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Co-occurrence structure of late Ediacaran communities and influence of emerging ecosystem engineers

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Understanding the roles of habitat filtering, dispersal limitations and biotic interactions in shaping the organization of animal communities is a central research goal in ecology. Attempts to extend these approaches into deep time have the potential to illuminate the role of these processes over key intervals in evolutionary history. The Ediacaran marks one such interval, recording the first macroscopic benthic communities and a stepwise intensification in animal ecosystem engineering. Here, we use taxonomic co-occurrence analysis to evaluate how community structure shifted through the late Ediacaran and the role of different community assembly processes in driving these changes. We find that community structure shifted significantly throughout the Ediacaran, with the most dramatic shift occurring at the White Sea–Nama boundary (approx. 550 Ma) characterized by a split between older, more enigmatic taxonomic groups (the 'Ediacara-type' fauna) and more recognizable ('Cambrian-type') metazoans. While ecosystem engineering via bioturbation is implicated in this shift, dispersal limitations also played apart in separating biota types. We hypothesize that bioturbation acted as a local habitat filter in the late Ediacaran, selecting against genera adapted to microbial mat ecosystems. Ecosystem engineering regime shifts in the Ediacaran may thus have had a large impact on the development of subsequent metazoan communities.

1. Introduction

Community structure is an integral facet of natural diversity, reflecting the intersection between ecological and evolutionary processes that shape the organization, distribution and interrelationships between species [1–3]. This is of principal importance to ecologists, as changes in community structure can record responses to environmental change through the effects on speciation and extinction patterns [4–6], dispersal limitations [7,8], environmental filtering [9,10] and biotic interactions [11–13]. Thus, community structure can not only signal how groups of species responded in tandem to shared environmental pressures [14] but also how interactions between those species may have mediated those responses [14,15]. Paleoecology has expanded on these insights by examining how community structure changes over larger timescales with broad ecological and/or environmental shifts [16–18]. This provides a powerful opportunity to explore how communities have responded to mechanisms of community assembly operating on temporal scales much longer than are recorded in modern communities [19]. Thus, in turn, a palaeoecological view of community structure allows us to ask how ecosystems arose from emergent ecological and evolutionary processes across Earth's history [19,20].

A key and emerging question in evolutionary ecology is: how have the emergence of new ecological behaviours shaped communities in deep time [21–23]? In this context, 'ecosystem engineers' [24] are of particular interest. The term 'ecosystem engineers' refers to organisms that have large impacts on resource flows (for example, by forming links between abiotic and biotic systems [25]) and thus can create, modify or destroy habitats, and exert powerful controls on the structure of communities [26,27]. On geological timescales, these effects may serve a foundational role in the creation of new ecological niches into which other species besides the engineer may evolve to exploit [25,28,29]. The Ediacaran is a pivotal interval in this regard, marking the first appearance of ecosystem engineering behaviours (for example, bioturbation; [30,31]) that continue to be a powerful influence on the structure and function of communities in the present day. The emergence of these new behaviours may have been critical for the evolution of more complex animal groups, via niche creation, species–habitat feedbacks and the appearance of new ecological interactions [25,32,33]. However, the degree to which ecosystem engineering shaped early animal evolution is still debated [33–36] and other community assembly processes—such as abiotic habitat filtering—may also have been important and even driven pulses of biotic turnover [34,37]. A closer evaluation of how different factors shaped Ediacaran community structure and evolution is therefore critical to understanding how community assembly rules may have emerged for macroscopic animal life.

The Ediacaran has been subdivided into three informal chronostratigraphic 'assemblages'—the Avalon, White Sea and Nama [38–40]; figure 1. The Avalon assemblage (*ca* 574–558 Ma) is best known from deep-water continental slope deposits around Mistaken Point in Newfoundland and marks the first appearance of complex macroscopic eukaryotes in the fossil record [43]. Avalon-aged communities are overwhelmingly dominated by rangeomorphs [43], an enigmatic clade of organisms possessing modular and fractal branching, and that may represent stem-group eumetazoans [44,45]. The succeeding White Sea assemblage (*ca* 558−550 Ma) marks the apex of Ediacaran diversity and a rise in ecological complexity [46]. Patchy resource distribution [47], competing grazing behaviours [47] (including the first weakly bioturbating animals [21]) and the evolution of new suspension feeding modes [48–50] may have contributed to this diversification through emergent niche partitioning [51]. Although several of these White Sea taxa are now recognized as metazoans [52,53], many others still have uncertain relationships to extant animal groups, and so their position on the animal tree of life remains enigmatic [54,55]. Finally, the Nama (*ca* 550−539 Ma) is the youngest Ediacaran assemblage and witnesses a decline in macrofaunal diversity, with rangeomorphs and erniettomorphs being the principal survivors from the White Sea [30,33,39,51]. The Nama assemblage also records a proliferation of tubular organisms [56,57], a diversification in bilaterian trace fossils [21,23,58], the appearance of metazoan biomineralization (and the first animals in reef communities; see [59,60]) and the first evidence for macroscopic predation [61,62]. This transition marks a fundamental shift to communities with a much higher proportion of metazoan groups associated with the Cambrian [51,63,64] and increasingly intense ecosystem engineering behaviours [58,60].

The Avalon–White Sea–Nama transition thus records a generalizable pattern of biotic turnover and ecological change. Relatively simple organisms possessing an (apparently) limited suite of ecologies and biotic interactions [65,66] are sequentially replaced by taxa with more energy-intensive behaviours, a wider diversity of feeding modes and a broader array of potential interactions, coinciding with a marked drop in the diversity of 'Ediacaran biota' and their eventual disappearance at the Ediacaran–Cambrian boundary [32,33,40,64]. Recent work has thus primarily focused on what led to the extinction of the Ediacaran biota, with a variety of biotic and abiotic drivers proposed [30,34,37,64,67,68]. For example, among biotic drivers it has been suggested that the rise of bioturbation may have contributed to the extinction of the 'Ediacaran biota' through changing the rheology of the sediment substrate and/or interfering with feeding mechanisms possessed by Ediacaran groups [23,32]. Other studies have suggested that a proliferation in macroscopic algae may have facilitated the evolution of more active metazoans through increased oxygenation and nutrients [69,70]. Among abiotic drivers, pulses of anoxia may have caused the extinction of some groups at the White Sea–Nama transition [37,67,71] and a sustained episode of rift-related volcanism has been hypothesized as a driver of extinction immediately prior to base of the Cambrian [72]. However, despite the wealth of new data and debate surrounding drivers of the Ediacaran–Cambrian transition [33,73], directly testing the influence of multiple factors simultaneously at broad spatial scales has proven difficult [34,36,47,74]. Thus, evaluating whether and how communities were structured by ecosystem engineering behaviours, ecological interactions and dispersal modes across major environmental fluctuations can provide more insight into the processes that potentially helped drive the emergence of modern-looking and animal-dominated marine biospheres.

Previous work examined community structure across the whole Ediacaran using co-occurrence analyses [36]. Co-occurrence quantifies the degree to which taxa form aggregated pairs (more likely to occur together than by chance), segregated pairs (less likely to occur together than by chance) or random pairs. As co-occurrence patterns are shaped by biotic interactions, dispersal limitations, habitat filtering, speciation and extinction [1,75,76], changes in the co-occurrence patterns of an assemblage can reflect shifts in underlying community structure and the factors influencing it [19,76]. Aggregations may result from mutualism and facilitation, a lack of dispersal barriers and shared habitat preferences. Conversely, segregations may result from competition, the presence of dispersal barriers or limitations (i.e. leading to non-overlapping geographic ranges) and disparate habitat preferences. Eden *et al*. [36] found that, in addition to regional metacommunity specialization, late Ediacaran community composition varied significantly with depth. Here we build on their analyses by quantifying the co-occurrence structure of ecological communities within the Avalon, White Sea and Nama using a more sensitive evaluation of co-occurrence and testing the importance of four potential drivers of these patterns: dispersal limitations, habitat filtering by depth, facilitation by algae and ecosystem engineering via bioturbation [27,77–79]. The results of this analysis potentially shed new light on the role of ecological processes in driving biotic change over evolutionary timescales and during a crucial interval in the early evolution of the first macrofaunal communities.

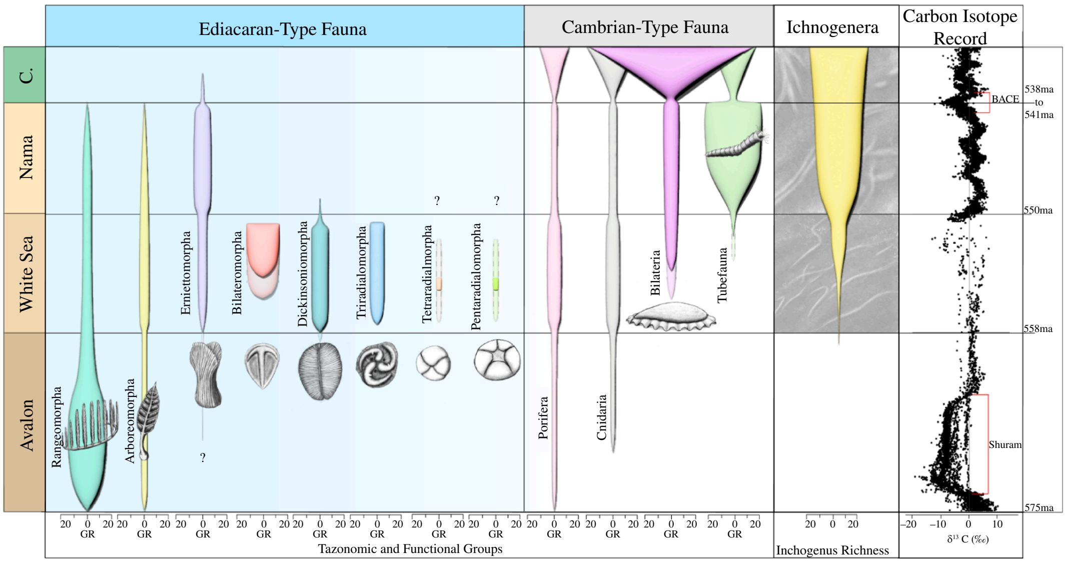

Figure 1. Relative generic richness (GR) of Ediacaran taxonomic groups over time, split between members of the Ediacaran-type and Cambrian-type biota. The Ediacaran–Cambrian boundary is included to highlight general patterns of diversification and extinction between biotas at the end of the Ediacaran. Also included is the abundance of ichnogenera through the Ediacaran and into the early Cambrian, as well as a carbon isotope curve (assembled from Yang *et al*. [41] and Bowyer *et al*. [42]) with major carbon isotope excursions (Shuram and Basal Cambrian carbon isotope excursion (BACE)) indicated. These excursions may signal major environmental shifts and correlate to the initial diversification of the Ediacaran biota (Shuram) and end-Ediacaran extinction (BACE; [41,42]). Modified from Darroch *et al*. [33].

2. Methods

(a) Data

We downloaded initial global genus-level macrofossil presence/absence data for the Ediacaran from the Paleobiology Database [80], selecting all occurrences between 575 and 538 Ma. We supplemented this dataset with an equivalent number of additional fossil occurrences from the recent primary literature (electronic supplementary material, DataSet). We manually reviewed and updated the taxonomic identification of each genus where justified by the latest consensus. We reviewed the geochronology of each collection and formation, allowing us to assign it to an assemblage zone (i.e. Avalon, White Sea or Nama) and confirm Ediacaran age. We also corrected missing or mistaken latitude and longitude data and recalculated estimated palaeo latitude and longitude using Wright *et al*. [81]'s continental reconstruction models, using the middle date of each assemblage zone. Collections with uncertain assemblage zones were excluded from analyses. We also removed algae genera from the occurrence dataset while recording their presence as a binary (1/0) variable for each collection, allowing us to test the effects that the presence of algae might have on communities (e.g. [69]). We also removed microfossil occurrences because these require different sampling techniques from macrofossils and they are reported only infrequently; retaining them might create spurious segregations between fossil types.

We reviewed the palaeoenvironment of each collection from the interpretations or sedimentological descriptions for host strata reported in primary literature. Collections were identified as either being shallow or deep water, following the classifications of Mitchell *et al*. [66] and Boag *et al*. ([39]; i.e. as shore-shelf and slope-basin assignments, respectively). To test whether bioturbation and algae may have contributed to habitat filtering or facilitated the co-occurrence of Ediacaran fauna, we scored each locality for whether bioturbation was present (1) or absent (0), and whether macroscopic algae (eg. *Doushantuophyton*) was present (1) or absent (0). To accommodate monographic effects [82] and other issues related to the geographic concentration of easily sampled localities repeating the same biotas, we lumped collections from the same formation and member that are within a 5 km radius of each other. Sites with fewer than three genera were excluded from our analyses to conserve statistical power and assess relatively complete communities for Ediacaran fauna. We also excluded 'singleton' genera because co-occurrence cannot be meaningfully assessed for single-occurrence taxa. These steps resulted in 17 localities for the Avalon, 32 for the White Sea and 35 for the Nama.

To examine the macroecological and evolutionary dynamics of this interval, we subdivide macrofossil occurrences into 'Ediacaran-type' or 'Cambrian-type'. With this, we attempt to separate morphogroups (sometimes clades [45]) that are thought to have become extinct at, or prior to, the base of the Cambrian (and thus have left no direct descendants in the post-Cambrian Phanerozoic) from more recognizable fossil groups that persist and diversify in the early Cambrian [32,40,51,73]. Subdividing taxa this way has a long history, although what this division actually represents—biologically and evolutionarily—has been in a state of flux since the 1970s. The bulk of soft-bodied Ediacaran macrofossils, commonly referred to as the 'Ediacaran biota', were at one stage considered non-metazoan [83]. However, although many among them are still enigmatic [55], recent work is increasingly showing that most (if not all) Ediacaran biota represent members of a polyphyletic grouping of stem-group metazoans or eumetazoans that share several ecological and taphonomic characteristics [45,53,84]. This has led recent reviews [33] to frame putative late Ediacaran extinction events in terms of competition between stem- and crown-group animals.

Rather than hinge our assignment of 'Ediacaran-type' or 'Cambrian-type' strictly on phylogenetic arguments (which are contentious for most of the taxa treated in this study), we instead use these terms in a broader context of evolutionary ecology.

For example, we use the term ‘Ediacara-type’ to refer to soft-bodied macrofossils that are thought to be—broadly—restricted to matground ecosystems, which disappear at or before the end of the Ediacaran and do not seem to possess close evolutionary links to fossil groups that radiate in the Cambrian. We use the term ‘Cambrian-type’ to refer to macrofossils (soft-bodied or mineralized) that belong to groups that cross the Ediacaran–Cambrian boundary, and that possess clearer links to extant metazoan phyla and their presumed ecological niches. Assignment to either ‘Ediacaran-type’ or ‘Cambrian-type’ was done with reference to the most recent papers and/or taxonomist consensus. For example, taxa assigned as ‘Cambrian-type’ include *Kimberella* (which is widely thought to be an early mollusc [52] and which moreover has recently been shown to persist beyond the White Sea [85]), *Cloudina* and other cloudinids (which are recognized as metazoans and that further diversify in the Cambrian [57,86]) and *Namacalathus* (a lophotrochozoan [87]). Taxa assigned as ‘Ediacara-type’ include groups such as the Rangeomorpha and Erniettomorpha (which, although likely metazoans [45], are also thought to represent once-successful clades that go extinct at, or shortly after the Cambrian boundary [33]) and the Dickinsoniomorpha, Triradialomorpha and Pentaradialomorpha (similarly, probable metazoan clades thought to be adapted to matgrounds [50], and that disappear in the last *ca* 10 million years of the Ediacaran [33]). A full list of taxa treated in this analysis, along with their assignments (with references), is included in electronic supplementary material, table 1.

The subdivision between ‘Ediacaran’ and ‘Cambrian’ types comes close to definitions of the ‘Ediacaran biota’ versus ‘Cambrian fauna’ that have been used in older work, while incorporating the most recent data on these fossils and remaining agnostic about their status as animals. As such, classifying taxa in this way provides a heuristic model with which to explore the ecological dynamics between Ediacaran- and Cambrian-type eukaryotic faunas, specifically in whether their patterns of association (quantified via subset co-occurrence distributions) change across assemblage boundaries. However, we acknowledge that even this subdivision is not without controversy [88], and thus we also apply a series of sensitivity analyses on faunal group assignments (see electronic supplementary material, Methods & Results) designed to test how our co-occurrence patterns and following inferences are sensitive to this classification scheme.

(b) Co-occurrence analysis

For each assemblage zone, we assessed genus pair-wise co-occurrence using Fisher’s Mid-P Transformation (FETmP) of Veech’s co-occurrence probabilities [77,78]. Co-occurrence is principally concerned with whether taxon pairs form aggregated pairs (more likely to occur than by chance; FETmP > 0) or segregated pairs (less likely to occur than by chance; FETmP < 0). Calculating co-occurrence scores via FETmP provides a continuous index of co-occurrence strength rather than a significance test for aggregation or segregation. This allows finer variation in the distribution of co-occurrence scores to be evaluated, which may contain information regarding smaller shifts in community structure and the effects of larger-scale biogeographic processes, for example, that are more difficult to detect with other co-occurrence methods [27]. To account for differing sample size between assemblage zones, each was randomly subsampled 100 times by the lowest number of sites between zones (n = 17). The co-occurrence scores for each genus pair were averaged across all subsamples. We tested for significant changes in co-occurrence distributions between zones with pairwise Kolmogorov–Smirnov tests. To further identify whether changes in community structure could be attributed to changes in association patterns between faunal groups, we subset pairs according to whether they represent Cambrian-type or Ediacaran-type taxa using the definitions outlined for these groups above.

(c) Assessing environmental effects on co-occurrence

We determine the strength of our environmental factors (dispersal, water depth, presence of algae and presence of bioturbation) as predictors of co-occurrence, using the decision tree and sequential testing framework of Blois *et al*. ([79]; figure 2). Pairs were first identified as either being aggregated (FETmP > 0) or segregated (FETmP < 0). We identified strong pairs as the top and bottom quartiles of each co-occurrence distribution. For aggregated pairs, sites where both or neither genus occurred (syntopic sites) were compared across subsequent tests. For segregated pairs, sites where only one but not the other genera occurred in the pair were compared (allotopic sites). We tested for the presence of dispersal barriers between site types with a one-way Multivariate Analysis of Variance MANOVA). Palaeolongitude and latitude were treated as two elements of a response vector that allowed us to evaluate whether spatial overlap occurs between site-type group centroids—that is, whether there was significant dispersion between site types selected for aggregated and segregated pairs. For an aggregated pair, a significant difference in site group centroids means that the locations at which both genera occurred differed significantly from where neither occurred. Thus, the genera likely shared broad dispersal limitations and aggregated within the same geographic regions. For a segregated pair, a significant difference in site group centroids would indicate that sites at which one genus (but not the other) occurred were separated in space from where the other genus occurred. That is, the pair was likely segregated by a broadly ranging dispersal barrier that neither genus could cross (for example, an open ocean). To test the influence of selected environmental factors (e.g. the presence of bioturbation and the presence of algae) on co-occurrence, we used the χ^2 statistic to test for significant differences in the chosen variable between site types for aggregated and segregated pairs. For aggregated pairs, a significant difference in the chosen environmental factor indicates that the genera are grouped by shared habitat preference (for or against the chosen variable). For segregated pairs, a significant difference in the presence of algae or bioturbation signifies that the factor likely structured that segregation by contrasting habitat preference.

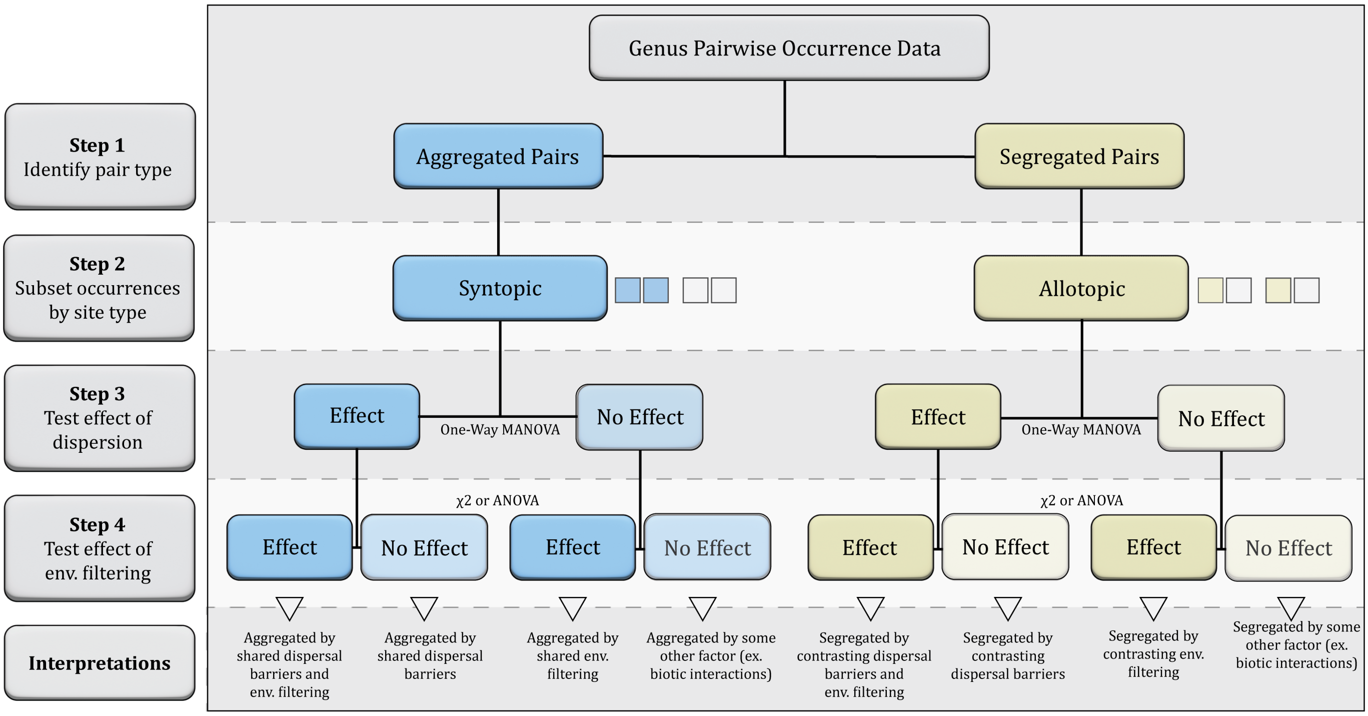

Figure 2. Decision tree framework from Blois *et al*. [79] describing the decision-making flow to evaluating the effect of different environmental factors and dispersal limitations on co-occurrence patterns. Syntopic sites are those where both genera occur or neither genus occurs. Allotopic sites are those where one genus in the pair occurs and not the other. The boxes next to the allotopic and syntopic cells visualize these definitions. Cell colours (yellow, blue) reflect whether a pair is aggregated or segregated, respectively, with lighter shades indicating test outcomes that found no significant effect of environmental factors or dispersal limitations on co-occurrence. env., environmental.

3. Results

(a) Co-occurrence

There are significant shifts in co-occurrence distributions between all three assemblages (figure 3*a*; Kolmogorov–Smirnov Tests: *p* value for AV–WS = 0.0165, *p* value for WS–NM = 7.94×10^{-11}). However, the shift between the Avalon and White Sea is subtler than between the White Sea and Nama. Global co-occurrence structure in both the Avalon and White Sea is characterized by a higher proportion of aggregated pairs to segregated pairs (0.65 in the Avalon and 0.68 in the White Sea), with no significant difference between these proportions (*t*-test: $p = 0.1956$). Nonetheless, these distributions differ in their shapes and range of occurrence values, with a decline in the maximum strength of segregated pairs observed at the White Sea from the Avalon (figure 3). The distribution shift at the White Sea to Nama is also driven by a dramatic decline in the proportion of aggregated pairs and an increase in the proportion of segregations (both strong and weak). This shift can be attributed to a change in the spatial relationship between Ediacaran- and Cambrian-type fauna (figure 3*d*) because these exclusively form segregated pairs in the Nama. In the White Sea, both aggregated and segregated pairs are present between biotas at roughly equal frequencies (figure 3*c*) and there is a smaller proportion of strong segregations (within the bottom quartile). Within-group pairs for both the Ediacaran- and Cambrian-type biotas form aggregated and segregated pairs at their initial appearance (figure 3*b*) but in the following interval (White Sea for the Ediacaran-type fauna and Nama for the Cambrian-type fauna) pairs within groups are almost entirely aggregated.

(b) Environmental effects

Barriers to dispersal was the most frequently detected environmental factor found associated with strong pairs in our analysis (figure 4). In the Avalon, barriers to dispersal was the only variable associated with pairs (11%; electronic supplementary material, table 2). Similarly, in the White Sea 20% of strong pairs were significantly associated with dispersal, and these were mainly aggregated. In the Nama, dispersal was associated with a greater proportion of segregations (38%) than aggregations (5%). However, we found that the presence of algae was associated with several pairs which account for 11% of segregations in the White Sea interval (specifically involving *Calyptrina*—an enigmatic tubular taxon—and common members of the White Sea Ediacaran-type biota such as *Dickinsonia*).

We also find that depth is important, being associated with 4% of strong pairs in the White Sea interval evenly split between aggregations and segregations. Segregated pairs associated with depth principally involved *Ventogyrus*—a triradial organism from modern Siberia found in deep-water habitats—and genera from South Australia (ex. *Dickinsonia, Kimberella, Spriggina* and *Rugoconites*), as well as between *Dickinsonia* and *Charniodiscus*, and between *Palaeopasichnus* and *Ediacaria*. We found that barriers to dispersal were also associated with some of these pairs (e.g. *Spriggina*/*Rugoconites* and *Ventogyrus*).

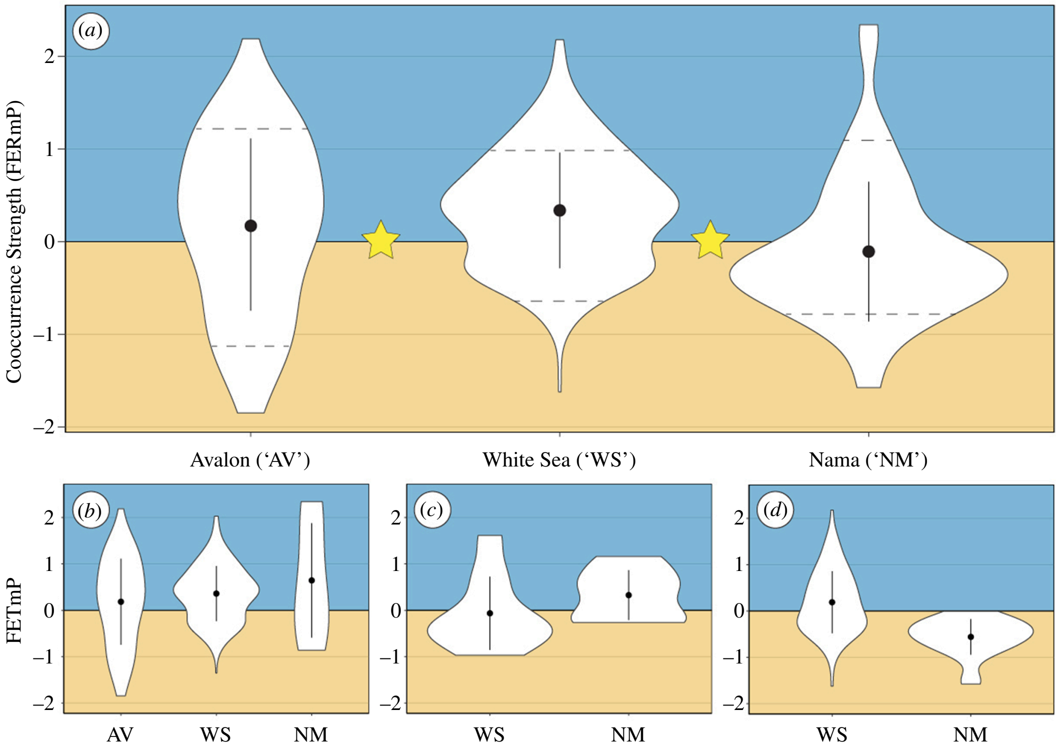

Figure 3. (*a*) Violin plots of co-occurrence scores between each assemblage zone. The blue background indicates aggregated pairs (FETmP > 0), while yellow indicates segregated pairs (FETmP < 0). Dashed lines indicate the cut-off for 'strong pairs' for each assemblage zone. Stars indicate significant difference ($p < 0.05$) between intervals. (*b*) Subset co-occurrence distributions for pairs between Ediacaran biota. (*c*) Subset co-occurrence distributions for pairs between Metazoan biota. (*d*) Co-occurrence distributions for pairs between Ediacaran and Metazoan biota.

Lastly, the impact of bioturbation—in terms of being associated with aggregated versus segregated pairs—is reversed between the White Sea and the Nama. In the White Sea, bioturbation was associated with 20% of strong aggregations, with most also being associated to some extent with dispersal. In the Nama, we found that bioturbation was associated with 19% of strong segregations and no aggregations. These strong segregations occurred between Cambrian-type fauna (*Cloudina, Namacalathus* and *Corumbella*) and classic Ediacaran-type genera (*Pteridinium, Ernietta* and *Rangea*), and we did not detect the influence of any other tested factor besides bioturbation on these pairs.

(c) Sensitivity tests

Our sensitivity tests that shift the identity of some taxonomic groups from 'Ediacaran-type' to 'Cambrian-type' (see electronic supplementary material, Results) have an influence on these results. Specifically, we find a broader-scale temporal separation of fauna types between intervals than we find with our original (and presently better supported) assignments. Our principal finding remains that community structure changed between the Ediacaran-type and Cambrian-type fauna (with a broad temporal rather than spatial component), and that this shift is still associated with changing impacts in bioturbation and barriers to dispersal between White Sea and Nama.

4. Discussion

Our analyses indicate a significant change in the structure of macrofaunal communities across the Ediacaran. We find that the co-occurrence patterns of genus pairs shifted between each successive assemblage zone. However, each of these steps differed both in the pattern of co-occurrence shift and the environmental factors associated with shifts, suggesting complex patterns of ecological and/or biogeographic change. Moreover, we found that the largest shift in co-occurrence structure occurred between the White Sea and Nama assemblages, marked by a shift from a majority of aggregated to segregated pairs. Moreover, our analysis suggests that this change was associated with changing patterns of spatial association between faunal groups (i.e. Ediacaran-type versus Cambrian-type), and that this was potentially a response to intensifying bioturbation and changes in dispersal limitations rather than a secular change in preserved environments (i.e. deep- versus shallow-water habitat).

(a) Avalon–White Sea transition

The overall proportion of aggregated and segregated pairs did not change substantially between the Avalon and White Sea. This is despite the emergence of new ecological behaviours (e.g. motile grazing and bioturbation; [89,90]), the colonization of shallow-water habitats [91] and general rise in community complexity [46]. Additionally, the change in co-occurrence strength between the Avalon and White Sea is relatively minor, marked only by a decline in the relative strength of strong pairs, which

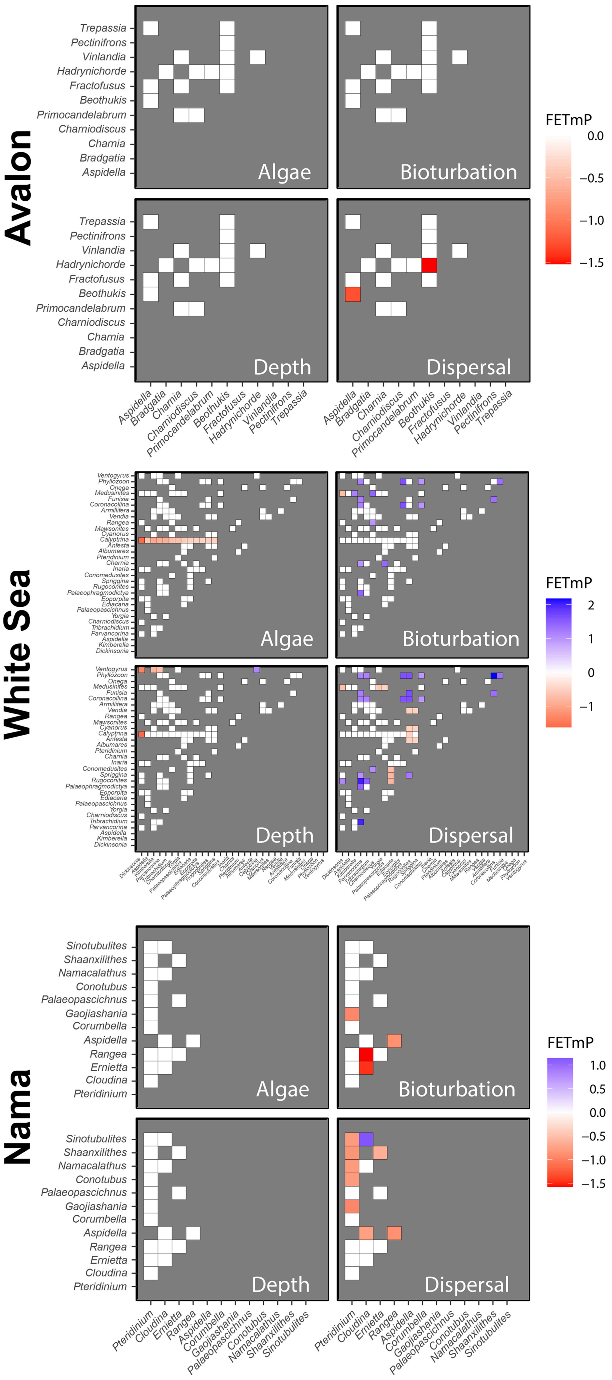

Figure 4. Matrix plots of strong pairs (top/bottom quartiles of each assemblage zone's co-occurrence distribution), with those significantly influenced by a tested environmental factor (presence of algae, bioturbation, depth category and dispersal) coloured. Blue cells indicate aggregated pairs structured by the indicated variable; red cells indicate segregated pairs structured by the indicated variable. The intensity of red or blue reflects the strength of aggregation or segregation (FETmP). White cells show pairs that were not significantly influenced by the indicated variable. Missing cells within the top triangle of the matrix reflect pairs that fell beyond the top or bottom quartiles of each co-occurrence distribution.

could be attributable to declining occupancy rates among genera (0.39 to 0.14 occupancy probabilities per Foote [92] estimates). With lower occupancy, co-occurrence scores (especially for segregated pairs) tend to decline in magnitude as the probability of two genera not occurring together by chance increases. Thus, the slight shift at the Avalon–White Sea could have been driven by a diversifying and geographically expanding White Sea assemblage as compared with the Avalon. While the White Sea represents an interval of major macroevolutionary change, innovations such as motility, suspension feeding and grazing may not have been widespread or intense enough to affect biotic interactions, habitat filtering and dispersal patterns at the global scales used here to compare co-occurrence distributions.

When examining the effect of our environmental variables on strong pairs, we find evidence for shifts in barriers to dispersal and habitat filtering by bioturbation, depth and the presence of algae (to minor extents) from the Avalon to White Sea. Notably, all White Sea pairs structured by bioturbation were also structured by shared dispersal barriers. This could reflect the emergence of a group of genera with similar dispersal limitations and habitat preferences, and which could coexist with early bilaterian tracemakers. This observation is consistent with the low inferred ecosystem engineering impact of these early burrowing behaviours. Bioturbation in the White Sea is restricted to simple, horizontal burrows at or shortly beneath the sediment–water interface, and with limited impacts on resource flows [31]. Bioturbation in the White Sea thus did not have a strong impact on community structure. However, almost all genera associated with bioturbation in the White Sea were absent by the Nama (see electronic supplementary materials, tables 3 and 4). This suggests that, while members of the White Sea assemblage may have tolerated bioturbation, intensification of bioturbation in the Nama [23,58] did not benefit these genera.

(b) White Sea–Nama transition

In contrast to the Avalon–White Sea transition, co-occurrence distributions between the White Sea and Nama assemblages changed significantly, both in the shape of the distribution of interaction strengths and in a shift towards majority segregated pairs (figure 3). Our analyses suggest that this is driven by a change in spatial associations between taxa defined as Cambrian-type and Ediacaran-type, as these groups exclusively formed segregated pairs with each other in the Nama. Furthermore, some of the strongest segregations between Cambrian-type (i.e. *Cloudina*) and Ediacaran-type taxa (i.e. *Rangea* and *Ernietta*) were influenced by the presence of bioturbation and no other tested factor (see electronic supplementary material, table 4). Although the group identity of aggregated and segregated pairs over the White Sea–Nama transition is sensitive to our assignment of taxa as 'Ediacaran type' or 'Cambrian type', the apparent drivers of this shift change very little. We speculate that, through the re-suspension of sediment particles, the more intense bioturbative behaviours that characterize the Nama may have interfered with feeding mechanisms present among some Ediacaran biota reconstructed as suspension feeders (a process termed 'trophic group amensalism', see [23,93]). Additionally, bioturbation may have begun to physically disrupt microbial matgrounds across large areas of shallow shelf, with bioturbators targeting matgrounds for consumption and oxygen refugia [94,95]. This is consistent with inferences made by Eden *et al*. [36], who suggested that the decline of Ediacara-type fauna in the Nama assemblage may have been resulted, in part, from bioturbation driving shifts in community structure and niche separation.

We also found that barriers to dispersal were associated with a larger portion of strong segregations than bioturbation in the Nama. Most of these occur between the erniettomorph taxon *Pteridinium* (Ediacara-type) and tubular suspension feeding metazoans such as *Cloudina* [57]. *Pteridinium* is most abundant in Namibia, and its dispersal-structured segregations with tubefauna occur with genera principally found in the United States and China. However, these tubefauna do not form strongly aggregated pairs among themselves, and only their pairs with *Pteridinium* are structured by dispersal. This indicates that a degree of endemism among tubefauna genera may be responsible for this signal. We note that Ediacaran-aged tubefauna need systematic revision [62,96], and thus the endemism inferred could reflect patterns of taxonomic assignment as opposed to differences in local species pools. Regardless, where *Pteridinium* (and other Ediacara-type fauna) occur in the same regions as Cambrian-type fauna, they occur in different communities and thus maintain a strong pattern of segregation. Thus, local barriers to dispersal may have complemented larger-scale dispersal barriers to structure Nama communities and segregate biota types.

(c) Drivers of changing community structure

Our analysis suggests that bioturbation may have been a driver of segregations between Ediacaran-type and Cambrian-type genera in the Nama assemblage; however, the differing styles of bioturbation and the timing of their appearance add nuance to this picture. Bioturbation is often split into biomixing behaviours—referring to solid particle transport through sediment—and bioirrigative behaviours, which create channels through which water is transported through sediment from the sediment–water interface [97]. While trace fossils with biomixing-type behaviours are first recorded in the White Sea assemblage, the first 'complex' trace fossils with biorrigative-type impacts—treptichnids—appear markedly later, above the transition between the White Sea and Nama assemblages, approximately 550 Ma [97]. In the Nama Group of southern Namibia where the dating of these innovations can be constrained, the first occurrence of treptichnids comes above an ash bed dated to 542.65 ± 0.15 Ma [98]. The record in Namibia thus potentially suggests a *ca* 7 million year gap between a White Sea–Nama turnover pulse and the emergence of more intense bioturbation behaviours, and in turn suggests that an intensification in biomixing, rather than the evolution of more complex bioirrigative behaviours, was a source of disruption to benthic macrofossil communities. This is perhaps not surprising, given that biomixing behaviours are known to be associated with a variety of powerful ecosystem engineering effects. These include the disruption of microbial mats, alteration of surface rheology and enhanced resuspension of sediment. In modern settings, these impacts are known to have powerful knock-on effects on benthic communities [93]. In addition, we acknowledge that previous work linking ecosystem engineering with biotic turnover in the Ediacaran has emphasized that bioturbation may represent just one family of interactions that apparently proliferated in this interval [33]. Predation, which may have been a source of ecological pressure on suspended larvae and/or community hydrodynamics [23,99], and competition for resources such as suspended food particles [55,60] are both supported by recent palaeobiological reconstructions of Nama-aged taxa [49]. Thus, while our analyses suggest an important and changing role for bioturbation in structuring Nama-aged communities, there are other ecological interactions that we do not test for here and that may have also been powerful drivers of change.

We do not find support for two other proposed drivers of late Ediacaran community structure shifts—segregation by depth and facilitation by algae. Both appeared to have very minor (if any) effects on community structure throughout the Ediacaran, as pairs structured by these factors were driven by one genus each in the White Sea. *Ventogyrus* was the only genus detected that formed pairs structured by water depth and thus may be considered a deep-water specialist, segregated from common shallow-water genera. However, it belonged to a taxonomic group (triradialomorphs) which had not evolved by the Avalon, whereas Avalon-type taxa (specifically rangeomorphs, which first appear in deep-water settings) were found across depth categories. This point emphasizes that Avalon taxonomic groups did not remain in deep-water habitats in the White Sea and Nama, even while unique shallow-water communities evolved, and despite the emerging split between Ediacaran-type and Cambrian-type fauna in the Nama. Shallow-water habitats may have still been partitioned at finer scales [36], but deep-water habitats (in which the Ediacaran-type fauna first evolved) apparently did not serve as refugia for waning taxonomic groups as shallow-water communities changed. Similarly, *Calyptrina* was responsible for all segregated pairs structured by algae (electronic supplementary material, table 4). Although macroalgae diversification is very similar to macrofaunal diversification during the Ediacaran [100], there does not seem to be a facilitative relationship between macroalgae and metazoans.

Lastly, we do not find support for preservation bias to be a driver of changes between White Sea and Nama communities (see electronic supplementary materials, tables 3 and 4). Previous taphonomic work has suggested that the preservation of soft-bodied Ediacaran-type fauna is reliant on both siliciclastic sediments and the presence of microbial mats [23,101]. We might, therefore, expect this to be reflected in segregations structured by the changing distribution of siliciclastic versus carbonate environments. However, there is little evidence in our supplemental analyses that this process is in effect (see electronic supplementary material, table 5). Moreover, more recent discoveries of Ediacaran-type fauna preserved in carbonates [102] suggest that the controls on Ediacaran preservation are still poorly understood. Alternatively, the rise of biomineralized Cambrian-type taxa in the Nama could be hypothesized to have yielded different preservation patterns from soft-bodied biota, and thus driven increased segregations in the Nama. However, there is no significant effect of genus biomineralization on co-occurrence distributions (electronic supplementary material, figure 2).

In summary, our analyses provide quantitative support for a model in which change in community structure between the White Sea and Nama Assemblages was linked, at least in part, to increasing intensity of bioturbation and the emergence of new ichnotaxa, which have been well documented from Nama-aged communities worldwide [23,58,62,94,95]. However, other ecological interactions (e.g. competition and/or predation) may have also been important drivers, which remain to be directly tested. Nonetheless, our data indicate an important (and changing) role for bioturbation in structuring faunal aggregations/segregations in the White Sea and Nama assemblages. We hypothesize that the emergence of ecosystem engineering behaviours—including bioturbation—was patchy in space (see e.g. [23]) and thus led to greater spatial heterogeneity in the character of shallow-marine settings according to physical habitat changes and/or regulating nutrient availability in the community. This, in turn, may have resulted in the emergence of more specific fauna–habitat associations and new ecological interactions. These interactions could have excluded soft-bodied Ediacaran-type fauna from certain environments and contributed to the increased importance of dispersal barriers for segregated pairs in the Nama assemblage. This finding is in line with recent work [103] suggesting the stepwise emergence of distinct ecosystem engineering regimes in deep time, and that may have played a crucial role in structuring the evolving animal biosphere.

Although speculative, our hypothesis is rooted in several key observations surrounding the latest Ediacaran palaeontological and palaeoecological records; specifically, bioturbation in the Nama assemblage is noticeably patchy at a wide range of time- and space scales. For example, on local scales, densely bioturbated horizons in southern Namibia are limited to only a few stratigraphic horizons, which moreover tend not to be laterally extensive [23]. On regional to global scales, dense accumulations of trace fossils (especially those comprising more 'complex' and energy-intensive behaviours) are well described from some localities (Namibia and China) but are rare or virtually unknown from others (e.g. the southwestern United States, several sites in Russia and Iran). This hints at significant geographic and temporal disparities in the emergence of intense burrowing behaviours (potentially driven by oxygen availability on local scales; [23,62,104], although, we acknowledge that these observations do not account for surface exposure or sampling effort). Furthermore, in many localities, soft-bodied Ediacara-type fauna rarely occur on slabs together with either metazoan tube-fauna or trace fossils left by bilaterians, which Darroch *et al*. [99] suggested may have been the result of niche partitioning, contributing to or driving other changes in ecological interactions. Moreover, the split between metazoan traces and Ediacaran-type fauna does not seem to have occurred for the White Sea Assemblage [105], supporting our suggestion that the palaeoecological influence of bioturbation may have changed through time, becoming an important driver of community structure in the Nama. We stress that the exact nature of antagonistic interactions (if they existed) between soft-bodied Ediacaran-type and Cambrian-type fauna in the Nama remains contentious (see discussion in Darroch *et al*. [23]), and thus that more detailed work focused on community palaeoecology will be needed to provide more focused tests.

At the broadest scale, our analyses provide evidence for a model wherein the rise of new ecosystem engineering behaviours reshaped late Neoproterozoic communities, perhaps by changing the suitability of different habitats for specific faunal groups, and/or by contributing to dispersal limitations. This intensification in ecosystem engineering may have acted as a new disturbance pattern, restricting potential habitat for organisms not evolved to exploit it, altering the distribution of resources and thereby acting as a powerful influence on the trajectory of animal evolution.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and r code for analyses have been included as a zip file with supplemental materials. These have also been deposited in Dryad [106].

Supplementary material is available online [107].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; P.J.W.: data curation, software, validation, writing—review and editing; D.K.W.: data curation, validation, writing—review and editing; S.A.F.D.: conceptualization, data curation, investigation, resources, supervision, validation, visualization, writing—review and editing; S.K.L.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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