High ecological complexity in benthic Ediacaran communities

Simon A. F. Darroch [1]*, **Marc Laflamme**[2] **and Peter J. Wagner**[3]

A long-running debate over the affinities of the Neoproterozoic 'Ediacara biota' has led to contrasting interpretations of Ediacaran ecosystem complexity. A 'simple' model assumes that most, if not all, Ediacaran organisms shared similar basic ecologies. A contrasting 'complex' model suggests that the Ediacara biota more likely represent organisms from a variety of different positions on the eukaryotic tree and thus occupied a wide range of different ecologies. We perform a quantitative test of Ediacaran ecosystem complexity using rank abundance distributions (RADs). We show that the Ediacara biota formed complex-type communities throughout much of their stratigraphic range and thus likely comprised species that competed for different resources and/or created niche for others ('ecosystem engineers'). One possible explanation for this pattern rests in the recent inference of multiple metazoan-style feeding modes among the Ediacara biota; in this scenario, different Ediacaran groups/clades were engaged in different methods of nutrient collection and thus competed for different resources. This result illustrates that the Ediacara biota may not have been as bizarre as it is sometimes suggested, and provides an ecological link with the animal-dominated benthic ecosystems of the Palaeozoic era.

The terminal Neoproterozoic Ediacara biota (570–541 Ma) represents the first major radiation of large, morphologically complex multicellular eukaryotes. Given their position at the dawn of animal life, Ediacaran ecosystems are typically interpreted to have been relatively simple, comprising few unique modes of nutrient acquisition and characterized by limited biotic interactions between organisms (the 'Garden of Ediacara')[1–3]. The subsequent Cambrian explosion is thus inferred to have been as much a behavioural and ecological revolution (including the appearance of macroscopic predation, infaunal deposit feeding, and active filtering and suspension feeding)[4], as a rise in metazoan diversity and morphological disparity[5,6]. However, recent work has challenged this view, suggesting that Ediacaran ecosystems may have been more complex than originally thought, through the identification of previously cryptic feeding modes[7] and inference of facultative mobility in taxa previously thought to have been sessile[8,9]. Testing between these two views of the Ediacara biota is crucial. Not only does it colour our view of where the Ediacara biota fit in the Cambrian 'explosion' of animals, and thus sheds light on the origins of the modern, metazoan-dominated biosphere, but it also carries implications for the relationship(s) between ecological and macroevolutionary theory and when we might see high ecological disparity among relatively closely related species. Because these two end-member models ('simple' and 'complex' ecosystems) predict different patterns of relative abundance within assemblages[10], we use rank abundance distributions (RADs)—distributions of species abundances within assemblages by rank order—to test between them and calculate temporal trends in the complexity of Ediacaran communities. Although recent studies have examined this question by investigating the biology of individual Ediacaran taxa[7,8,11,12], here we perform a test of these hypotheses given their predictions about general RAD models.

RADs can test ideas about the variety of ecological types among Ediacaran taxa because the ecological theory underlying different RAD models reflects not simply resource partitioning, but the number of basic resource types being partitioned[13]. One class of RAD models supposes that species in a community compete for roughly the same resources. Relative abundances thus reflect how rapidly populations expand[14] and variation in migration, origination and extinction within the larger metacommunity[15,16]. If those latter factors governed Ediacaran communities while Ediacaran taxa exploited the same basic resources, then their RADs for Ediacaran taxa should fit one of these models. The second class includes models assuming some disparity in basic resource demands among members of a community. If different groups of species target different resources (that is, different basic niche types), then emigration of species can result in the hierarchical partitioning of a variety of those different basic niches. We expect this to create log-normal RADs[13]. New species might expand the ecospace, either by making new resources available for additional species[17] or by employing niche construction to expand the available resources[18]. We expect these scenarios to create Zipf distributions. Finally, the presence of multiple basic niche types within the same community with geometric, log-series or zero-sum distributions within each basic ecospace type can generate Zipf or log-normal distributions for the entire community, depending on the similarity of the RADs within each ecospace. Thus, if different groups of Ediacaran taxa exploited very different resources, then we expect the RADs for Ediacaran assemblages to best fit one of those two models.

Mathematically, log-normal and Zipf distributions are similar in complexity to geometric, log-series and zero-sum multinomial distributions. However, the former set is 'complex' in that they invoke 2+ basic resource or niche types, whereas the latter set is 'simple' by invoking only one. Thus, we refer to the geometric, log-series and zero-sum multinomial group as 'simple', and the log-normal and Zipf group as 'complex'. The number of basic niche types is a different aspect of community complexity than is the evenness of species abundances within basic niche types. All of the models considered here can generate very even distributions or distributions dominated by a one or two species[19]. Even given very uneven
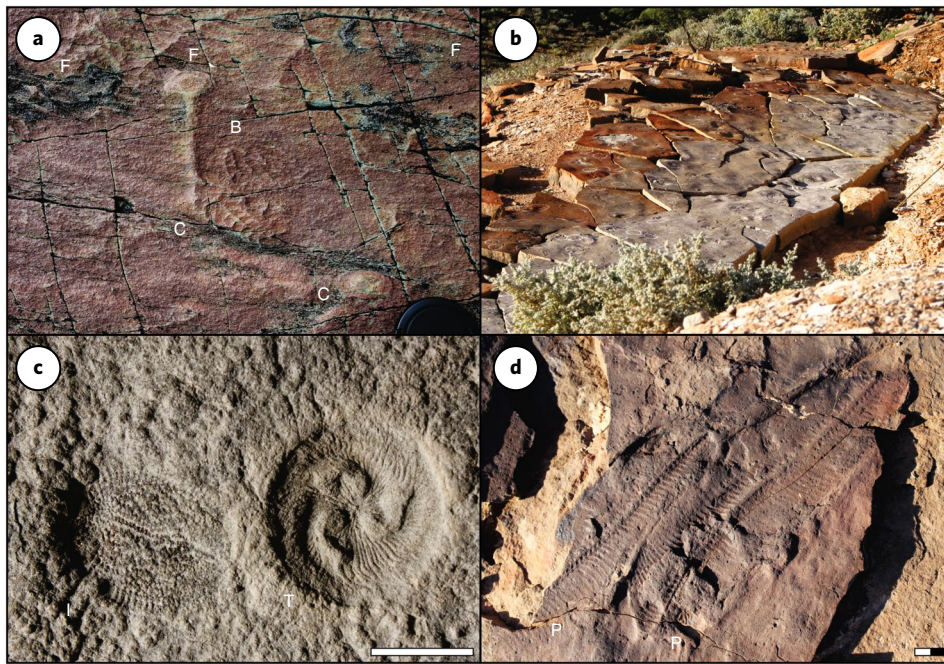
Fig. 1 | Examples of Ediacaran in situ communities preserved on bedding planes. a, Mistaken Point 'E' surface from the Avalon Peninsula in Newfoundland (Avalon assemblage) preserving *Fractofusus* (F), *Charniodiscus* (C) and *Bradgatia* (B). **b**, Exhumed and flipped storm bed from Nilpena, South Australia (White Sea assemblage); organisms are circled in white chalk. **c**, Bedding plane assemblage from the White Sea area of Russia (White Sea assemblage), preserving *Ivovicia* (I) and *Tribrachidium* (T). **d**, Bedding plane from Swartpunt Farm, Namibia (Nama assemblage), preserving multiple *Pteridinium* (P).

distributions, complex models should generate a longer tail of (very) rare species than should simple models[19], implying that one ecological type is both much more pertinent than others and dominated by one or two species. Thus, the questions we seek to answer here concern the disparity of ecological types rather than the extent to which individual ecological types are dominated by particular species.

When considering models of ecological complexity, an intuitive null hypothesis is to assume simple distributions controlled by a single primary resource, demanding evidence for complex distributions influenced by multiple resource types and/or interactions among species. This null model is especially appealing when considering ecosystem models for the Ediacara biota; historically, Ediacaran organisms have been thought to be anatomically simple relative to most Phanerozoic metazoans[20] and many Ediacaran communities have low species richness relative to their Phanerozoic counterparts[2,3]. Although neither of these is necessary for low ecological complexity, both can contribute to forming simple RAD models such as the geometric, log-series or zero-sum multinomial distributions. In addition, the view that the Ediacara biota represent a closely related group of organisms has been prominent; given that recent studies corroborate a close association between phylogenetic diversity and functional diversity[21], this would suggest low ecological disparity among the Ediacara biota as a whole. Lastly, many Ediacaran communities (especially those from deep-water settings) are overwhelmingly dominated by taxa possessing a common body plan, leading to assumptions that they all fed in the same manner (osmotrophy[22,23]) and thus likely competed for a common resource. This first general model, therefore, suggests that communities fitting simple RADs should predominate. Conversely, anatomical disparity among different Ediacaran groups is large (Fig. 1), to the point where researchers have struggled to identify homology schemes that can be shared between putative clades[5,24–29]. High anatomical disparity need not reflect high ecological variation. The morphologically disparate groups of brachiopods, bryozoans, echinoderms, molluscs and corals all relied primarily on suspension during much of the Palaeozoic. However, it is possible that the variety of Ediacaran

body plans represent adaptations to exploiting a wider range of basic ecological types (for example, suspension feeding, saprophagy and osmotrophy)[7,8,30,31]. In addition, several shallow-water Ediacaran communities exhibit richness and evenness values on a par with their Phanerozoic counterparts[32]. Therefore, this second complex general model predicts that Ediacaran assemblages should fit either the log-normal or Zipf RADs. We test between these two models for Ediacaran ecosystems—'simple' and 'complex'—by assessing RAD fits for all Ediacaran fossil assemblages with relative abundance data (see Supplementary Table 1). These fossil assemblages span the three Ediacaran chronostratigraphic divisions (Avalon, White Sea and Nama) that are used to subdivide the Ediacara biota, including the oldest Ediacaran communities from Newfoundland[33,34], apex diversity communities from South Australia and Russia[35–38], and the youngest Ediacaran communities from Namibia[39] (Supplementary Tables 1 and 2). These data sets also represent a variety of palaeoenvironments, including both deep-shelf and shallow-marine settings (although none from carbonates)[40].

Results
We first considered the distribution of best-fitting RADs among all assemblages and then split them between chronostratigraphic divisions: Avalon (Mistaken Point, Newfoundland, $n=8$); White Sea (Nilpena, South Australia, $n=6$; Flinders, South Australia, $n=6$; White Sea area of Russia, $n=2$); and Nama (Witputs sub-basin, Namibia, $n=1$). RAD fits for each assemblage are illustrated in Supplementary Figures 1 and 2.

Overall (Fig. 2a), the highest number of best fits are for the Zipf, geometric and log-normal models (eight, five and five, respectively), with fewer assemblages best fitting the log-series (one) and zero-sum (one) models (see also Supplementary Tables 3, 5). When split between chronostratigraphic divisions, the Avalon assemblages were evenly split between geometric and Zipf (three each), with two assemblages best fitting the log-normal model. The 'combined' Mistaken Point assemblage also best fitted the log-normal model. White Sea assemblages produced a majority of complex-type
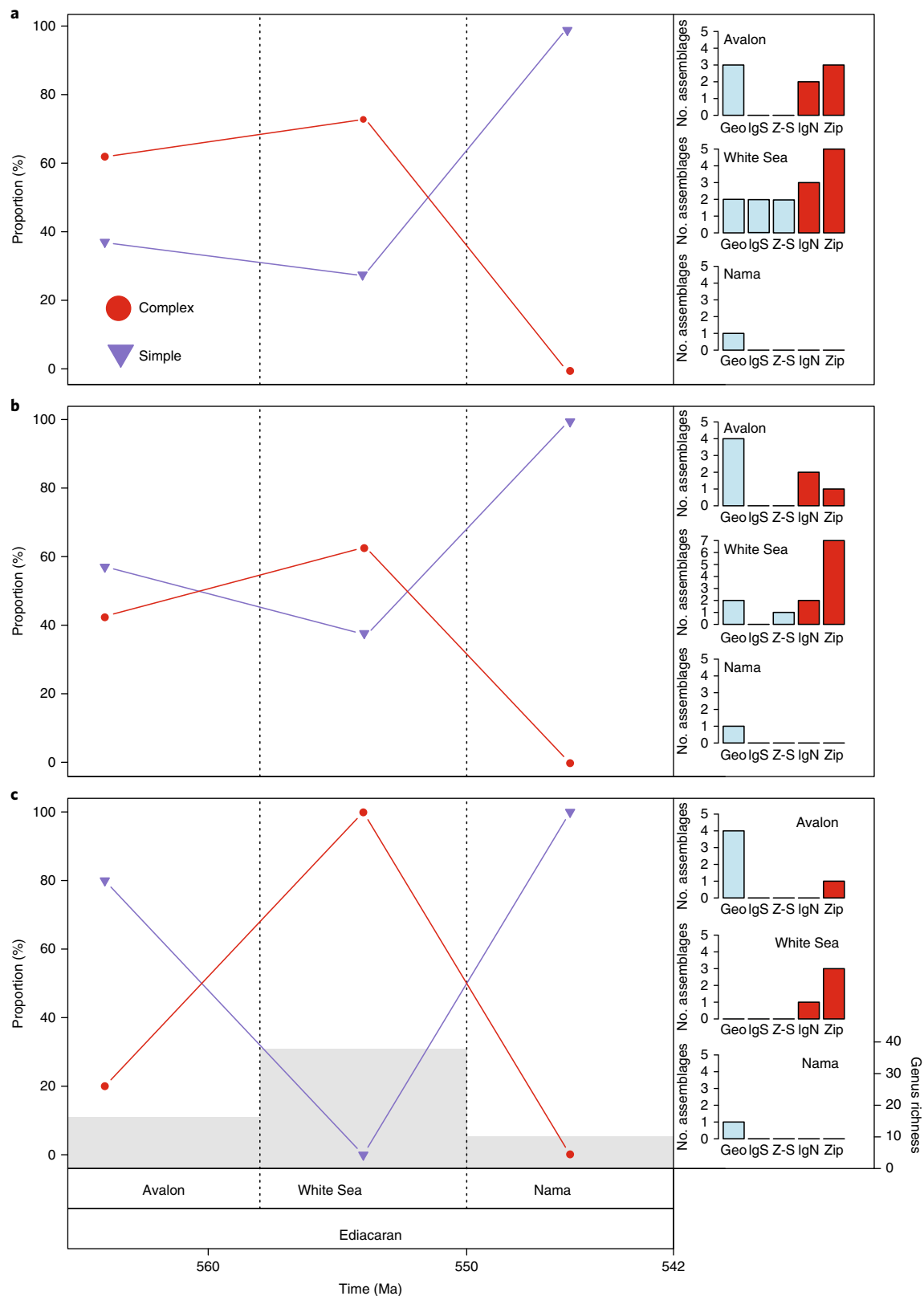
Fig. 2 | Distribution of 'simple' (geometric, log-series and zero-sum multinomial) and 'complex' (log-normal and Zipf) RADs throughout the Ediacaran period. a, Untreated species occurrence data. **b**, Data with *Aspidella* removed. **c**, Data with individual genera binned into Ediacaran clades (see Supplementary Table 1).

RADs (five fitting the Zipf and three fitting the log-normal models), with relatively few fitting simple RADs (one zero-sum and one log-series). The lone assemblage falling within the Nama division (Swartpunt Farm) best fitted the geometric RAD model.

Excluding the form taxon *Aspidella* produced a very similar pattern of results (Supplementary Tables 4, 6); among all the assemblages taken together, 8 best fitted simple RADs, while 12 best fitted complex RADs. When split between chronostratigraphic divisions,

Avalon assemblages were approximately equally split between simple and complex-type RADs (four simple versus three complex), with the combined assemblage again fitting a log-normal distribution. However, two assemblages that best fit Zipf distributions have higher Akaike weights for simple models due to comparable support for two best simple models (see Supplementary Fig. 3). White Sea assemblages showed nine examples best fitting a complex distribution and three best fitting a simple one (Fig. 2b). The one assemblage recorded from the Nama interval remains simple. Across all analyses and chronostratigraphic assemblages, there was no systematic difference between single-bed and amalgamated data sets, suggesting that this distinction does not have a significant effect on RAD fits.

When data sets were broken up into broader taxonomic groups and clades (Fig. 2c), only the Rangeomorpha and the Erniettomorpha clades had enough genera in single localities, which nonetheless included sites in all three Ediacaran assemblages, to produce interpretable RAD fits. The results indicate an approximate 50:50 split between geometric and Zipf distributions, with one log-normal distribution (Supplementary Table 7).

Zipf and log-normal distributions both assume a tail of moderately rare species, which may be easier to detect with larger sample sizes and/or with more sampled taxa. Richness also affects the power of our tests; as the simplest distribution (geometric) is an ecologically simple model, low richness should also encourage relatively higher Akaike information criterion (AIC) scores for geometric distributions. However, the split between simple and complex RAD fits did not show any correlation with the number of individuals within communities, nor the number of genera (Supplementary Fig. 4). Indeed, several of the richest and most heavily sampled assemblages best fit simple models, particularly when *Aspidella* is included, and a simple Mann–Whitney U test reveals no systematic bias ($P = 0.29$).

Discussion

In terms of simple- versus complex-type models, both the Avalon and White Sea assemblages contain fossil communities with a relatively even split of simple and complex RADs. This result does not change when the form taxon *Aspidella* is removed. Furthermore, splitting data sets into broader taxonomic groups and clades illustrates a proportion of complex-type RAD fits even within the Erniettomorpha and Rangeomorpha clades in both the Avalon and White Sea assemblages, indicating that complex-type RAD fits in these intervals are not produced merely by the presence of multiple simple-type communities in the same ecosystem. This suggests that at least some communities in each of these chronostratigraphic divisions comprise species that are competing for different resources or creating niches for others (that is, ecosystem engineering). This result is perhaps not surprising in the context of the White Sea assemblage where diverse Ediacaran fossils are thought to represent a variety of positions on the eukaryotic tree of life, including stem-group metazoans, crown-group metazoans and total group-bilaterians[20]. Taxa from these beds are also recognized as utilizing a relatively diverse array of feeding modes; *Kimberella* from these beds is probably a stem-group mollusc and surficial grazer[41–43], whereas *Dickinsonia* possibly fed saprophytically by absorbing organic matter through its ventral surface[30,44]. Rahman et al.[7] also make a case for *Tribrachidium* representing an early suspension feeder. However, it is a surprising result in the Mistaken Point sites from the Avalon assemblage, where communities are overwhelmingly dominated by rangeomorphs[22,23,45], all of which are thought to represent macroscopic osmotrophs[22,23] and thus might be expected to have competed for a single resource. Of the non-rangeomorph taxa represented in complex-looking Avalon assemblages (the Mistaken Point 'G' surface), *Charniodiscus* belongs to the Arboreomorpha and may have been a filter feeder, although it preserves no evidence for feeding structures[11].

One consideration centres on the presence of rare unsampled taxa in assemblages; rarefaction curves produced for many of the data sets treated here, for example[38,39], illustrate varying amounts of undersaturation, illustrating that more species may remain to be discovered at these sites. However, rare taxa will produce long tails in the RAD distributions, which will typically produce better fits with log-normal and Zipf (that is, 'complex') models. This expectation holds when evenness is very low and/or when dominance by a single taxon is high[19]. Therefore, the discovery of additional rare taxa in these sites will most likely result in a higher proportion of complex-type RADs, strengthening the inference of predominantly complex ecosystems existing throughout the Ediacaran period. However, a possible caveat revolves around the identity of the form taxon *Aspidella*; although we find evidence for complex-type ecosystems both when we include and exclude *Aspidella*, an alternative possibility is that this form represents more than one species, which is possible given that similar holdfast structures apparently evolved independently in multiple Ediacaran clades. In this scenario the distribution of RAD fits could conceivably be changed depending on how many species were represented within *Aspidella*; however, we note that inference of complex-type ecosystems as early as the Avalon assemblage (where *Aspidella* is particularly numerous) is in agreement with spatial analyses showing evidence for a complex web of interactions and associations among rangeomorph taxa on the Mistaken Point 'E' surface[12].

Our one site from the Nama assemblage preserves a simple-type geometric RAD; although there is only one data point from this interval (and thus is not a robust result), this is interesting in the context of suggestions that soft-bodied Ediacara biota in this interval were undergoing a protracted extinction event that may have been driven by the radiation of metazoan ecosystem engineers, in a process referred to as 'biotic replacement'[3,39]. Darroch et al.[39] established that the Ediacaran biota preserved at Swartpunt Farm had significantly lower diversity than all other White Sea- and Avalon-aged assemblages, while other studies[46–48] document a substantial increase in both the diversity and intensity of bilaterian infaunal activity at this time. These data are consistent with a biotic turnover event separating the White Sea and Nama assemblages[4,39,49,50]. Given that both extant communities undergoing substantial stress[51–54] and fossil communities from intervals of catastrophically rapid environmental change[55] have been shown to exhibit simple-type RADs, the finding that latest Ediacaran fossils from Swartpunt Farm best fit a geometric-type model supports the inference that communities of Ediacara biota were 'stressed' towards the end of the Ediacaran period. However, we emphasize that more data sets from the Nama interval are needed before these latest Ediacaran communities can be shown to fit broader narratives surrounding the Ediacaran–Cambrian transition[50].

In sum, although the number of Ediacaran communities recording relative abundance data is still relatively low, the results of RAD analyses illustrate that at least some (if not most) Ediacaran communities were ecologically complex. In contrast to a 'Garden of Ediacara' scenario[1] with little ecosystem engineering and few unique methods of nutrient acquisition, RADs suggest that species within Ediacaran communities possessed multiple basic ways to partition resources and thus occupied multiple basic niche types in both shallow- and deep-water settings. This supports a more contemporary view of Ediacaran communities as possessing a sophistication of community assembly on par with the Phanerozoic eon[31,32]. We note that this is not an explicitly phylogenetic argument; we cannot leverage the results of RAD analyses to say whether the Ediacara biota represent metazoans. Rather, these results support the notion that the Ediacara biota (even within single Ediacaran clades) formed complex communities comprising species with different ecologies and/or species that acted as ecosystem engineers, creating resources for others; thus, it provides an ecological link with
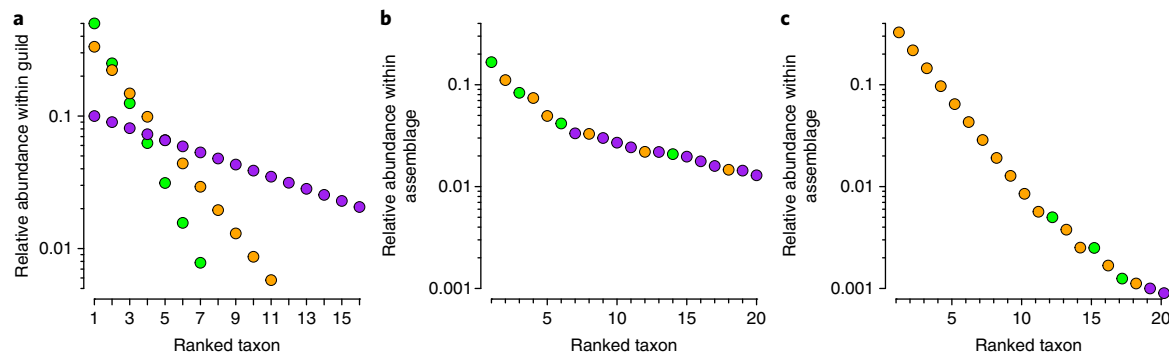
Fig. 3 | The effects of three 'guilds' within a community (illustrated using different colours) utilizing separate resources and following independent geometric RADs. a, Relative abundances within each guild. **b**, Relative abundances within the total assemblage when each guild represents one-third of the assemblage. **c**, Relative abundances when one guild represents 80% of the assemblage and the other two represent 10% each.

the metazoan-dominated benthic ecosystems of the Phanerozoic Eon. We also note that this inference of ecological complexity is independent of evidence for more cryptic ecological diversity in Ediacaran ecosystems. We find complex RAD fits, for example, in the Avalon assemblage, even without considering the presence of (albeit still controversial) trace fossils on the same surfaces[56], which hint at the presence of more complex and mobile bilaterians in rangeomorph-dominated communities. Although the authenticity of many Ediacaran-aged trace fossils is still the topic of debate[57], the occasional discovery of trace fossils and, for example, macroalgae on the same surfaces as Ediacara biota hint at hidden complexity in Precambrian ecosystems, which may ordinarily require different circumstances to be preserved.

On the other hand, standard interpretations of Zipf and log-normal distributions assume that interactions among species generate some of the occupied niches. This tacitly assumes fairly high richness. However, richness in the Ediacaran assemblages that we examine typically is quite low relative to Phanerozoic assemblages[2,3]. Incomplete sampling does not easily explain this. Zipf and log-normal distributions generate a large middle class of moderately common species; as such, we expect to sample a greater proportion of the true richness than if the other models applied[19]. This also could reflect unfossilised species. However, all of the fossils represent soft-bodied forms, which provide a taphonomic control suggesting that this is a less viable explanation than it would be if we had only skeletonized taxa[58]. Moreover, there is no association between the sample size and whether best-fit RADs are 'simple' or 'complex' (Supplementary Fig. 1E,F).

One possible explanation for these findings hinges on understanding the character of limiting nutrients in Ediacaran oceans and the diversity of Ediacaran feeding modes. Although many Ediacaran groups were almost certainly osmotrophic[22,23] and fed via direct absorption of dissolved organic matter, a growing body of evidence suggests that other groups of Ediacara biota more likely fed via a primitive form of suspension feeding[7]. The appearance of these more complex feeding modes may owe a lot to top-down engineering of the marine environment; although cyanobacteria were still major primary producers in the Ediacaran period, biomarker data point to increasingly greater contributions by eukaryotic algae[59]. The appearance of sponge-type filter feeding in particular would have helped to oxygenate the water column and create conditions where eukaryotes could thrive[60]. Therefore, the Ediacaran period may represent the critical transition interval where the controls on community assembly stopped reflecting the availability of a single resource (primary production) and began reflecting the availability of other resources, such as suspended organic particles. Consider a hypothetical community in which three groups of organisms

partition three basic nutrient sources following different simple geometric distributions (Fig. 3a). If all three basic nutrient sources are approximately equal, then unless the three groups follow very similar geometric distributions, the total distribution will instead resemble a Zipf or log-normal distribution, with a relatively long tail following the initial decay visible after only a few species that could be distinguished from a simple geometric distribution with dozens of specimens (Fig. 3b). On the other hand, if one of the nutrient sources predominates over the other two, then the mixed community will effectively resemble the geometric distribution for those taxa using that resource (Fig. 3c). In this case, where the dominant resource accounts for 80% and the other two account for 10% each, we would need thousands of specimens to recognize that a simple geometric distribution is inadequate. In other words, high disparity in basic ecological modes among Ediacaran taxa might have generated complex relative abundance structures with relatively few species. The subsequent decrease in basic ecological disparity in the Palaeozoic era due to the ascension of suspension-feeding clades might then have led to the preponderance of simple RAD patterns[10].

Lastly, we suggest that Ediacaran communities have frequently been thought of as simple both as a result of the bizarre nature of many Ediacaran body plans (making them difficult to interpret) and as the result of taphonomic overprint. In terms of the first point, although comparative morphological approaches to interpreting Ediacaran palaeobiology have been historically unsuccessful[3,31], sophisticated palaeoecological and computational modelling techniques are starting to shed new light on how many enigmatic Ediacaran organisms moved, fed and reproduced[7,8,33,61]; the results of these studies almost always expand the known range of Ediacaran behaviours and life histories. In terms of the second point, Ediacaran fossils are typically preserved in 'death mask' style, which involves an interplay between rapid burial, anoxia driven by the onset of aerobic decay and sulphate-reducing bacteria, leading to the precipitation of pyrite on the outer surfaces of carcasses[62]. Although this taphonomic pathway is frequently assumed to preserve fossil anatomy with high fidelity, some researchers have suggested that death masks may be inadequate for preserving delicate feeding structures (as well as key metazoan synapomorphies) that would illustrate the true range of ecologies present in Ediacaran communities[63]. This point has received support from decay experiments, which show key metazoan characters decaying faster in Ediacaran-style scenarios[64]. The typical mode of Ediacaran preservation may thus be making communities look simpler than they actually are by obscuring the anatomical information required to reconstruct ecologies.

In summary, our analysis of RADs from a large number of Ediacaran fossil data sets supports the interpretation of complex Ediacaran ecosystems and supports the inference of cryptic

Ediacaran complexity obscured by non-analogue body plans and/or an imperfect late Neoproterozoic taphonomic window. Although new data sets will refine this picture, our analyses suggest that the Ediacara biota may have partitioned resources in a fashion analogous to modern benthic communities and provides an ecological link with the animal-dominated benthic ecosystems of the Palaeozoic era.

Methods

We used only data sets that preserve > 50 specimens and > 2 non-*Aspidella* species. This is a lower threshold for species than previous studies[10], but it is conservative with respect to the null hypothesis because the power to reject the simplest RAD models decreases with the number of sampled taxa.

Several of the data sets in this analysis include the genus *Aspidella*, which is a form taxon that most likely represents the holdfast to a frondose organism[65–67]. Given that a wide variety of Ediacaran groups contain species possessing a discoidal holdfast (including other genera in these analyses, such as *Swartpuntia*[39]), *Aspidella* in any one assemblage may represent a variety of different Ediacaran genera rather than any one single taxon. Therefore, we ran RAD analyses both with (Supplementary Table 3) and without *Aspidella* (Supplementary Table 4).

For each assemblage of X species with n_i specimens each and N total specimens, we determined the specific RAD that maximizes the probability of observing $n_{1...X}$ given a sample size of N for each of the five general models[10]. Mathematically, the different RAD models differ in the numbers of parameters without any being special cases of another. Therefore, we used a modified AIC (AICc), which adjusts the log-likelihood both by the number of freely varying parameters and the size of the data set (here, the number of specimens)[68]. We identified which of the five models had the lowest AICc. We also identified which class of models (simple versus complex) had the highest Akaike weights. Because we examined one more simple model than complex models, the Akaike weights for the simple class is based on the two best models.

Because complex-type RADs (that is, Zipf or log-normal) can also be produced by multiple groups in an ecosystem with geometric, log-series or zero-sum distributions, we also performed likelihood analyses on data sets with component species broken up into clades and/or broader taxonomic groups (for example, the Rangeomorpha and the Erniettomorpha[5]; Supplementary Table 2). Species within these groups share similar body plans and most likely utilized similar methods of nutrient acquisition[3]. The Rangeomorpha, Erniettomorpha and Arboreomorpha in particular emerge as distinct monophyletic groupings in a recent cladistic analysis[29], lending support to the notion that these clades share a common ancestor and likely possessed similar ecological and life history traits.

Lastly, our Ediacaran communities compiled from the literature comprise species counts from both single and multiple-amalgamated bedding planes (see Supplementary Table 1). Ediacaran organisms are typically inferred to have been fossilized in situ as pyritic death masks[38,62]; thus, single bedding plane assemblages are considered by most (but not all[69]) authors to represent instantaneous snapshots of the Ediacaran seafloor[38]. In principle, amalgamating beds should bias results towards log-normal distributions, as mixing exponential distributions tends to generate log-normal distributions[70]. Thus, we considered each category separately. As a partial test of the idea that mixing assemblages might generate log-normal RADs, we also analysed an artificial amalgamation of the seven single bedding plane Mistaken Point assemblages (MP_Combined). Community data sets from all assemblages contain both single-bed and amalgamated species counts.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All R code and data are provided in the online supplementary materials.

References

1. McMenamin, M. A. S. The Garden of Ediacara. *PALAIOS* **1**, 178–182 (1986).
2. Bush, A. M., Bambach, R. K. & Erwin, D. H. in *Quantifying the Evolution of Early Life Topics in Geobiology* 1st edn (eds Laflamme, M. et al.) 111–133 (Springer, Berlin, 2011).
3. Laflamme, M., Darroch, S. A. F., Tweedt, S., Peterson, K. J. & Erwin, D. H. The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat?. *Gondwana Res.* **23**, 558–573 (2013).
4. Schiffbauer, J. D. et al. The latest Ediacaran wormworld fauna: setting the ecological stage for the Cambrian explosion. *GSA Today* **26**, 4–11 (2016).
5. Erwin, D. H. et al. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097 (2011).
6. Erwin, D. H. & Valentine, J. W. *The Cambrian Explosion: The Construction of Animal Biodiversity*. (Roberts & Company: Greenwood Village, 2013).
7. Rahman, I. A., Darroch, S. A. F., Racicot, R. A. & Laflamme, M. Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. *Sci. Adv.* **1**, e1500800 (2015).
8. Darroch, S. A. F., Rahman, I. A., Gibson, B., Racicot, R. A. & Laflamme, M. Inference of facultative mobility in the enigmatic Ediacaran organism *Parvancorina*. *Biol. Lett.* **13**, 20170033 (2017).
9. Paterson, J. R., Gehling, J. G., Droser, M. L. & Bicknell, R. D. Rheotaxis in the Ediacaran epibenthic organism *Parvancorina* from South Australia. *Sci. Rep.* **7**, 45539 (2017).
10. Wagner, P. J., Kosnik, M. A. & Lidgard, S. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* **314**, 1289–1292 (2006).
11. Laflamme, M., Gehling, J. G. & Droser, M. L. Deconstructing an Ediacaran frond: three-dimensional preservation of *Arborea* from Ediacara, South Australia. *J. Paleontol.* **92**, 323–335 (2018).
12. Mitchell, E. G. & Butterfield, N. J. Spatial analyses of Ediacaran communities at Mistaken Point. *Paleobiology* **44**, 40–57 (2018).
13. Gray, J. S. in *Organization of Communities Past and Present* (eds Gee, J. H. R. & Gillier, P. S.) 53–67 (Blackwell, Oxford, 1987).
14. Root, R. B. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* **37**, 317–350 (1967).
15. Fisher, R. A., Corbet, A. S. & Williams, C. B. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**, 42–58 (1943).
16. Hubbell, S. P. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* **16(Suppl 1)**, S9–S21 (1997).
17. Frontier, S. in *Oceanography and Marine Biology: An Annual Review* (ed. Barnes, M.) 253–312 (Aberdeen Univ. Press, Aberdeen,1985).
18. Laland, K. N., Odling-Smee, F. J. & Feldman, M. W. Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl Acad. Sci. USA* **96**, 10242–10247 (1999).
19. Kosnik, M. A. & Wagner, P. J. Effects of taxon abundance distributions on expected numbers of sampled taxa. *Evol. Ecol. Res.* **8**, 195–211 (2006).
20. Xiao, S. & Laflamme, M. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol. Evol.* **24**, 31–40 (2009).
21. Tucker, C. M., Davies, T. J., Cadotte, M. W. & Pearse, W. D. On the relationship between phylogenetic diversity and trait diversity. *Ecology* **99**, 1473–1479 (2018).
22. Laflamme, M., Xiao, S. & Kowalewski, M. From the cover: osmotrophy in modular Ediacara organisms. *Proc. Natl Acad. Sci. USA* **106**, 14438–14443 (2009).
23. Sperling, E. A., Peterson, K. J. & Laflamme, M. Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans. *Geobiology* **9**, 24–33 (2011).
24. Glaessner, M. F. in *Treatise on Invertebrate Paleontology. Part A* (eds Robison, R. A. & Teichert, C.) A79–A118 (Univ. Kansas Press, Boulder, 1979).
25. Jenkins, R. J. F. The enigmatic Ediacaran (Late Precambrian) genus Rangea and related forms. *Paleobiology* **11**, 336–355 (1985).
26. Gehling, J. G. The Case for Ediacaran Fossil Roots to the Metazoan Tree Vol. 20, 181–224 (Geological Society of India, Bangalore, 1991).
27. Antcliffe, J. B. & Brasier, M. D. *Charnia* at 50: developmental models for Ediacaran fronds. *Palaeontology* **51**, 11–26 (2008).
28. Budd, G. E. & Jensen, S. The origin of the animals and a 'Savannah' hypothesis for early bilaterian evolution. *Biol. Rev. Camb. Philos. Soc.* **92**, 446–473 (2017).
29. Dececchi, T. A., Narbonne, G. M., Greentree, C. & Laflamme, M. Relating Ediacaran fronds. *Paleobiology* **43**, 171–180 (2017).
30. Sperling, E. A. & Vinther, J. A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evol. Dev.* **12**, 201–209 (2010).
31. Droser, M. L., Tarhan, L. G. & Gehling, J. G. The rise of animals in a changing environment: global ecological innovation in the Late Ediacaran. *Annu. Rev. Earth. Planet. Sci.* **45**, 593–617 (2017).
32. Droser, M. L. & Gehling, J. G. The advent of animals: the view from the Ediacaran. *Proc. Natl Acad. Sci. USA* **112**, 4865–4870 (2015).
33. Darroch, A. F., Laflamme, M. & Clapham, M. E. Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland. *Paleobiology* **39**, 591–608 (2013).
34. Clapham, M. E., Narbonne, G. M. & Gehling, J. G. Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology* **29**, 527–544 (2003).
35. Gehling, J. G. & Droser, M. L. How well do fossil assemblages of the Ediacara biota tell time?. *Geology* **41**, 447–450 (2013).

36. Zakrevskaya, M. Paleoecological reconstruction of the Ediacaran benthic macroscopic communities of the White Sea (Russia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **410**, 27–38 (2014).

37. Coutts, F. J., Gehling, J. G. & García-Bellido, D. C. How diverse were early animal communities? An example from Ediacara Conservation Park, Flinders Ranges, South Australia. *Alcheringa* **40**, 407–421 (2016).

38. Droser, M. L., Gehling, J. G. & Jensen, S. R. Assemblage palaeoecology of the Ediacara biota: the unabridged edition? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**, 131–1457 (2006).

39. Darroch, S. A. F. et al. Biotic replacement and mass extinction of the Ediacara biota. *Proc. Biol. Sci.* **282**, 20151003 (2015).

40. Boag, T. H., Darroch, S. A. F. & Laflamme, M. Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* **42**, 574–594 (2016).

41. Fedonkin, M. A. & Waggoner, B. M. The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**, 868–871 (1997).

42. Gehling, J. G., Runnegar, B. N. & Droser, M. L. Scratch traces of large Ediacara bilaterian animals. *J. Paleontol.* **88**, 284–298 (2014).

43. Ivantsov, A. Y. New reconstruction of *Kimberella*, problematic Vendian metazoan. *Paleontol. J.* **43**, 601–611 (2009).

44. Ivantsov, A. Y. & Malakhovskaya, Y. E. Giant traces of Vendian animals. *Doklady Earth Sci.* **385A**, 618–622 (2002).

45. Liu, A. G., Kenchington, C. G. & Mitchell, E. G. Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. *Gondwana Res.* **27**, 1355–1380 (2015).

46. Jensen, S. & Runnegar, B. N. A complex trace fossil from the Spitskop Member (terminal Ediacaran–? Lower Cambrian) of southern Namibia. *Geol. Mag.* **142**, 561–569 (2005).

47. Mángano, M. G. & Buatois, L. A. Decoupling of body-plan diversification and ecological structuring during the Ediacaran–Cambrian transition: evolutionary and geobiological feedbacks. *Proc. Biol. Sci.* **281**, 20140038 (2014).

48. Buatois, L. A., Wisshak, M., Wilson, M. A. & Mángano, M. G. Categories of architectural designs in trace fossils: a measure of ichnodisparity. *Earth Sci. Rev.* **164**, 102–181 (2017).

49. Smith, E. F. et al. The end of the Ediacaran: two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA. *Geology* **44**, 911–914 (2016).

50. Darroch, S. A. F., Smith, E. F., Laflamme, M. & Erwin, D. H. Ediacaran extinction and Cambrian explosion. *Trends Ecol. Evol.* **33**, 653–663 (2018).

51. Gray, J. S. Pollution-induced changes in populations. *Phil. Trans. R. Soc. Lond. B* **286**, 545–561 (1979).

52. Hamer, K. C., Hill, J. K., Lace, L. A. & Langan, A. M. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *J. Biogeogr.* **24**, 67–75 (1997).

53. Hill, J. K., Hamer, K. C., Lace, L. A. & Banham, W. M. T. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *J. Appl. Ecol.* **32**, 754–760 (1995).

54. Mouillot, D. & Lepretre, A. Introduction of relative abundance distribution (RAD) indices, estimated from the rank-frequency diagrams (RFD), to assess changes in community diversity. *Environ. Monit. Assess.* **63**, 279–295 (2000).

55. McElwain, J. C., Wagner, P. J. & Hesselbo, S. P. Fossil plant relative abundances indicate sudden loss of Late Triassic biodiversity in Greenland. *Science* **324**, 1554–1556 (2009).

56. Liu, A. G., McIlroy, D. & Brasier, M. D. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology* **38**, 123–126 (2010).

57. Buatois, L. A. & Mángano, M. G. *Ichnology: Organism–Substrate Interactions in Space and Time* (Cambridge Univ. Press, Cambridge, 2011).

58. Bottjer, D. J. & Jablonski, D. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *PALAIOS* **3**, 540–560 (1988).

59. Brocks, J. J. et al. The rise of algae in Cryogenian oceans and the emergence of animals. *Nature* **548**, 578–581 (2017).

60. Butterfield, N. J. Early evolution of the Eukaryota. *Palaeontology* **58**, 5–17 (2015).

61. Mitchell, E. G., Kenchington, C. G., Liu, A. G., Matthews, J. J. & Butterfield, N. J. Reconstructing the reproductive mode of an Ediacaran macro-organism. *Nature* **524**, 343–346 (2015).

62. Gehling, J. G. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *PALAIOS* **14**, 40–57 (1999).

63. Budd, G. E. & Jensen, S. A critical reappraisal of the fossil record of the bilaterian phyla. *Biol. Rev. Camb. Philos. Soc.* **75**, 253–295 (2000).

64. Gibson, B. M., Schiffbauer, J. D. & Darroch, S. A. F. Ediacaran-style decay experiments using mollusks and sea anemones. *PALAIOS* **33**, 185–203 (2018).

65. Gehling, J. G. Sequence stratigraphic context of the Ediacara Member, Rawnsley Quartzite, South Australia: a taphonomic window into the Neoproterozoic biosphere. *Precambrian Res.* **100**, 65–95 (2000).

66. Tarhan, L. G., Droser, M. L. & Gehling, J. G. Taphonomic controls on Ediacaran diversity: uncovering the holdfast origin of morphologically variable enigmatic structures. *PALAIOS* **25**, 823–830 (2010).

67. Burzynski, G. & Narbonne, G. M. The discs of Avalon: relating discoid fossils to frondose organisms in the Ediacaran of Newfoundland, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **434**, 34–45 (2015).

68. Sugiura, N. Further analysis of the data by Akaike's information criterion and the finite corrections. *Commun. Stat. Theory Methods* **A7**, 13–26 (1978).

69. Liu, A. G., McIlroy, D., Antcliffe, J. B. & Brasier, M. D. Effaced preservation in the Ediacara biota and its implications for the early macrofossil record. *Palaeontology* **54**, 607–630 (2011).

70. Plotnick, R. E. & Sepkoski, J. Jr. A multiplicative multifractal model for originations and extinctions. Paleobiology 27, 126–139 (2001)..

Author contributions

S.A.F.D. and M.L. collected and compiled the data. P.J.W. and S.A.F.D. performed the analyses. All authors contributed to writing the paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-018-0663-7.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to S.A.F.D.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

nature research

Corresponding author(s): Simon A.F. Darroch

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☒	☐	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	Data was collected from published sources, and from the Paleobiology Database (paleobiodb.org) where this data is accessioned.
Data analysis	Our analyses were performed using a custom code written in the statistical programming language R (R Development Core Team, 2015). A full copy of our code is included in the submission.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All R code and data are provided in online supplementary materials.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☒ Life sciences ☐ Behavioural & social sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Life sciences

Study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	This study uses published species-occurrence data from all Ediacaran localities worldwide where this data has been collected. All of these datasets have different sample sizes; we test for the possible effects of sample size on RAD distributions ('simple' or 'complex') using Mann-Whitney tests.
Data exclusions	(Text copied from Supplementary Materials) We have updated the taxonomic assignments of many taxa from Mistaken Point from those originally provided in Clapham et al. (2003) to reflect more recent systematic work (see Darroch et al. 2013 for additional details). Field and taxonomic studies of Charnia by Laflamme et al. (2007), Brasier and Antcliffe (2009), and Narbonne et al. (2009) have led to the attribution of the vast majority of specimens of "Charnia" from the Bristy Cove and Mistaken Point D and E surfaces to new genera, most notably Beothukis. Although two species of Fractofusus have been identified, they are easily differentiated by overall shape and are effectively temporally restricted in the Mistaken Point Ecological Reserve: oval shaped F. andersoni is restricted to the BC and LMP surfaces, whereas the spindle shaped F. misrai is restricted to the D, E, and G surfaces of the upper Mistaken Point Formation (Gehling and Narbonne 2007). The 'dusters' described by Clapham et al. (2003) have been formally described as Plumeropriscum hoffmani by Mason and Narbonne (2016). Lastly, Liu et al. (2011, 2012) suggested that several of the more enigmatic fossils preserved on the Mistaken Point surfaces (specifically the Ivesheadiomorphs) actually represent taphomorphs of other taxa whose morphology has been decayed and obscured by the growth of microbial mats over carcasses, rendering their identification difficult. To avoid this potential problem, we omitted Ivesheadiomorphs from analyses. A small number of modifications were also made to the Nilpena datasets taken from Gehling and Droser (2013). Helminthoidichnites is a convincing bilaterian trace fossil (Buatois et al., 2014). As such, counts of this ichnotaxon cannot be used to infer the relative abundance of the associated tracemaker, and so were removed. Aulozoon has also been claimed as a trace fossil by Seilacher (2007) and Seilacher and Gishlick (2014; although see Buatois and Mangano, 2016), and so has also been removed.
Replication	For ease of replication, all datasets and code are included in the submission.
Randomization	Samples (species-occurrence data) were grouped by Ediacaran chronostratigraphic 'assemblages', in order to see how the distribution of 'simple' and 'complex' communities changes through time. Consequently, randomization was not required.
Blinding	As above, palaeontological species-occurrence samples were analyzed to see how the distribution of 'simple' and 'complex' communities changes through time. Consequently, blinding was not required.

Materials & experimental systems

Policy information about availability of materials

n/a	Involved in the study
☒	☐ Unique materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Research animals
☒	☐ Human research participants

Method-specific reporting

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ Magnetic resonance imaging