wave base) during the Cambrian Epoch 2, argues against a laterally extensive, horizontally stratified ocean and in favor of laterally impersistent, wedge-shaped oxygen minimum zones (17). The pattern of delayed colonization of environments below storm wave base is consistent with geochemical proxies that indicate that these settings were prone to episodes of bottom-water anoxia (20). The drop of metrics in shelf settings during the Cambrian Epoch 2 also supports the hypothesis that the onset of bioturbation in the early Cambrian may have contributed to a decrease in oxygenation (8, 9, 21), although we argue that this impact was mostly restricted to settings below storm wave base.

Colonization of marginal-marine and deep-sea settings lagged behind that of fully marine, siliciclastic offshore environments. Therefore, our study supports the hypothesis of a protracted invasion of the benthos into highly stressed, brackish-water settings during the whole Paleozoic (22). In turn, exploitation of microbial mats persisted in the deep sea during all the Cambrian, as indicated by the dominance of various types of microbial feeding strategies in shallow tiers. In contrast, the GOBE was associated with the establishment of deep-marine communities of “modern aspect” (23) dominated by shallow-tier farming and trapping structures (i.e., graphoglyptids), deep- to mid-tier trace fossils of deposit feeders, and, to a lesser extent, deep-tier trace fossils produced by deposit feeders and chemosymbionts. This biotic turnover in the deep sea was coincident with an increase in oxygenation in slope and base-of-slope settings (24). Therefore, our study indicates that deep-sea bottoms were oxygenated much earlier than previous estimations on the basis of the ratio of Fe^{3+} to total Fe in oceanic basalts, which indicated that deep-ocean oxygenation may have been delayed until the late Paleozoic (25).

Recurrent dysoxia and hypoxia during the middle and late Cambrian (i.e., Miaolingian and Furongian) may have negatively affected reef-building communities (26). Substantial diversification of reef organisms took place during the Middle to Late Ordovician, coincident with an increase in marine oxygenation (24). This diversification trend may reflect, at least in part, the establishment of novel modes of life and styles of ecosystem engineering in an extensive shallow carbonate belt that formed in Equatorial Laurentia and Baltica during the Late Ordovician. Overall, evolutionary innovations for level-bottom communities during the GOBE preceded those of carbonate reef communities (2). In addition to innovations in carbonate softground communities, the increase in all metrics revealed by bioerosion structures in hard substrates underscores a major breakthrough in hardground communities during the GOBE (11). However, the fossil record of microbial bioerosion during the Ediacaran and early Paleozoic is strongly biased by a relative scarcity of biogenic skeletal substrates, diagenetic overprint, and a lack of studies for this interval. The body-fossil record of microendolithic cyanobacteria and algae indicates that the endolithobiontic ecological niche was already exploited during the Proterozoic [e.g., (27)].

This study demonstrates, in a global and quantitative fashion, that bioturbation was a major force during the CE and GOBE, with bioerosion having a notable impact only during the latter. Analysis of our robust dataset yields insights into ecospace utilization and ecosystem engineering along the depositional profile during these two major evolutionary events, helping to constrain with more precision the role of oxygen minimum zones as limiting factors of benthic colonization. By adopting a refined sedimentological framework, we show that ichnologic data have the potential to provide high-resolution information to differentiate between environmental and evolutionary constraints. Our approach to quantify ecospace utilization and ecosystem engineering opens a new line of research that can be used to explore multiple evolutionary events from the perspective of animal-substrate interactions.

MATERIALS AND METHODS

Dataset compilation

Data were compiled at the series level from 1367 stratigraphic units on the basis of an exhaustive literature review and personal data from Ediacaran-Cambrian sedimentary basins worldwide, including both ichnofossiliferous and non-ichnofossiliferous units. Source literature on Ediacaran-Ordovician stratigraphic units was collated by the use of various search engines (e.g., Google Scholar) and by examination of edited and monographic series on stratigraphy and regional geology (e.g., Geological Society “Geology of” series). The dataset was compiled over a period of 20 years with constant updating (6,11). Searches specific to ichnology and associated sedimentary environments were performed. Of all the units compiled, 364 (209 of these containing trace fossils) have been examined by at least one of the authors in outcrop or in core. Official subdivisions established in the geological time scale were used. An informal subdivision of the Ediacaran between Avalon, Vendian, and Nama was adopted following a previous proposal (19). Data from 28 units of Avalon age were not considered in the final analysis because, with the exception of one case, these were barren in trace fossils. Accordingly, our analysis is restricted to the Vendian-Late Ordovician time span. Age is based on the original study documenting the trace fossils or in biostratigraphic and geochronologic studies of the same unit. In

many instances, the age in the primary literature was expressed in local subdivisions and, accordingly, conversions to the international standard were performed.

Of all the units compiled, 639 contain trace fossils. Standard ichnotaxonomic practices (e.g., use of ichnotaxobases) were followed in the construction of the dataset. We checked synonymies to adopt a consistent ichnotaxonomic approach. Ichnotaxonomic reviews were regularly checked to update original assignments. In addition to those units where direct observations of trace fossils were performed in outcrop and core, analysis of collected specimens was performed for another 81 units. In those cases where no direct observation has been done, each original ichnotaxonomic determination has been checked on the basis of photographs and descriptions in the primary literature. Details on ichnotaxonomic decisions and their underlying rationale have been provided elsewhere [e.g., (6, 28)]. A total of 162 ichnogenera are identified across the Ediacaran-Ordovician time interval.

Occurrences from these units were, in turn, subdivided into discrete trace fossil assemblages for seven standardized environmental categories at the series level. Of the 1367 units analyzed, 1165 represent single environmental zones and 202 multiple zones, ranging from two to five discrete environmental zones per unit. This scheme follows current subdivisions used in the sedimentological and applied ichnology literature and has a higher resolution than the one usually used in paleobiologic analysis. In addition, this scheme reflects both location of ichnofaunas along a depositional gradient and potential responses of the benthos to environmental factors, such as energy, oxygen, substrate, and salinity. Placement in environmental categories is based on the original studies performed in the different units, either in the papers documenting the trace fossils or in sedimentologic studies of the same unit. Each unit was critically assessed for potential discrepancies between the provided sedimentologic evidence and the proposed interpretation to attain consistent placement in the pertinent environmental zones according to the standardized scheme. Initially, data were compiled for six discrete environmental categories for siliciclastic systems (see below), four for carbonate systems (restricted carbonate platform, open carbonate platform and ramp, reef, and slope to basin plain), and three for volcanoclastic systems (marginal marine, shelf, and volcanoclastic slope). However, the amount of ichnologic data available was not substantial enough to support the latter two subdivisions. Accordingly, for the final analysis, only one category was considered for carbonate settings, and the categories for volcanoclastic settings were merged with those of similar environments in siliciclastic systems. Therefore, the following seven standardized environmental categories have been adopted: (i) siliciclastic marginal marine; (ii) siliciclastic supratidal to intertidal; (iii) siliciclastic foreshore, shoreface, and subtidal; (iv) siliciclastic offshore; (v) siliciclastic shelf; (vi) siliciclastic slope to basin plain; and (vii) carbonate settings. No specific subdivisions are used for mixed siliciclastic-carbonate systems. Instead, discrete ichnofaunas within these systems are placed in the categories previously defined, depending on the characteristics of the predominant associated facies, and evaluated on a case-by-case basis. More detailed subdivision can be established for certain depositional environments (e.g., subdividing the offshore into offshore transition, upper offshore, and lower offshore), but this degree of definition is not available in most studies. In addition, the present scheme is considered accurate enough to detect trends in colonization. The different environmental categories are defined as follows.

(i) Siliciclastic marginal-marine environments in this scheme comprise all those settings strongly affected by rapid salinity fluctuations, therefore representing brackish-water environments. Bays, estuarine channels and basins, distributary channels, interdistributary bays, lagoons, and mouth bars are all included in this category. In terms of the ichnofacies model, the depauperate *Cruziana* ichnofacies is typical of these settings.

(ii) Siliciclastic supratidal to intertidal environments include settings formed above the high tide line and between the high and low tide lines in systems that are either tide dominated or strongly affected by tides. Stress factors associated with periodic subaerial exposure (e.g., desiccation and temperature) are expected in these environments. Backshore regions of wave-dominated settings share the same stress factors and are, therefore, included here. According to the energy regime, the *Cruziana* and *Skolithos* ichnofacies occur along the depositional profile.

(iii) Siliciclastic foreshore, shoreface, and subtidal environments encompass nearshore settings of a wave-dominated shoreline, as well as high-energy subtidal areas of tide-dominated systems. The foreshore and shoreface illustrate the former, whereas the latter is represented by a wide variety of subtidal sand bodies. The foreshore comprises the area between high and low tide, and the shoreface is located between the low tide and the fair-weather wave base. The shoreface is subdivided into the following three main zones: upper, middle, and lower. The upper shoreface is located immediately below the low tide line and is subjected to multidirectional current flows. The middle shoreface is a transition zone that may experience both unidirectional and oscillatory flows. The lower shoreface is located immediately above the fair-weather wave base and is strongly affected by both oscillatory and combined flows. Because high hydrodynamic energy is considered the key controlling factor on the benthos in these settings, lower shoreface ichnofaunas in low-energy shorelines with a low intensity and frequency of storms have been clustered with the adjacent environmental zone in a seaward direction. The sand bodies of tide-dominated environments include sand sheets, compound dunes, tidal sand ridges, and isolated dune patches. Some of these nearshore clastic settings may show variable degrees of deltaic influence, which is hard to evaluate in the case of many of the examples compiled in our dataset. Accordingly, delta-front sandstones, the bathymetric equivalent of the shoreface, are included here. In terms of the ichnofacies model, the *Skolithos* ichnofacies is typical of nearshore settings, although departures may occur under increasing deltaic influence.

(iv) Siliciclastic offshore environments comprise the region located between the fair-weather wave base and the storm wave base. This environment encompasses the offshore transition, upper offshore, and lower offshore. As in the case of the nearshore, deltaic influence may be present in some cases and so the prodelta, which occurs at the same depth as the offshore, is included here. In terms of the ichnofacies model, the *Cruziana* ichnofacies is typical of offshore settings, although a more stressed version may occur under increasing deltaic influence.

(v) Siliciclastic shelf environments occur below the storm wave base and extend to the slope break. This definition is a strict use of the term “shelf” different from the broad sense adopted in some schemes in which the shelf comprises all settings from the fair-weather wave base to the slope break, therefore also including the environment referred to as offshore in our study. The *Zoophycos* ichnofacies is typical of shelf settings, although its applicability to the study of Paleozoic strata is not free of controversies.

(vi) Siliciclastic slope to basin plain environments are located beyond the shelf break. These environments include mostly turbidite systems that may be present on the slope or at the base of slope, comprising, in turn, various subenvironments, such as channels, levees, crevasse splays, and terminal splays. We note that this use is consistent with the one used by sedimentary geologists in facies analysis and paleoenvironmental reconstructions. However, the term “deep marine” is commonly used in geochemical and paleobiologic studies in a very broad sense, including not only environments beyond the shelf break but in the shelf as well. In terms of the ichnofacies model, the *Nereites* ichnofacies is typical of deep-marine settings, although the *Zoophycos* ichnofacies is typical of the slope and the *Skolithos* ichnofacies may occur in high-energy channelized areas and proximal zones of levees and splays (sometimes referred to as the *Ophiomorpha rudis* ichnosubfacies).

(vii) Carbonate settings include a wide variety of environments, encompassing restricted carbonate platforms, open carbonate platforms and ramps, reefs, and carbonate slopes to basin plains. Restricted carbonate platforms include protected settings, such as rimmed platforms, in which a rim, ooid shoal, or barrier precludes ocean waves to impart an energy stress on the benthos. Typically, a low-energy lagoon is formed in this protected area. Open carbonate platform and ramp environments include shallow-marine carbonate settings that are exposed to ocean waves because they lack any type of physiographic barrier, being directly connected with the open ocean instead. These settings comprise a wide variety of subenvironments along the depositional profile, such as backshore, foreshore, inner ramp-platform, middle ramp-platform, and outer ramp-platform. Reefs comprise not only coral reefs but also various types of bioherms, including archaeocyathid reefs and microbial buildups. Reefs can be subdivided into different subenvironments, namely, back reef, reef flat, reef crest, reef front, and fore reef. Carbonate slope to basin plain environments include both flanking reefs and platform margins. In comparison with their siliciclastic counterparts, ichnofacies models are less developed for carbonate systems. Regardless, the *Cruziana* ichnofacies is expected in most of these settings, although the *Skolithos* ichnofacies may occur in high-energy areas exposed to wave action, such as a shoal. A transition from the *Skolithos* to the *Cruziana* ichnofacies is expected along the depositional profile of carbonate ramps and platforms with increasing water depth. In addition to marine softground ichnofacies, bioerosion ichnofacies, such as the *Trypanites* ichnofacies, tend to be dominant in reefs, and the *Glossifungites* ichnofacies may develop in firmgrounds in many of these carbonate settings.

The definitions of ichnodiversity and ichnodisparity used in this paper follow previous schemes (28). Global ichnodiversity refers to the total number of ichnogenera at a certain environment during a certain time. Alpha ichnodiversity refers to the number of ichnogenera for each specific trace fossil assemblage, therefore providing information on the ecologic structure of discrete communities. Beta and gamma ichnodiversity were not assessed in this study. Architectural designs were defined to address the basic morphologic plans involved in animal-substrate interactions. Each ichnogenus was included in one category of architectural design following previous proposals (table S1).

The multidimensional ecospace and ecosystem engineering analysis has been used (22, 29). Previous schemes developed to assess ecospace utilization based on body fossils (4) have been adapted for trace fossils (22, 29). Occupied ecospace is quantified on the basis of

the number of modes of life, as indicated by the following three parameters: (i) tiering, (ii) motility, and (iii) feeding mode. Ecospace categories are summarized in table S1.

Tiering is subdivided into five categories: surficial, semi-infaunal, shallow infaunal, intermediate infaunal, and deep infaunal tiers (4, 6, 22, 29). In particular, tiering refers to the position occupied by an animal vertically with respect to the sediment surface. Because trace fossils essentially reflect interactions of the benthos with the substrate, ichnologic data are restricted to infaunal tiering rather than epifaunal tiering (i.e., the vertical distribution of organisms above the sediment surface). Surficial tier refers to animals living on the sediment surface. Semi-infaunal tier comprises animals that are partly infaunal and exposed to the overlying water. A shallow infaunal tier refers to animals living up to 6 cm deep within the sediment. An intermediate infaunal tier includes those animals occupying depths between 6 and 12 cm. A deep infaunal tier corresponds to those animals living at depths between 12 and 100 cm. A very deep infaunal tiering is defined for animals occupying depths greater than 1 m, but this tier was not occupied before the Mesozoic marine revolution (6). Tier position can be estimated for both bioturbation and bioerosion structures, irrespective of the type of hard substrate or the type of bioerosion, including macroborings, microborings, attachment etchings, predation traces, and grazing traces. In all those cases, tier position reflects maximum penetration into the hard substrate.

Motility is subdivided into motile, facultatively motile, and non-motile (4, 22, 29). Most animal trace fossils reflect some degree of motility, although attachment structures and some microbioerosion structures are produced by non-motile organisms. In general, any organism capable of producing temporary bioturbation structures that reflect continuous or semicontinuous movement is considered motile. Animals that are generally stationary but are capable of movement are included in the category of facultatively motile.

Feeding mode includes suspension feeding, nonspecialized deposit feeding, specialized deposit feeding, predation, parasitism, chemosymbiosis, farming and trapping, autotrophy, and matground feeding (4, 22, 29). Suspension feeding is represented by those animals that obtain food particles from the water column. These animals are typically illustrated by permanent vertical burrows or borings. Deposit feeding includes those animals that actively ingest food particles from the sediment, including both particles within the sediment (i.e., deposit feeding *sensu strictum*) and from the sediment surface (i.e., detritus feeding). Typical trace fossils produced by deposit feeders include horizontal trails and burrows of variable complexity, including spreite and branching structures, as well as vertical to inclined burrows showing concentric infills. In turn, deposit feeding is subdivided into nonspecialized deposit feeding (i.e., animals that left simple and self-overcrossing trails) and specialized deposit feeding (i.e., those animals leaving non-overcrossing and meandering trails). Predation refers to those animals able to capture prey. In the trace fossil record, predation is mostly but not exclusively recorded by bioerosion structures, such as durophagy and drilling. Parasitism represents a feeding mechanism in which one species benefits to the detriment of the other. In the present study, parasitic activities are represented by some microborings. Chemosymbiosis involves animal endosymbiosis with chemoautotrophic bacteria. This feeding mode has been inferred for burrows with shafts or bunches with downward radiating probes. Farming involves the culturing of suitable bacteria or fungi for feeding purposes, which

can take place on large internal surfaces of burrows or chambers, whereas trapping refers to the passive capture of migrating meiofauna or other microorganisms. Although, conceptually, these are two different mechanisms, in practice, they may be difficult to differentiate on the basis of ichnologic data because both are represented by complex, regular, patterned, meandering, spiral, radiating, and network structures, collectively referred to as graphoglyptids. Autotrophy is represented by organisms capable of synthesizing their own food from inorganic substances by means of light or chemical energy. From an ichnologic standpoint, autotrophy is illustrated mostly by microborings produced by algae and cyanobacteria. The category of “matground feeding” includes various types ascribed to exploitation of microbial mats. These types are mat grazing (organisms browsing through the microbial mat), undermat mining (organisms constructing tunnels below the active mat), mat scratching (organisms rasping on the microbial mats), and mat digestion (organisms feeding from direct external digestion of the mat). The latter illustrates a variety of osmotrophy, which refers to absorption of dissolved nutrients directly from seawater and (or) from the underlying substrate across the lower surface of organisms. For the sake of simplicity, all these interactions have been plotted as a single category in the diagrams but have been counted separately for the analysis. Matground feeding has been inferred for a wide spectrum of Ediacaran organisms.

Ecosystem engineering is categorized on the basis of three parameters: (i) tiering, (ii) mode of sediment interaction, and (iii) mode of sediment modification (22, 29). Ecosystem engineering is summarized in table S1. Tiering categories have been characterized above. Organisms may interact with sediment by intrusion, compression, backfilling, and excavation (22, 29). Intrusion comprises displacement of sediment as the animal moves through, but the sediment closes up behind it. Compression consists of movement and compaction of sediment around the animal as it passes through. Backfilling is the process of active backward movement of sediment around or through the animal. Excavation involves active loosening and bulk transport of sediment from one location to another. These four categories have been used to classify bioturbation ichnogenera with respect to styles of animal-substrate interaction (table S1). In hard substrates, animals bioerode by mechanical excavation, chemical dissolution, or a combination of both mechanisms. Accordingly, bioerosion ichnogenera have been classified on the basis of these categories (table S1).

Modes of sediment modification can be evaluated by categorizing bioturbation structures in a way that reflects how animals affect and rework sediment. This scheme has been adapted from the conceptual framework of marine benthic ecology (12). The categories of modes of sediment modification are biodiffusors, gallery biodiffusors, conveyors, and regenerators (22, 29). Biodiffusors are those animals responsible for the movement of sediment particles over short distances. In this case, particle transport is analogous to molecular or eddy diffusion. Gallery biodiffusors are animals responsible for the rapid redistribution of sediment particles from one part of the sediment profile to another. These organisms typically construct dwelling burrows, resulting in diffusive local biomixing of particles. Conveyors are those vertically oriented organisms that actively transport sediment particles across and within tiers. Both upward conveyors (i.e., organisms feeding head down within the sediment) and downward conveyors (i.e., organisms feeding head up within the sediment) are included. Particle movement is nonlocal, beyond that capable

by only biodiffusion. Regenerators are animals that actively move sediment from below to the surface, where it may be transported away by currents. These burrows are continuously maintained by the producer. In many instances, individual ichnogenera are ascribed to one of these categories on the basis of the identification of modern analogs (table S1). In other cases, where modern analogs are not known, classification becomes more speculative. Unfortunately, a similar scheme of ecosystem engineering that can be used for bioerosion structures is not available at this time.

The Ecosystem Engineering Index (EEI) has been developed as a way of assessing the impact that a particular trace fossil might have on its environment (30). The EEI is defined on the basis of a simple sum of the tier, functional group of the bioturbator, and the likelihood of bioirrigation. We choose not to include this index in its present formulation because it conflates several things across the measures, most notably in relation to tiering, because certain functional groups, such as epifaunal bioturbators and surficial modifiers, are, by definition, already spatially restricted in their distribution within the sediment profile. The likelihood of bioirrigation is a useful additional parameter but is somewhat interpretative, and animals may perform different activities within their burrows, depending upon the environmental conditions.

Dataset analysis

Observed patterns of ichnodiversity through the rock record may be affected by the availability of rock and intensity of sampling for different time intervals. These relations may conform to (i) the bias model, whereby observed diversity is driven by the number of formations; (ii) the redundancy model, whereby diversity drives the number of discovered formations; or (iii) a combination of these models. Potential biases affecting raw paleodiversity data are often attempted to be corrected by using (i) standardization on the basis of subsampling of large datasets or (ii) the residual modeling technique. The latter is frequently used when the data are too limited for standardization by subsampling, although the underlying methodology and use of the number of fossiliferous or clade-bearing formations as sampling proxies have been critiqued (31). Here, we do not attempt to correct the raw ichnodiversity plots but instead evaluate whether there are statistically significant correlations between the data and the sampling proxies.

Different proxies have been used as measures of sampling intensity in the fossil record. Because data used in macroevolutionary studies are commonly harvested from the Paleobiology Dataset, these proxies are commonly the easily gleaned number of clade-bearing formations or the total number of fossiliferous formations for each particular time bin. However, such proxies have been critiqued on the basis of empirical and simulation data because the proxies are not truly independent and, instead, there is redundancy of information between formation counts and diversity data, with each time series as likely to drive the other (31). Simulations involving potential clade-bearing formations, in which units representing environments from which a clade is likely to occur, found that lithostratigraphic units constituted a better proxy because they are an a priori better measure of total sampling effort and underlying drivers such as sedimentary rock volume (31). The alternative sampling measure of rock volume has been demonstrated previously to be independent and not correlated with diversity measures (21); however, the compiled data available do not extend to the Ediacaran and do not provide data at the temporal and paleoenvironmental

scale required for this study. More recent compilations of formation counts are geographically restricted (32). Accordingly, we need to derive our own proxy for rock volume, namely, the total number of lithostratigraphic units. This compilation was achieved through a systematic evaluation of the literature on Ediacaran and lower Paleozoic stratigraphy, summarizing information of the different sedimentary basins (table S2). To provide a better temporal and paleoenvironmental resolution, lower-rank units (e.g., members) were considered wherever possible. This is equivalent to the potential clade-bearing formations used in previous simulations, because it includes lithostratigraphic units where, from an environmental perspective, a particular fossil group could be present during a certain time interval, but that group has not been recovered and so is more akin to ecological sampling practices.

To evaluate the quality of our dataset and confidence that we could have in the observed patterns through time, we tested the null hypotheses that observed ichnodiversity was uncorrelated with the following variables: (i) the number of trace fossil assemblages, (ii) the number of ichnofossil-bearing units, and (iii) the total number of lithostratigraphic units. The alternative hypotheses were that these variables were correlated and so we could be confident that the observed patterns in ichnodiversity reflected a biological signal and were not an artifact of sampling.

There is an expected trade-off between temporal resolution and the overall reliability of observed patterns reflecting a biological signal. From an a priori perspective of trying to maximize the macroevolutionary information, the Ediacaran was subdivided into Vendian and Nama following previous schemes (18) to account for possible changes in ecospace utilization and ecosystem engineering. This temporal resolution is consistent with ongoing work attempting to subdivide the Ediacaran. The Fortunian and Cambrian Stage 2 were also collated as discrete units to detect potential changes that otherwise would have been overlooked at the series level. The correlations between observed ichnodiversity and sampling measures were compared between this temporally higher resolution dataset and the series level dataset to test for any artifacts and dampening effects related to trade-offs between temporal resolution and accuracy of observed patterns.

Statistical analysis

The hypotheses that observed ichnodiversity correlates with (i) the number of trace fossil assemblages, (ii) the number of ichnofossil-bearing units, and (iii) the total number of lithostratigraphic units were tested using Spearman's rank-order correlation (table S3). This test determines the probability that two independent variables are uncorrelated. The nonparametric Spearman's rank-order correlation was selected because of the small number of pairs of independent variables being considered, and it does not assume that data are normally distributed and so is not sensitive to outliers of time bins with larger or small numbers of known lithostratigraphic units or ichnogenera. All statistical tests were conducted using PAST [version 4.03 for Mac; (33)].

There is a trade-off between the temporal resolution and the reliability of observed patterns that reflect a biological signal over sampling efforts. This trade-off has been demonstrated before in the analysis of the trace fossil record for the colonization of land (21). For the Ediacaran to Ordovician marine trace fossil record, however, there are a priori reasons to wish to split the Ediacaran into the Nama and Vendian (18) and to split the Terreneuvian

series into the Fortunian Stage and Cambrian Stage 2 in an attempt to avoid missing information in a critical interval. However, when the Ediacaran and Terreneuvian are split into stages, more of the environmental subdivisions have significant correlations between global ichnodiversity and the total number of lithostratigraphic units in comparison to when the stages are pooled into the series (table S3). Only for siliciclastic marginal marine, siliciclastic supratidal to intertidal, and siliciclastic shelf environments is global ichnodiversity not correlated with the total number of lithostratigraphic units when data are split into Nama, Vendian, Fortunian, and Cambrian Stage 2 time bins. In contrast, when data are analyzed at the series level, the correlations between global ichnodiversity and the total number of lithostratigraphic units are nonsignificant for siliciclastic marginal marine, siliciclastic intertidal to supratidal, siliciclastic offshore, and siliciclastic shelf environments. This lack of correlations indicates that any effects of sampling intensity on global ichnodiversity trajectories are minimized when data are pooled into geological series, and thus, we analyze and present our results at this temporal resolution. Accordingly, we have used bins at the series level, with the exception of Ediacaran, which is considered as a single bin.

Comparison of correlations between different diversity measures and different sampling proxies for each environment reveals a greater number of significant correlations when using the number of trace fossil-bearing lithostratigraphic units or number of trace fossil assemblages compared to the total number of lithostratigraphic units (tables S2 and S3). This supports the argument that proxies for sampling intensity derived from counts of ichnofossiliferous units are not independent of diversity measures and there will be information redundancy between them. The total number of ichnofossiliferous and non-ichnofossiliferous lithostratigraphic units takes into account relevant units from the same environment that could potentially bear trace fossils (but do not bear them) and so gives a better indicator of available sedimentary rock volume.

No significant correlations between any of the diversity metrics and the total number of lithostratigraphic units were obtained for siliciclastic marginal marine, siliciclastic supratidal to intertidal, siliciclastic offshore, and siliciclastic shelf environments (table S3). Therefore, the observed patterns in the raw data reflect a biotic signal rather than sampling artifacts. However, there is a significant correlation between global ichnodiversity and the total number of lithostratigraphic units for siliciclastic foreshore, shoreface, and subtidal environments ($P = 0.0382$). The other diversity metrics for this environmental subdivision do not have significant correlations with the total number of lithostratigraphic units (table S3). All diversity metrics apart from average alpha ichnodiversity are statistically significantly correlated with the total number of lithostratigraphic units for siliciclastic slope and basin plain environments and carbonate environments (table S3). Therefore, the raw data for these environments cannot be read literally, and they are excluded from further analysis herein.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/33/eabb0618/DC1>

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