

Early bursts of diversification defined the faunal colonization of land

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Abstract

The colonization of land was one of the major events in Earth history, leading to the expansion of life and laying the foundations for the modern biosphere. We examined trace fossils, the record of the activities of past life, to understand how animals diversify both behaviourally and ecologically when colonizing new habitats. The faunal invasion of land was preceded by excursions of benthic animals into very shallow, marginal-marine environments during the latest Ediacaran Period and culminated in widespread colonization of non-marine niches by the end of the Carboniferous Period. Trace-fossil evidence for the colonization of new environments shows repeated early-burst patterns of maximal ichnodisparity (the degree of difference among basic trace-fossil architectural designs), ecospace occupation, and level of ecosystem engineering prior to maximal ichnodiversity. Similarities across different environments in the types of behavioural programmes employed (as represented by different trace fossils), modes of life present, and the ways in which animals impacted their environments, suggest constraints on behavioural and ecological diversification. The early-burst patterns have the hallmark of novelty events. The underlying drivers of these events likely were the extrinsic limitation of available ecospace and intrinsic controls of genomic and developmental plasticity that enabled trace-maker morphological and behavioural novelty.

Introduction

The colonization of land by animals was a fundamental transition in the development of the biosphere¹. The initial colonization of each new continental environment during the Palaeozoic may be viewed as a series of repeated experiments that allowed the morphological, behavioural, and ecological penetration of ecospace during successive evolutionary radiations. Preceding faunal colonization, a diverse continental microbiota of prokaryotes and eukaryotes existed during the Precambrian, as evidenced by molecular clocks², microbially induced sedimentary structures³, microfossils⁴⁻⁶, and various proxies⁷⁻⁹. However, such microbially-based communities were physically-passive occupants of quiescent patches within landscapes¹⁰, and later were joined during the Cambrian and Ordovician by fungi¹¹ and land plants¹², which had ecosystem engineering capabilities. Continental habitats thus were relatively well-established before their invasion by motile ecosystem engineers (i.e. animals), but debate surrounds the timing and palaeoenvironmental context of this invasion in the history of life^{13,14}. Molecular clock studies increasingly point to a Precambrian-Middle Cambrian origin for myriapods¹⁵⁻¹⁷, a Cambrian-Ordovician origin for arachnids^{15,16}, and an Ordovician origin for hexapods^{15,16,18}, and argue for initial colonization of land by these groups during the Cambrian (myriapods), Ordovician-Silurian (arachnids) and Ordovician (hexapods)¹⁶. These estimates agree with the oldest known body fossils of arachnids (Silurian)¹⁶ but pre-date the oldest known terrestrial myriapods (mid Silurian)¹⁶ and hexapods (Early Devonian)¹⁸. Trace fossils (known also as ichnofossils: the burrows, trails and trackways left behind by the activities of animals) provide a unique, but complementary, alternative record to molecular clock or body fossil data that further refines our understanding of the advent of motile life on land¹⁹⁻²². The oldest known non-marine trackways, from rocks of Middle-Late Cambrian age²⁰, include those of a myriapod-like animal that are more

congruent with molecular clock estimates of terrestrial myriapod origins. In addition to commonly pre-dating body fossils of their inferred producers, trace-fossil archives of animal behaviour: (i) record the activities of both soft- and hard-bodied organisms; (ii) provide *in situ* evidence and precise environmental contexts of animal habitats; and (iii) may represent archetypal, sediment-modifying, ecosystem engineers, altering their environment in ways that affect other organisms²³ with potential macroevolutionary consequences²⁴.

Analyses of macroevolutionary patterns during evolutionary radiations frequently focus on the relationship through time between disparity (range of morphological variety) and taxonomic diversity (number of taxa, typically assessed at the family or genus level). Most studies reveal a “disparity first” pattern, whereby an early burst in morphological diversification produces maximal disparity early within a lineage²⁵⁻²⁷, followed by a subsequent and pronounced rise in taxonomic diversity after a significant time interval. This contrasts with a null pattern wherein disparity and diversity are approximately coupled, and a “diversity first” pattern where disparity initially is constrained and exceeded by taxonomic diversification²⁵⁻²⁷. Here, we present a new framework for macroevolutionary analysis of behavioural diversification²⁸, ecospace occupation, and ecosystem engineering²⁹. This new approach allows: (i) analysis of the timings of colonization of different continental environments; (ii) identification of commonalities and differences in patterns of behavioural and ecological diversification across continental environments during the colonization of land; and (iii) elucidation of causative macroevolutionary processes. Behaviour is just as integral to organismal phenotype as is morphology²³. Consequently, analyses of disparity and diversity can be extended to behaviour through the concepts of ichnodisparity and ichnodiversity. Ichnodiversity is a measure of ichnotaxonomic richness. Ichnotaxa are biogenic sedimentary structures formally classified on the basis of their morphology as a reflection of tracemaker behaviour. By contrast, ichnodisparity is a measure of the variability

of trace-fossil morphological plans, quantified as the number of architectural designs, such as simple horizontal trails or vertical unbranched burrows²⁸. Architectural designs reflect broad behavioural programmes, wherein variations are represented by a variety of ichnotaxa. The amount of occupied ecospace is quantified as the number of modes of life, and the amount of ecosystem engineering is quantified as the number of ichnological impacts upon a sedimentary stratum. These concepts are intended to foster a commonality of language and analysis between ichnologists and benthic ecologists. The results below are based on an exhaustive search of published accounts of Palaeozoic trace fossils worldwide. Caveats regarding strengths and limitations of trace-fossil analysis are discussed in the Methods and Results sections.

Results

Continental and shallow marginal-marine trace-fossil record. Subaqueous coastal (Fig. 1), transitional coastal (Fig. 2), and transitional alluvial environments (Fig. 3) have the most extensive and complete Palaeozoic trace-fossil records of the environments considered in this study. The trace-fossil records for other environments are incomplete and trends should be treated cautiously (Supplementary Figs 1-6). Data from at least one geological period are lacking for subaerial coastal, subaqueous alluvial, aeolian, and ephemeral lacustrine environments. Subaqueous lacustrine and marginal lacustrine environments are represented only by a short interval of occupation within the temporal scope of this study.

Analyses of potential sampling biases demonstrate no significant correlations between observed ichnodiversity and the independent sampling measure of terrestrial clastic rock volume when data are considered at both sub-period and period levels for subaqueous coastal, transitional coastal, and transitional alluvial environments (Supplementary Table 1).

There are statistically significant correlations (Bonferroni corrected α' -level for multiple comparisons = 0.0167) between observed ichnodiversity and the numbers of trace-fossil-bearing formations and/or the numbers of trace-fossil assemblages when the data are pooled by geological sub-period, but not when data are pooled by geological period (Supplementary Table 1). At the sub-period level, low observed values for ichnodiversity are associated with low numbers of trace-fossil bearing formations and trace-fossil assemblages (Supplementary Fig. 7). This relationship may reflect observed ichnodiversity being driven by the number of formations (the bias model), ichnodiversity driving the number of discovered formations (the redundancy model), or a combination of these effects³⁰. There clearly is a trade-off between temporal resolution and the overall reliability of observed patterns. Ichnodiversity trajectories are strongly related to sampling intensity at the sub-period level, but this effect is dampened when data are pooled into geological periods, as is done for presentation, analysis and discussion of data in this study.

At the level of the geological period, there are no statistically significant correlations (Bonferroni corrected α' -level = 0.0167) amongst the diversity measures of ichnodiversity, ichnodisparity, ecospace occupation and ecosystem engineering versus the sampling measures of the numbers of trace-fossil bearing formations and trace-fossil assemblages (Supplementary Table 2). Rank-order correlation plots identify those geological periods with the lowest residuals from the fitted models (Supplementary Figs 8-10), and for which diversification metrics are most closely related with sampling intensity. Decreases in ichnodiversity observed for Devonian and Permian subaqueous coastal environments probably are constrained by the number of trace-fossil bearing formations. This relationship also explains the decrease in ichnodisparity for Permian subaqueous coastal environments. Increases in ichnodisparity during the Devonian and in ecosystem engineering for Cambrian transitional coastal environments probably are related to greater sampling intensity. Some

observed values may be underestimates and might be greater with comparable sampling intensity. These analyses identify limitations to the trace-fossil record of continental and shallow marginal-marine environments, but the limitations do not compromise the overall patterns.

Patterns of behavioural and ecological diversification. By the end of the geological period following initial colonization of a particular continental environment (e.g. transitional alluvial environments by the end of the Silurian), global ichnodisparity, ecospace occupation and ecosystem engineering began to reach a plateau with little subsequent numerical or compositional change. Although ichnodiversity shows greater variation (Figs 1-3, Supplementary Figs 1-6), this does not affect the overall pattern of requiring additional time to achieve an asymptote or continuation of an increase across the temporal range of this study. Variation from these trends in observed ichnodiversity is attributable to sampling intensity (Supplementary Figs 7-10; Supplementary Table 2). In transitional alluvial environments, ichnodiversity follows an approximately linear increase from the Ordovician to Permian, and shows no sign of reaching an asymptote within the temporal range of this study (Fig. 3). However, the Devonian has one of the greater numbers of trace-fossil bearing formations for transitional alluvial environments, and observed ichnodiversity during the Ordovician, Silurian and Permian may be limited by the lower number of trace-fossil bearing formations (Supplementary Fig 7f). Global ichnodisparity, ecospace occupation and ecosystem engineering rose sharply from the Ediacaran to Cambrian in subaqueous and transitional coastal environments before becoming fairly constant through the rest of the Palaeozoic. This pattern is similar for transitional alluvial environments, with initial colonization during the Ordovician, reaching an asymptote by the end of the Silurian.

Initial infaunal occupation was limited to shallow and semi-infaunal tiers, respectively, in subaqueous coastal and transitional coastal environments. Facultatively motile, suspension-feeding animals created horizontal to obliquely inclined burrows in subaqueous coastal environments, whereas freely motile, non-specialized deposit-feeding animals were responsible for making horizontal burrows with horizontal to vertical branches in transitional coastal environments. Each type of structure was produced by compressional forces and acted as gallery biodiffusive structures (Figs 1,2), in which sediment particles may be rapidly redistributed from one part of the sediment profile to another. Transitional alluvial environments initially were colonized by freely motile, non-specialized deposit-feeding animals and possible predators occupying the surficial tier. These colonizers left trackways and scratch imprints that had minimal, compressive, biodiffusive impact upon the sediment (Fig. 3).

Occupation of the deep infaunal tiers of subaqueous coastal, transitional coastal, and transitional alluvial environments continued during the geological interval following initial colonization and were dominated by facultatively motile suspension-feeding animals and possible predators. Such infaunal organisms used compression of the sediment to create stable, vertical, unbranched and single U- and Y-shaped burrows that acted as gallery biodiffusive structures. The same types of structure also were produced at this time and subsequently further expanded into the shallow and intermediate-level infaunal tiers. In transitional coastal and transitional alluvial environments, the deep infaunal tier also was colonized by freely motile, non-specialized deposit-feeding animals. In transitional coastal environments, organisms of this tier created burrows with complexly oriented spreiten; by contrast, in transitional alluvial environments they created simple, actively filled (meniscate), horizontal to obliquely inclined structures. Both types of architectural design were produced by animals moving through the sediment by backfilling and transporting sediment in a

manner similar to a conveyor belt. With the exception of subaerial coastal environments where colonization was limited to the surficial tier (Supplementary Fig. 1), expansion to the deep infaunal tier in other environments occurred within the geological period of initial invasion (Supplementary Figs 2,3,6) or the following period (Supplementary Figs 4,5).

Modes of life increased in number for other tiers of subaqueous coastal, transitional coastal, and transitional alluvial environments in the geological period following initial colonization. Freely motile, non-specialized and specialized deposit-feeding animals and predators colonized the semi-infaunal tier. Among other activities, they were responsible for: (i) movement by backfilling and acting as sediment conveyors to produce simple horizontal trails; (ii) use of compression to produce horizontal burrows with horizontal to vertical branches that acted as gallery bioturbative structures; and (iii) excavation and regeneration of sediment from below the sediment–water interface during the production of bilobate trails and paired grooves, and bilaterally symmetrical short, scratched imprints. The process of regeneration provides sediment for transportation by physical processes. The shallow infaunal tier was colonized by freely motile, non-specialized deposit feeders and possible predators that moved by backfilling as they acted as sediment conveyors in the production of simple, actively filled, massive and meniscate, horizontal to obliquely inclined structures.

The number of ichnogenera within each architectural design for each tier remains fairly constant across the swath of geological time represented by each environmental category. However, for the surficial tier, there is a greater increase in ichnodiversity compared to ichnodisparity. This pattern is most pronounced in transitional alluvial environments (Fig. 4; Supplementary Fig. 11). Principal co-ordinates analyses show that architectural designs, modes of life, and impacts upon the sediment are remarkably consistent through time and across environments (Supplementary Fig. 12).

Discussion

The prologue to the colonization of land by animals began during the latest Ediacaran and was limited to subaqueous and transitional coastal environments. During the Cambrian, some animals, principally arthropods, were capable of making amphibious excursions into subaerial coastal environments²⁰. The first evidence of animals in fully continental settings possibly occurs during the Ordovician³¹, although this may be questionable¹⁴. These events were followed by expansion of animals, plants and fungi into subaqueous alluvial and ephemeral freshwater environments during the Silurian³². The Devonian records the first trace-fossil evidence of organisms inhabiting aeolian environments³³ and lake margins³⁴. Subaqueous environments in the centres of deep lakes were not colonized until the Carboniferous¹⁹. These data support a marine route for the colonization of land, via transitional coastal environments into subaerial coastal and transitional alluvial environments before subaqueous alluvial and ephemeral lacustrine environments were colonized, followed by aeolian and marginal lacustrine environments, and finally subaqueous lacustrine environments.

Environmental expansion was coupled with increases in several parameters. In general, ichnodisparity, the volume of occupied ecospace, and the level of ecosystem engineering reached a plateau soon after colonization of a new environment, with little subsequent change for the duration of the Palaeozoic. The trend for global ichnodiversity is more variable, taking longer to reach a plateau in many environments and also exhibiting intervals of apparently decreasing ichnodiversity. In transitional alluvial environments, ichnodiversity increases linearly from the Ordovician to Permian, whereas ichnodisparity, occupied ecospace and ecosystem engineering reached asymptotes from the Silurian to Devonian. The decoupling between ichnodiversity and ichnodisparity is exaggerated during

this interval, attributable to increasing numbers of surficial tier trackway and scratch imprint ichnogenera. This increase is in part a function of the diversification of trace-making organisms that produce trackways and scratch imprints because the morphology of these ichnogenera is strongly influenced by the anatomy of the producer. In addition, the paucity of deep-tier bioturbators may have increased the preservation potential of trackways and other trace fossils formed at the sediment surface.

There is strong trace-fossil evidence that Cambrian arthropods and mollusks had begun to adapt to marginal-marine settings. One or more lineages of annelids, nematodes and nemerteans also may have exhibited adaptation to this environment. A range of arthropods was responsible for trackways and scratch imprints, including trilobites, aglaspidids, chasmataspidids, and marellamorphs in shallow marginal-marine environments, as well as myriapod-like animals and euthycarcinoids in subaerial coastal environments. Trilobites were the most likely producers of bilobate trails and paired grooves, and bilaterally symmetrical, short, scratched impressions and burrows in marginal-marine settings³⁵. Oval imprints and trails with undulating transverse bars and furrows likely were produced by mollusks. Worm-like animals and possibly crustaceans were responsible for a variety of burrows and trails. Infaunal cnidarians likely also were present and produced vertical plug-shaped burrows in marginal-marine environments. Chordates appeared during the Ordovician, with body fossils of early fish lineages preserved in coastal settings³⁶. Possible trace-fossil evidence in the form of flattened trilobate trails, affiliated with flatworms is present in Ordovician strata³⁶. Many of the body fossils of terrestrial arthropod, fungal, and plant lineages appear initially during the latter part of the Silurian³², including the earliest representatives of at least five major groups of chelicerate and myriapodan arthropods that became prominent later in the Palaeozoic: scorpions, trigonotarbid arachnids, arthropleurids, kampecarid millipedes, and centipedes^{32,37}. Trackways likely produced by members of these arthropod groups

(*Diplichnites*, *Paleohelcura*) are known from a variety of Silurian marine littoral and terrestrial environments^{38,39}. Sister-group relationships suggest a marine route for myriapods and arachnids¹⁶, which is consistent with the oldest known trace fossils for these groups respectively occurring from Cambrian²⁰ and Silurian³⁹ transitional coastal environments. Whether hexapods colonized the land via a marine or freshwater route is dependent upon the identity of their sister group, which currently is unresolved¹⁶. Hexapods are first recorded during the Early Devonian^{18,37}. Trackways attributable to apterygote insects (*Stiaria*) have been described from Devonian alluvial and lacustrine environments^{34,40} and possibly from Silurian transitional coastal environments^{40,41}, although they may have been produced by a scorpionid⁴¹.

Microbially induced sedimentary structures occurred in association with many trace fossils in early emergent tidal-flat settings, and microbial mats could have provided a food source for the above-mentioned animals. In addition, microbial mats likely increased trace-fossil preservation potential⁴². Similarly, early land plants potentially could have provided a source of nutrients for pioneer continental metazoans in the earliest, simple, terrestrial food webs^{32,37}. The search for food and lack of competition for terrestrial organic matter may have spurred the earliest stages in the colonization of land. Another likely initial driver of terrestrialization was predator avoidance³⁷. Reproduction, particularly for establishment of mating sites, has been suggested as an alternative hypothesis²². In addition to these potential causative mechanisms, the colonization of continental environments took place during an interval of Earth history when landscapes were being fundamentally and irreversibly altered by land-plant evolution. Until the Silurian, colonization occurred among landscapes that were dominated by unconfined, braided alluvial systems. The rise of land plants expanded the variety of fluvial styles, including the first mixed sand-mud meandering rivers by the end of the Silurian^{43,44}. This increase in alluvial geomorphological and sedimentary diversity

increased the potential physical habitats for biotas through the latest Palaeozoic⁴⁵, and ecological studies of modern alluvial environments show that biodiversity increases toward more geomorphologically complex reaches of river systems⁴⁶. The increasing variety of continental landscapes is stratigraphically consistent with the first appearances of continental ichnofaunas, followed thereafter by their subsequent expansion and diversification.

Adaptive radiations *sensu stricto* correspond to portions of evolutionary radiations that involve a single clade⁴⁷. An early-burst, “disparity first” pattern is most prevalent amongst studies based on single clades of body fossils²⁵⁻²⁷. The colonization of each continental environment recorded by trace fossils occurred across independent animal lineages. Novelty events and broad diversification events are two types of evolutionary radiation that involve independent lineages, with novelty events demonstrating a “disparity first” pattern, and broad diversification events a “diversity first” pattern⁴⁷. With minor exceptions, the phyla involved in subsequent waves of colonization during the later Palaeozoic largely were the same as the founding colonists during the mid Palaeozoic. The colonization of each new continental environment therefore may be viewed broadly as a series of repeated-measures experiments through which commonalities and differences in the exploration and occupation of ecospace can be analyzed. Despite differing environmental contexts, the results of each colonization event are largely similar, characterized by initial rapid realization of maximal ichnodisparity and a later increase in ichnodiversity. This pattern conforms to an early-burst model⁴⁷. Maximal numbers of architectural designs, modes of life, and ichnological sediment impacts appear to have arisen rapidly but diachronously across continental environments, once they were colonized. Except for the first geological period of occupation, the constituent architectural designs, modes of life, and ichnological sediment impacts are remarkably similar across time and environments (Supplementary Fig. 12). The colonization of different continental environments therefore has the hallmark of “novelty

events” associated with evolutionary radiations. A similar early-burst relationship between ichnodisparity and ichnodiversity has been documented for marine softgrounds and hardgrounds, respectively, following their initial colonization during the Cambrian Explosion and Great Ordovician Biodiversification Event²⁸.

Two principal process models have been proposed to explain disparity-first diversification patterns. The first is the ecospace model, whereby the success of new forms is controlled by variation in ecological opportunities. The second is the genetic/developmental model, whereby increasing genetic/developmental constraints reduce the potential for innovation through time^{27,47}. Most studies support the ecospace model, with exploitation of new ecological opportunities following colonization of a new environment or by ecological release after a mass extinction that leads to rapidly increasing disparity⁴⁷. However, in one clade of vertebrates, disparity was found to decline throughout the Permian and Triassic and did not return to pre-extinction levels, whereas taxonomic diversity decreased at the boundary but afterwards rebounded⁴⁸. This supports the genetic/developmental hypothesis whereby the capacity of the clade to generate disparate life forms was reduced by the genetic bottleneck induced by the Permo-Triassic mass extinction⁴⁸. However, the ecospace and genetic/developmental models are not necessarily mutually exclusive⁴⁷, particularly as certain genetic abilities are required to generate varied forms to exploit and create ecological opportunities. Indeed, novelty events are enabled by the combination of extrinsic control of available ecospace and intrinsic control of sufficient genomic and developmental plasticity to allow phenotypic novelty^{26,47}. This enablement occurred through both morphology and behaviour.

Our results show that largely the same architectural designs, modes of life, and ichnological sediment impacts occur across subaqueous coastal, transitional coastal, and transitional alluvial environments (Figs 1-3; Supplementary Fig. 12). This suggests some

constraints on the behavioural and ecological roles fulfilled by independent groups of organisms within continental environments. It remains to be investigated if these are “local maxima” for the Palaeozoic and what trends occurred during the Mesozoic and Cenozoic with such events as the evolution of social insects⁴⁹ and the Mesozoic Lacustrine Revolution⁵⁰. With an evolutionary experiment that ran its course several times, a pattern emerges that is characterized by: (i) colonization of a new environment; (ii) relatively rapid infilling of available ecospace through modification of the environment by the activities of animals; (iii) diversification of new behavioural programmes expressed as new trace-fossil architectural designs; and (iv) diversification of ichnogenera within already occupied ecospace representing variation on previously established, behavioural themes.

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Methods

Material. Data (Supplementary Table 3) were obtained from compilations of marginal-marine to continental trace-fossil occurrences for the Ediacaran to Ordovician¹⁴ and Silurian to Permian⁴⁰. Analyses are restricted to biogenic sedimentary structures that resulted from behavioural interactions between animals and sediments and excludes structures produced by plants and fungi. Assignment of trace fossil occurrences to particular environmental categories was based upon information from the primary literature. Original environmental

interpretations were adjusted based on information in additional primary literature sources. Regional chronostratigraphy in the primary literature was converted to International Chronostratigraphic divisions^{14,40}. Uncertainty in temporal designations is negated by our use of analyses at the level of the geological period. Ichnotaxonomic assignments were revised where necessary in the source compilations^{14,40} with reference to monographic treatments and other substantial ichnotaxonomic works. Often, ichnotaxa are inherently long ranging and many of the ichnogenera found in the Cambrian are present throughout the rest of the Palaeozoic and extend to more recent time. Few ichnotaxa are restricted to only one geological period. Ichnotaxonomic principles have undergone a period of rationalization⁵¹⁻⁵³ and, coupled with the above patterns, the effects of differences in ichnotaxonomic practices amongst researchers are likely to be minimized. For each geological period and environmental category, global raw counts were obtained for each of the following diversification metrics: ichnodiversity, ichnodisparity, ecospace occupation, and ecosystem engineering. Ichnodiversity and ichnodisparity are quantified respectively as the numbers of ichnogenera and architectural designs. Ecospace occupation is quantified as the number of modes of life, and ecosystem engineering as the number of impacts upon the sediment.

Raw counts were used to enable identification of patterns of appearance and also potential disappearance and reappearance of behavioural strategies, modes of life, and impacts upon the sediment. Range-through data may be used to ameliorate the effects of a patchy body-fossil record because species cannot re-evolve and so must be present in between their first and last appearances. However, the trace-fossil record is a different entity in this regard. A variety of organisms can make the same ichnotaxon by performing the same behaviour, and the same organism can make different ichnotaxa by performing different behaviours. As such, ichnotaxa are generally long-ranging but there may be valid gaps in their record. If a particular ichnotaxon disappears from an environment for an interval of

time, it may reappear in younger strata if the environment is re-colonised by a producer that had sought a temporary refugium or, alternatively, the responsible behavioural programme could re-evolve by convergence or parallelism in a different organism. The use of raw counts enables the identification of a behavioural programme or mode of life that disappears from a particular environment. An example is disappearance resulting from an extinction event, followed by subsequent reappearance during the recovery interval. Consequently, keystone functions performed by organisms and resulting patterns of ecological succession may be assessed.

Potential biasing factors in the continental and shallow marginal-marine trace-fossil record. Sub-sampling⁵⁴ and residual diversity estimates^{55,56} are the two principal methods for controlling the patchiness of the fossil record when analyzing patterns of diversity through time. The sub-sampling method involves randomly drawing a pre-determined sub-sample of fossil assemblages from a pool for each time bin in order to produce a normalized diversity curve⁵⁴; whereas the residual diversity estimate method involves a comparison of observed diversity values to a null model in order to find the residuals for producing a de-trended diversity curve^{55,56}. Sub-sampling is best performed with large sample sizes, whereas the residuals method does not require a large sample size⁵⁶. As our data are sample-limited, with fewer than 10 trace-fossil bearing formations or trace-fossil assemblages for some time intervals and environments, we employed the underlying principles of the residuals method over the sub-sampling method. The algorithms developed for producing de-trended diversity curves from residuals have been questioned⁵⁷. However, the principle of testing for correlations between diversity and sampling measures and obtaining residuals of observed values from a null model is valid as a test of the quality of the fossil record. Potential sampling biases on observed diversification metrics were tested using Spearman Rank-Order

Correlation. Normality tests are unreliable for relatively small samples of observations and so the non-parametric Spearman Rank-Order Correlation was used because it does not assume that data are normally distributed. The potential sampling biases that were considered were: terrestrial clastic rock volume⁵⁸, the number of trace-fossil bearing formations, and the number of trace-fossil assemblages. The former is an independent measure of the rock record and the latter two are likely to be dependent to some degree with observed diversification metrics³⁰. More recent compilations of rock volume exist but are not used in our analysis because they are restricted geographically to North America⁵⁹ and Western Europe⁵⁵. Trade-offs between the influence of sampling biases and the temporal resolution of identified patterns were investigated by testing for rank-order correlations between each of the potential sampling biases and ichnodiversity counts for data pooled at the levels of the geological period and geological sub-period. For the sub-period analysis, when testing for correlations with the numbers of trace-fossil bearing formations and trace-fossil assemblages, the data were separated into the following time bins: Ediacaran, early Cambrian, middle-upper Cambrian, Early Ordovician, Middle Ordovician, Late Ordovician, Silurian, Early Devonian, Middle Devonian, Late Devonian, Mississippian, Pennsylvanian, Early Permian, and Late Permian. Ordovician sub-period data were pooled when testing for a correlation with terrestrial clastic rock volume in order to relate them to this dataset⁵⁸. Analyses were conducted for subaqueous coastal, transitional coastal, and transitional alluvial environments because they have the most complete trace-fossil records. There are three repeated comparisons (for the three environments) for each of the comparisons of a sampling measure and diversity index, and so we apply a Bonferroni corrected α' -level for multiple comparisons = 0.0167. Data and patterns for other environments are presented for completeness in the supplementary material (Supplementary Figs 1-6).

Analytical frameworks. We use trace fossils as a unit of measurement and incorporate them into the frameworks for macroevolutionary analysis of behavioural diversification^{28,60}, ecospace occupation, and ecosystem engineering²⁹ during evolutionary radiations. Trace fossils provide *in situ* evidence and precise environmental contexts of animals for revealing the timing, routes ashore, and initial colonization of different continental environments.

Behavioural diversification. Analysis of behavioural diversification is based upon comparisons of ichnodiversity and ichnodisparity^{28,60}. Ichnodiversity is a measure of ichnotaxonomic richness. Ichnotaxa are biogenic sedimentary structures that are produced by behavioural interactions between organisms and their inhabited substrates⁵¹. They are classified on the basis of their morphology, which is the product of the anatomy of the producer, its behaviour, and the substrate⁵². A variety of organisms may produce the same ichnotaxon by performing the same behaviour; equally, the same organism may produce different ichnotaxa by performing different behaviours or by interacting with different substrates, or both⁶¹. Ichnodisparity is a measure of the variability of trace-fossil morphological plans, quantified as the number of architectural designs such as simple horizontal trails or vertical unbranched burrows^{28,60}. Architectural designs reflect broad behavioural programmes, within which there may be variations represented by different ichnotaxa. There are a variety of many-to-one relationships between ichnogenera and architectural designs.

Ecospace occupation. The amount of occupied ecospace is quantified as the number of modes of life, categorized on the basis of three parameters: (i) tiering, subdivided into surficial, semi-infaunal, shallow infaunal, intermediate infaunal, and deep infaunal tiers; (ii) motility, subdivided into motile, facultatively motile, and non-motile types; and (iii) feeding

mode, subdivided into suspension feeders, non-specialized deposit feeders, specialized deposit feeders, predators, and others. There are a variety of one-to-one, many-to-one and one-to-many relationships between ichnogenera and modes of life. In the latter case, an ichnogenus may have more than one possible tier and feeding mode. Architectural designs have one-to-one, one-to-many and many-to-one relationships with modes of life.

Tiering refers to the life-position level of an animal vertically in the sediment. For a trace fossil to form, an animal must interact with a substrate. Therefore, the realm of trace-fossil analysis largely is restricted to those organisms at or below the sediment surface. However, there are exceptions: for example, terrestrial animals such as termites may construct a structure above ground and animals may interact with substrates that are above ground, such as soil nests lodged on plants, or with mobile substrates such as logs. For the purposes of this analysis of subaqueous to subaerial habitats, tiering categories are limited to occurrences at or below the sediment surface. Surficial tier animals are those living on the sediment surface and not extending significantly upward, whereas semi-infaunal tier animals are partly infaunal and exposed to the overlying water or air^{62,63}. Trace fossils provide direct information on the life positions of animals, and so it is possible to be rather precise regarding infaunal tiering levels. The system adopted here comprises a shallow infaunal tier for depths up to 6 cm from the upper substrate surface, an intermediate infaunal tier for depths of 6 to 12 cm, and a deep infaunal tier for depths of greater than 12 cm⁶⁴⁻⁶⁶. This allows for the differentiation of an intermediate tier and a truly deep tier of infaunal animals.

Trace-fossil producing animals generally have some degree of motility, the exception being non-motile animals that leave attachment structures. Frameworks for ecospace occupation developed for body fossils have defined three major levels of motility: motile, facultatively motile and non-motile, each with two sublevels of fast and slow^{62,63}. This

analysis restricts categorization of motility to the three higher levels. Facultatively motile animals are those that are generally stationary but are capable of movement.

The mode of feeding is constrained to five categories in this analysis. Suspension feeders are those that obtain and capture food particles from the water column. Deposit feeders are those that actively ingest particles of food from a substrate. To avoid spatial segregation, the deposit-feeder category is used in a broad sense to include those organisms that obtain their food from the surface, are buried within the substrate, or feed by grazing (categories of surface deposit feeding, mining, and grazing^{62,63}). Nevertheless, deposit feeders are categorized on the basis of trace-fossil morphology into non-specialized deposit feeders with non-patterned and overcrossing trails, and specialized and systematic deposit feeders with patch exploration and non-overcrossing locomotory motifs. Predators are those trace-makers inferred to have been able to capture prey. The final category of 'other' includes chemosymbiosis as suggested for *Chondrites*; as well as farming activities as exemplified by complex, regular, patterned, meandering, spiral, radiating and network trace fossils known as graphoglyptids.

Ecosystem engineering. The amount of ecosystem engineering is quantified as the number of impacts on a sedimentary stratum, based on three parameters: tiering (as above); the mechanisms by which organisms interact with the sediment (intrusion, compression, backfilling, and excavation); and the basic modes by which production of a trace fossil modifies the sediment (biodiffusion, gallery biodiffusion, conveyors, and regenerators). There are a variety of one-to-one, many-to-one and one-to-many relationships between ichnogenera and the impacts upon a sedimentary stratum. In the latter case, an ichnogenus may have more than one possible tier. Architectural designs may have one-to-one, one-to-many and many-to-one relationships with the impacts upon a sedimentary stratum. Modes of

life may have one-to-one, many-to-one and one-to-many relationships with impacts upon a sedimentary stratum.

Animals may interact with a substrate by four principal means: intrusion, compression, backfilling, and excavation^{61,67}. Intrusion involves displacement of sediment as the animal moves through, resulting in the modified sediment closing-up behind the motile organism. Compression involves the movement and compaction of sediment around the animal as it passes through. Backfilling involves the active backward passage of sediment either around or through the animal. Excavation consists of the active loosening and transport of sediment from one location to another^{61,67}.

Categorization of the modes in which production of a trace fossil modifies the sediment used in this analysis are borrowed and adapted from concepts developed by marine benthic ecologists⁶⁸⁻⁷⁰. As well as being well suited for this purpose, this approach fosters commonality of language between ichnologists and benthic ecologists. In this analysis, consideration of modes of sediment modification is limited to biodiffusion, gallery biodiffusion, conveyors, and regenerators⁶⁸⁻⁷⁰. Biodiffusion is the movement of sediment particles over short distances, whereas gallery biodiffusion involves the rapid redistribution of sediment particles from one part of the sediment profile to another⁶⁸⁻⁷⁰. Upward and downward conveyors^{68,70} are subsumed within the simpler concept of conveyors, with animals also able to convey sediment laterally. This category refers to animals that actively transport sediment particles across and within tiers. Regenerators are animals that actively move sediment to the surface from below, where it may be transported away by physical sedimentary processes such as currents^{68,70}. Categories of epifaunal bioturbators and surficial modifiers⁷⁰ are omitted because of their spatial constraints, and are covered potentially by any of the other four means of sediment reworking in the epifaunal and semi-infaunal tier. Sediment reworking categories relate to movement of particles within fluids, and so are

applicable to scenarios where the ambient medium is water or air. There are constraints on what is possible in terms of ecosystem engineering. Certain methods of sediment modification and interactions with the sediment tend to go together, such as excavation and regeneration, whereas others are unlikely to go together, such as backfilling and gallery biodiffusion.

Environmental framework. Three principal environmental settings were considered in this analysis: (i) coastal, (ii) alluvial, and (iii) lacustrine. Each of these categories may be further subdivided in order to reflect an environmental or ecological gradient from those that are: (a) permanently subaqueous, (b) transitional between subaqueous and subaerial within a confined stratigraphic interval, or (c) subaerially exposed¹⁴. This generates both a seaward-to-landward gradient and an additional gradient based upon the availability of water.

The three categories included within coastal settings of subaqueous, transitional and subaerial can be understood as reflecting an environmental gradient along a coastal plain. The first two categories reflect for the most part the activity of brackish-water faunas. Fjord areas are affected by strong freshwater discharge, whereas tidal flats from the innermost zones of estuarine systems formed between the maximum landward limit of tidal influence and the maximum landward limit of the marine saline wedge. Both therefore represent a departure from typical marginal-marine conditions because they host freshwater faunas^{71,72}. The subaerial category reflects the activity of terrestrial biotas. The three categories included within alluvial settings (subaqueous, transitional, subaerial) also illustrate a gradient from active channels to riparian overbank settings and ultimately zones affected by aeolian processes. This is more an ecological gradient than an environmental gradient because aeolian depositional systems are not necessarily associated with riverine systems. The subaqueous category reflects the activity of freshwater biotas, while the transitional one

accommodates the work of freshwater to terrestrial faunas. The subaerial category reflects the work of fully terrestrial animals. The three categories included within lacustrine settings (subaqueous, marginal, ephemeral) illustrate an ecological gradient, from fully subaqueous settings to lake margins affected by a fluctuating water table and ultimately to ephemeral water bodies that experienced longer periods of subaerial exposure. While the first two categories reflect adjacent environments within a depositional system, the latter typically illustrates arid to semi-arid conditions that occur in the context of aeolian or ephemeral fluvial systems.

Ordination of behavioural and ecological diversification. The constituent components of ichnodisparity, ecospace occupation, and ecosystem engineering that occur through time intervals of occupation of subaqueous coastal, transitional coastal, and transitional alluvial environments were investigated using principal co-ordinate analyses. Data analyzed were separate presence-absence matrices for each of: (i) architectural designs, (ii) modes of life, and (iii) impacts upon the sediment (Supplementary Tables 4-6). The Jaccard index was used as the similarity measure due to the binary nature of the data, and because it was computed on shared occurrences.

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Data availability. All datasets generated or analysed during this study are included in this published article (and its supplementary information files).

Author contributions. N.J.M., L.A.B. and M.G.M. conceived the study. N.J.M., L.A.B., M.G.M., N.S.D., M.R.G., R.B.M. and C.C.L. contributed data to the analysis. N.J.M. performed the analysis and analysed the results. N.J.M. led the writing of the paper, with inputs from the other authors.

Conflicts of interest. The authors declare no conflicts of interest.

Figure 1 | Colonization of subaqueous coastal environments (estuaries and shallow subtidal flats) through the Ediacaran to Permian periods. (a) Ecospace occupation. (b) Ecosystem engineering. (c) Plot of changes in ichnodiversity, ichnodisparity, ecospace occupation and ecosystem engineering. Ichnodiversity and ichnodisparity are global counts of the numbers of ichnogenera and architectural designs by geological period. Ecospace occupation and ecosystem engineering are quantified, respectively, as the global number of modes of life and number of different ichnological impacts upon the sediment during each geological period. Counts are cumulative for each geological period and therefore plotted at the end of the intervals.

Figure 2 | Colonization of transitional coastal environments (coastal plains and tidal flats) through the Ediacaran to Permian periods. (a) Ecospace occupation. (b) Ecosystem engineering. (c) Plot of changes in ichnodiversity, ichnodisparity, ecospace occupation and ecosystem engineering.

Figure 3 | Colonization of transitional alluvial environments (floodplains and abandoned channels) through the Ediacaran to Permian periods. (a) Ecospace occupation. (b) Ecosystem engineering. (c) Plot of changes in ichnodiversity, ichnodisparity, ecospace occupation and ecosystem engineering.

Figure 4 | Number of global ichnogenera per global architectural design occupying different tiers through time in different environments. (a) Subaqueous coastal environments. (b) Transitional coastal environments. (c) Transitional alluvial environments.

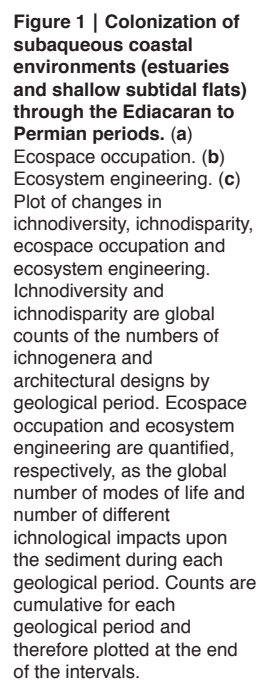


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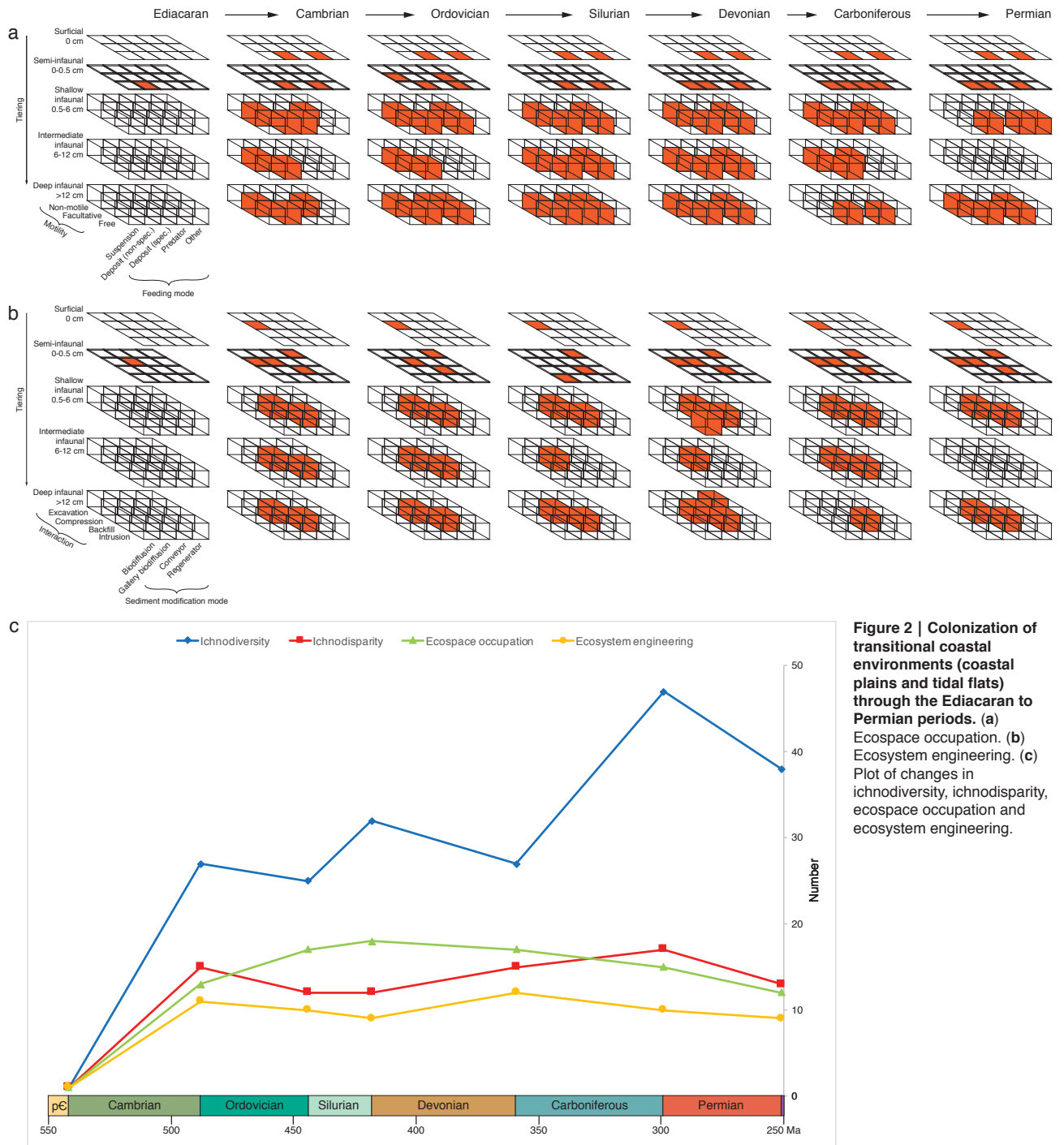


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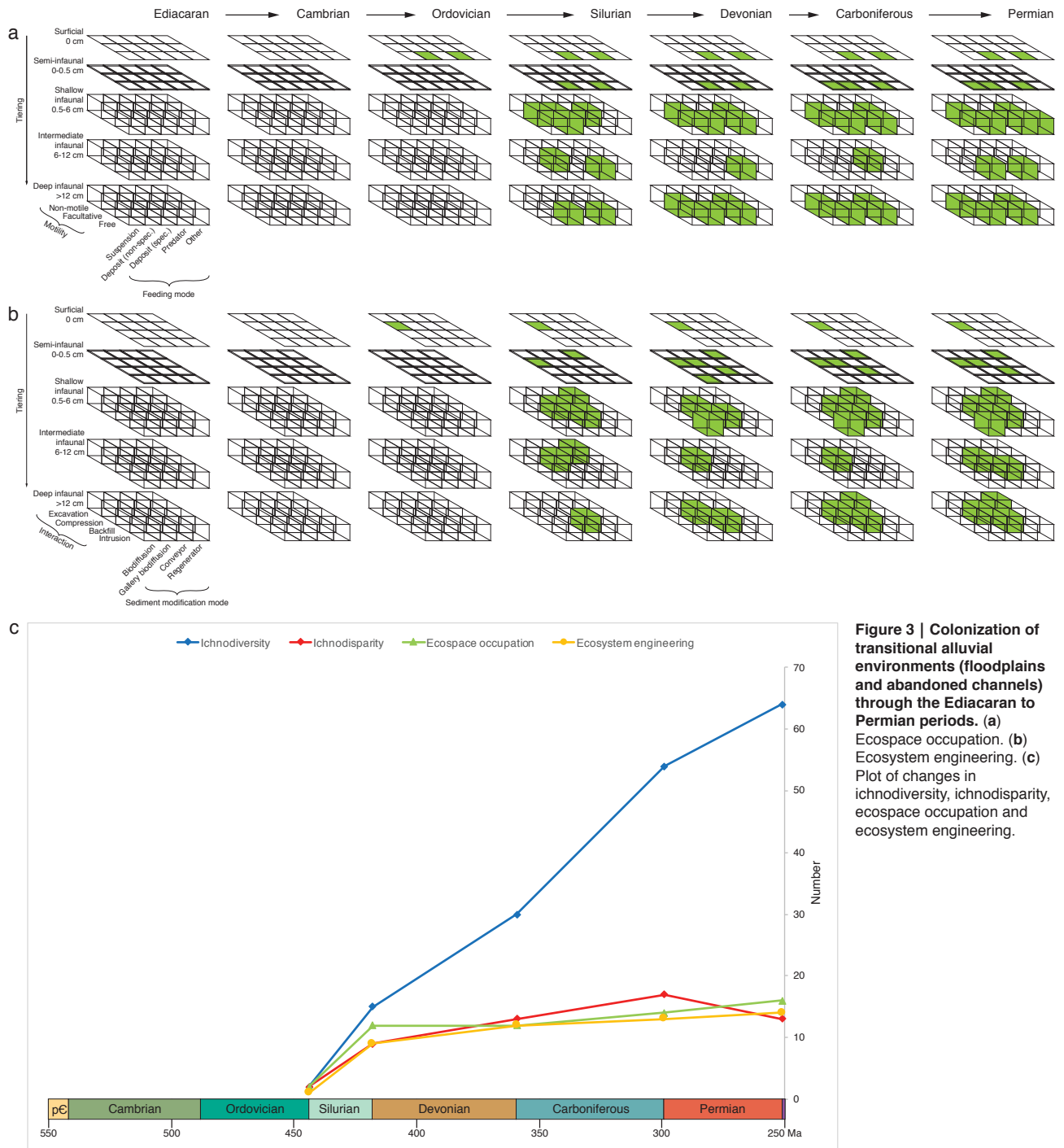


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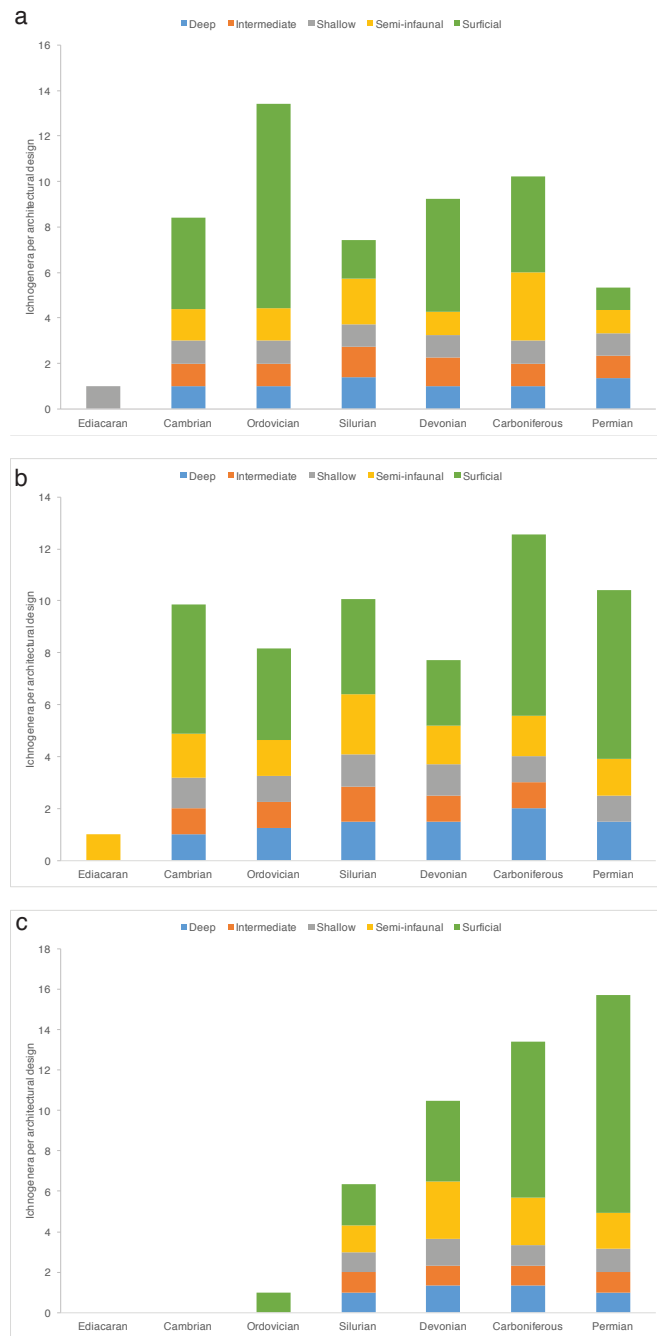


Figure 4 | Number of global ichnogenera per global architectural design occupying different tiers through time in different environments. (a) Subaqueous coastal environments. (b) Transitional coastal environments. (c) Transitional alluvial environments.