# From organisms to biodiversity: The ecology of the Ediacaran-Cambrian Transition

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RRH: ECOLOGY OF THE EDIACARAN CAMBRIAN TRANSISTION

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## Non-technical abstract

Animals first evolved over 550 million years ago, during the Ediacaran time period, but it wasn’t until well into the Cambrian time period, around 520 million years ago that animal evolution really took off, and most modern animal groups first evolved. It is over this Ediacaran to Cambrian transition that we not only see animals first appear, but also the evolution of movement, the ability to burrow and to swim and the very first reefs and macroscopic predators. There are likely many different factors that shaped this radiation of animal life, so in this review paper we discuss the ecology underlying this Ediacaran to Cambrian transition, and place the individual specimens and taxa in the context of the environment in which they lived. After all, it is the interactions that organisms experienced in their daily lives with each other and their environment that led to the diversification of animal body-plans, and the evolutionary patterns we observe over these crucial 75 million years. As early animals evolved, we see diversification in feeding, biological and environmental interactions. These ecological interactions started off relatively weak, with few interactions between organisms, but then increased throughout the Ediacaran and into the Cambrian. By 500 million years ago, the ecosystem structure is similar to that of marine systems today. However, there are time-delays between the origins of structuring processes and the time when they have an observed impact on other organisms and their ecosystem. As such, while the key building blocks of ecosystem structure were in place by the end of the Cambrian, it takes evolutionary time-scales for the impact of them to be realised.

## Abstract

The Ediacaran – Cambrian transition (ECT; ~575–500 Ma) captures the early diversification of animals, including the oldest crown group taxa of most major animal phyla alive today. Key to understanding the drivers underneath the ECT macroevolutionary patterns are the interactions of animals with each other and their environment, and how these interactions scale-up to global diversity patterns.  Understanding the ecology of ECT organisms is enabled by the abundance of Lagerstätten over this time period, with a relative large proportion of soft-bodied organisms preserved, often within the communities in which they lived.  Here, we review our understanding of organismal, community and macroecology of the ECT, and how these different scales of ecological analyses relate to the macroevolutionary diversification patterns we see over this 75 million year time period. Across all ecological scales, we find clear trends, starting with stochastic ecosystem dynamics dominated by generalist taxa in the first Ediacaran communities, to more structured, niche-driven specialist dynamics by Cambrian Epoch 2.  These trends are reflected in organism functional morphology, the complexity and strength of organism interactions within their communities, and large-scale metacommunity, biogeographical and biodiversity patterns.  Yet, there is often a time-delay between the origination of a new type of ecological interaction, and when it is observed to impact the ecosystem as a whole.  As such, while many modern ecological innovations were in place by the end of the Cambrian, the knock-on effects and complexity of these interactions continued to build up throughout the Phanerozoic, leading to the complex biosphere we have today.

## 1 Introduction

One of the most important evolutionary innovations in the history of life on Earth was the evolution of animals, transforming the biosphere. The appearance and diversity of trace and body fossils in the Cambrian is sufficiently quick that it was termed the Cambrian Explosion in the 1970s (cf. Brasier 1979), with a rapid expansion of taxonomic and morphological diversity occurring in the Cambrian Epoch 2, where many animal phyla crown groups are first found (e.g. Erwin et al. 2011, Zhang et al. 2021*b*). These likely represent accurate timescales for animal origination and early diversification *contra* (dos Reis et al. 2015) due to the systematic errors in molecular clock estimates of animal origination times (Budd and Mann 2020, 2023). Since the 1970s, our understanding of the Cambrian Explosion and the origins and early evolution of metazoans have changed dramatically, with an appreciation that animals pre-date the Cambrian (Ford 1958). Indeed it was only in the 1950s that complex, macroscopic fossils were established to have been found in rocks known to be pre-Cambrian (Ford 1958), with six other localities known which are now dated as Ediacaran age (Billings and Billings 1872; Gürich 1933; Sprigg 1947; Misra 1969; Sokolov 1972; Figure 1A-D). Yet it is only in the last few years that taxonomic affinities of Ediacaran macrofossils have been resolved, with support from phylogenetic analyses, as total and/or crown-group animals (Budd and Jensen 2017; Bobrovskiy et al. 2018; Chen et al. 2019; Dunn et al. 2021), supporting the diversification of early animals in the Ediacaran. The presence of Ediacaran animals (Bobrovskiy et al. 2018; Chen et al. 2019; Dunn et al. 2021), coupled to differences in when different groups radiated (Servais et al. 2023) means that the term Ediacaran-Cambrian Transition (ECT) (cf. Narbonne et al. 1987) is a more appropriate term for the radiation and diversification of early animals across the Ediacaran and Cambrian (e.g. Wood et al. 2019).

Our understanding of the evolutionary relationships of Cambrian organisms has similarly shifted since the 1970s, greatly influenced by research effort on exceptionally preserved fossils. Detailed redescriptions of Burgess Shale animals first described by Walcott in the 1910-20s e.g. (Walcott 1911*a*, *b*, *c*, 1912, 1918, 1920) by Whittington and colleagues, alongside descriptions of new taxa, highlighted the unusual morphology of many Cambrian soft-bodied animals. While these fossil taxa were recognisable as metazoans, they were not always straightforward to place within extant classes or even phyla (Whittington 1971, 1975; Hughes 1975; Briggs 1976; Conway Morris 1976, 1977; Conway Morris and Robison 1982; Bruton and Whittington 1983; Whittington and Briggs 1985). Over the last 50 years, the integration of these previously problematic Cambrian animals into cladograms (Briggs and Fortey 1989; Budd 1993, 1998) and phylogenetic analyses including extant groups  allowed these and other soft-bodied fossil taxa to be recognised as stem-group representatives of modern classes and phyla (Daley et al. 2009; Legg et al. 2013; Smith and Caron 2015; Park et al. 2024; Rahman and Zamora 2024). These exceptional fossils have provided critical data for understanding the evolution of disparate body plans (Figure 1E-H), although not always without controversy (Daley et al. 2018; Nanglu and Caron 2018; Zhao et al. 2019, Nanglu et al. 2020*a*, 2023; Kihm et al. 2023; Park et al. 2024).

Other substantial insights into the ECT since 1975 have been gained through the large increase in terms of number of localities and sites (Fig. 2), geographic distribution of these sites, and new data collection strategies. These data have been leveraged to further our understanding in terms not only of ECT evolutionary relationships, but also their evolutionary drivers through interrogating the ecology and ecological relationships. Whereas historically specimens were often collected in isolation, so taken out of their population and community context, now this information is commonly kept intact, enabling us to reconstruct the interactions and ecology of these organisms on ecological, not only geological, timescales. These data are further leveraged by the vast improvements in computational and imaging power since 1975, enabling more detailed studies of organisms anatomy through photographic and scanning methods (Liu et al. 2015*b*), complex ecological statistical analyses (e.g. Clapham et al. 2003; Mitchell et al. 2015) as well as new computationally intensive analyses, such as computational fluid dynamics (e.g. Rahman et al. 2015*a*) and finite element analysis (Bicknell et al. 2018, 2021) to investigate ECT organisms. This change in ECT palaeontology is also mirrored in extant ecology, with a shift from largely descriptive and observational work, to that which is more hypothesis-testing based and data-driven (Anderson et al. 2021).

### *1.1 Diversity patterns over the ECT*

The term "Cambrian Explosion" conjures up images of low (or no) animal life prior to the Cambrian, followed by a rapid/exponential radiation in terms of taxonomic diversity. This pattern was visualised first in (Sepkoski 1978) who showed that the number of orders from the Ediacaran time period (then known as the Vendian) through the Cambrian followed an exponential curve which plateaued out in the Cambrian Epoch 2. This historical pattern is seen across multiple groups, including trace fossils, commonly preserved fossil groups such as trilobites and brachiopods (e.g. Zhang et al. 2008*b*; Managano and Buatois 2017; Paterson et al. 2019). Almost 50 years later, diversity patterns appear much more complex, with an increase and subsequent decrease in the Ediacaran, followed by a large increase in the Cambrian at the base of Stage 3, with the rapid diversity increase that we associate with the Cambrian Explosion, which then plateaus (Na and Kiessling 2015). Yet these patterns are not robust across all taxa, environments, or metrics. Ichnodiversity follows the classic ECT increase (Mángano and Buatois 2014), some groups show a pulsed radiation (Zhuravlev and Wood 2018) through the ECT, and others begin to radiate at different times, some even starting their radiation in the Ordovician (Servais et al. 2023).

With the variation in timings, and distribution of radiations across different groups, it is likely that a range of different processes drove the ECT. Indeed, the exponential increase in the diversity of a group follows a null model with background rates of origination and extinction leading to crown group radiation (Budd and Mann 2020), so arguably requires no drivers. However, in order to describe the processes behind these patterns, we need to resolve which key mechanisms were operating. Even if the ECT diversification was driven purely by abiotic factors, we still need to understand how animals interacted with these abiotic factors, enabling diversification.

### *1.2 Ecology*

Ecology is a very broad field, which includes a range of different sub-topics that consider organism interactions on a variety of different scales. On an individual specimen level, organism ecology describes aspects of the individual that reflect aspects of an organism's behaviour, functional morphology and/or life style. In a palaeontological context, functional morphology, ichnology and ecospace studies fall within organism ecology.

Organism ecology is the product of how different organisms interact with their local environment and other taxa, and these interactions and associations build up to form the network on interactions that form the ecosystem, the community ecology. Community ecology includes interactions such as competition, facilitation as well as trophic interactions between organisms, i.e. food webs. Community ecology can also include the interactions of organisms with their local habitat, and how that then impacts the organisms themselves. Population ecology also acts at a community level (communities are after all just collections of interacting populations), so includes analyses of population size distributions, for example, and can also include behavioural ecology, such as the interactions between predators and prey (e.g. the landscape of fear (Laundré et al. 2001)). In a palaeontological context, community ecology can be inferred from organisms' functional morphology (Haug et al. 2012), with hypotheses now often interrogated with computational methods (Rahman et al. 2015*b*; Bicknell et al. 2021), gut contents and morphology (trophic ecology and food webs)

(Butterfield 2002; Vannier and Chen 2005; Vannier 2012; Vannier et al. 2014; Strang et al. 2016; Peel 2017; Park et al. 2024), trace fossils including predation traces (Seilacher et al. 2005; Jensen et al. 2006; Chen et al. 2013; Bicknell and Paterson 2018; Mángano and Buatois 2020; Bicknell et al. 2022), and with exceptional preservation, from quantitative analyses of census populations or communities (Wood et al. 2003; Darroch et al. 2013; Zhao et al. 2014; O'Brien and Caron 2016; Mitchell et al. 2019, Nanglu et al. 2020*b*).

The ecological mechanisms which shape and drive evolutionary patterns act at and within community scale, which over time lead to changes in organism ecology and to broad patterns across space and time (between community ecology, or macroecology). Comparisons between different communities encompasses metacommunity (and metapopulation) ecology, landscape ecology, biogeography, global ecology movement ecology and macroecology. As such, diversity trends over geological and evolutionary time scales are the result of organism, community and global ecological interactions of organisms with each other and their environment.

In order to understand the long-term diversity and evolutionary patterns over the ECT, this review outlines our current knowledge in ECT organism ecology, community ecology and macroecology, and how these different scales of interactions feed into and influence the broad-scale diversity patterns we observe over the ECT. Of course, preservational biases can have huge impacts on palaeoecological studies (Nanglu and Cullen 2023). However, the exceptional preservation for many fossil localities spanning the ECT means that analytical techniques normally only applicable for extant systems can be used. The preservation of Ediacaran macrofossil communities is commonly in-situ, creating near-census preservation, with burial under volcanic ash flow (Benus et al. 1988; Wood et al. 2003; Noble et al. 2015) and pervasive microbial mat coverage of the sea floor leading to widespread in-situ preservation of benthic communities between 572 Ma and 550 Ma (Gehling 1999; Grazhdankin 2004; Fedonkin et al. 2007; Laflamme et al. 2011; Darroch et al. 2012; Tarhan et al. 2015, 2017). The terminal Ediacaran (550-539 Ma) also has exceptional soft-bodied preservation, but many of these were transported in mass flow events (Hall et al. 2013; Meyer et al. 2014), as well as biomineralized reefs preserved within carbonate platforms (Hofmann and Mountjoy 2001; Grotzinger et al. 2005; Warren et al. 2011).

Dozens of deposits with exceptional soft-bodied preservation are known from the Cambrian (Gaines 2014; Muscente et al. 2017). These provide census-level data for deposits which have not undergone significant transport, as well as a rich record of the anatomy of animals completely lacking hard-parts, as well as soft tissues such as appendages, nervous tissues and guts not usually preserved in the shelly fossil record (Gaines 2014), just as for Ediacaran deposits with similar preservation. However the oldest of these Cambrian deposits are known from Stage 3 (Figure 2), leaving a large gap in the soft-bodied fossil record spanning the entire Terreneuvian. Insights into the organism ecology of Terreneuvian animals can be gleaned from trace fossils, for which a continuous record exists (Seilacher et al. 2005; Managano and Buatois 2017; Buatois et al. 2018, 2020), as well as the small shelly and small carbonaceous fossil records (SSF and SCF respectively) (Butterfield and Harvey 2012; Kouchinsky et al. 2012), however the lack of exceptional deposits precludes community ecology studies. Compared to the Ediacaran, exceptional soft-bodied deposits from the Cambrian Series 2 and 3 provide a more heavily sampled interval including multiple deposits of similar age from geographically constrained areas (e.g. Burgess Shale and nearby localities, Collins et al. 1983, Caron & Jackson 2008a, Caron et al. 2010, Nanglu et al. 2020b; the Great Basin of the USA, Lieberman 2003, Lerosey-Aubril et al. 2018, 2020, Kimmig et al. 2019; South China, Hou et al. 2017, Fu et al. 2019, Steiner et al. 2005, Zhang et al. 2008*a*). Just as for soft-bodied preservation in the Ediacaran and post-Cambrian, these deposits provide a rich record important for our understanding of organism ecology. Compared to Ediacaran macrofossils, Cambrian macrofossils are generally more readily identifiable to the Phylum or Class level, facilitating a more straightforward comparison with modern analogues to infer aspects of their ecology (§2 below). Importantly, alongside the temporal gap in the Terreneuvian, there are geographic limitations to our understanding of soft-bodied Cambrian animals. Most pressingly, there are a paucity of deposits preserving soft-tissues from high latitudes, and those that are known do not have the same fidelity or abundance of fossils as the best low latitude Lagerstätten (they are Tier 3, rather than Tier 1, *sensu* Gaines 2014). Thus comparable preservation modes and types facilitate comparison of organism, community and macroecology across the ECT, albeit with some temporal and geographical gaps, and differences in sampling intensity.

## 2 Organism ecology

Organismal, or autecology, focuses on the adaptations that an individual organism has in response to its biotic and abiotic environment. These changes include morphological, physiological and behaviour adaptations. Insights into autecology can be gained through functional ecology analyses such as CFD and FEA to infer trophic relationships (e.g. Gibson et al. 2020; Bicknell et al. 2021), trace fossil analyses to understand habitat and feeding modes (Seilacher et al. 2005; Jensen et al. 2006; Mángano and Buatois 2020). These analyses can also be visualised in ecospace, whereby different axes are used to quantify the different niches that organisms can live and how this niche or ecospace occupation changes through time (Bambach 1983). For marine organisms, the axes used are normally: extent of mobility, position relative to the substrate, and feeding modes (Bambach et al. 2007). Body and trace fossil data are used to determine whether an area of ecospace (or ‘Bambach cube’) is occupied for a particular time slice. During the ECT, ecospace occupation changed dramatically between the Ediacaran and Cambrian, with the advent of animals, mobility and many new feeding modes. In the Ediacaran 12 Bambach cubes were occupied, with 30 in the Cambrian, and 92 in the modern (Bambach et al. 2007; Bush et al. 2011).

### *2.1 Marine animal forests: Lantian and Avalon assemblages: Pre- 558 Ma*

The first putative animals are sessile, benthic organisms which lived attached to the sea floor. The oldest are putative cnidarians from the Lantian biota, China (Wan et al. 2016) (up to 600 Ma), and widespread, abundant, large, complex fossils found predominantly in Newfoundland, Canada and Charnwood Forest, UK 572 - 560Ma, known as the Avalon assemblage (Waggoner 2003; Noble et al. 2015; Matthews et al. 2021). Avalon communities are dominated by rangeomorphs, a group of fractally branching organisms unique to the Ediacaran (Narbonne 2004; Brasier et al. 2012; Hoyal Cuthill and Conway Morris 2014), with large numbers of arboreomorphs (Laflamme and Narbonne 2008) also present (Clapham et al. 2003; Wilby et al. 2011). Phylogenetic analyses have resolved rangeomorphs as eumetazoans (Dunn et al. 2021). Other taxonomically-resolved taxa include crown-group cnidarians (Liu et al. 2014; Dunn et al. 2022) and putative sponges (Sperling et al. 2011; Suarez and Leys 2022). In these early Ediacaran assemblages, namely the Lantian and Avalon, there is no evidence for mobility within animal communities. Putative cnidarian trails have been found in nearby strata (Liu et al. 2010), but these may instead be microbial aggregates (Mariotti et al. 2016; Warren et al. 2020).

Feeding modes for these sessile, benthic organisms are hard to establish because comparisons with extant sessile benthic organisms such as sponges and sea pens are limited (Antcliffe and Brasier 2007; Laflamme et al. 2009). The widespread presence of rangeomorphs in deep-water strata below the photic zone demonstrates these sessile organisms were not algae or photosynthetic (Benus et al. 1988; Wood et al. 2003). Instead, the fractal-style branching of rangeomorphs (Hoyal Cuthill and Conway Morris 2014) suggests utilisation of resources from the water column (Narbonne 2004, 2005). This feeding could be through suspension or filter feeding, cf. extant sessile benthic animals, or osmotrophy like giant bacteria and other micro-organisms. As rangeomorphs exhibit similar surface area to volume ratios to extant osmotrophs, and no feeding apparatus for suspension or filter feeding is preserved at a micron-level scale, this unusual mode of feeding was thought likely (Laflamme et al. 2009). However, suspension feeding is now considered the most likely mode for rangeomorphs as osmotrophy could not occur at the high Raleigh numbers and advective fluid dynamics that operate at macroscopic scales (Butterfield 2022). Furthermore, if the filter/suspension feeding apparatuses were sufficiently small (< 8 microns) they might not have been preserved (Riisgård and Manríquez 1997), especially due to the preferential loss of labile tissue (Gibson et al. 2018). Lastly rangeomorphs display growth patterns that put them within Eumetazoans (Dunn et al. 2021), where osmotrophy is unknown. Computational fluid dynamics (CFD) simulations have led further support for suspension feeding in Ediacaran organisms. *Tribrachidium* and *Ernitetta* are now interpreted as a suspension feeders (Rahman et al. 2015*b*; Gibson et al. 2021), whereas the rangeomorph *Pectinifrons* shows feeding modes inconsistent with suspension feeding, osmotrophy and carnivory (cf. the carnivorous sponges *Lyra*; Darroch et al. 2023*b*).

The passive uptake of food from the water (by osmotrophy or passive suspension feeding) can be supplemented by making the most of canopy flow (Ghisalberti et al. 2014), but these are not active feeding modes as they do not expend energy in order to gain further energy. This contrasts with filter feeding, the active pumping of water through feeding apparatuses. Prior to 559 Ma the putative sponge *Thectardis,* (572Ma) is the only organism for which filter feeding has been proposed. Support for this feeding mode is based on length width ratios and comparisons of the morphology of Cambrian and extant sponge osculums and surface area of flattened specimens with *Thectardis* (Sperling et al. 2011). As such, prior to 559 Ma, known life modes are limited to non-mobile, exclusively passive feeders, attached to the substrate (Bush et al. 2011).

### *2.2 Origins of mobility and morphological diversification: White Sea assemblage: 558-550Ma*

Taxonomic, morphological and functional diversity increases dramatically ~ 555Ma during the Avalon Explosion or Ediacaran second wave (Shen et al. 2008; Droser and

Gehling 2015; Evans et al. 2018) with key localities for this time period in South Australia, and the White Sea Region, Russia (Boag et al. 2016). In contrast to the deep-water Avalon assemblage, the White Sea assemblage records a shallow water environment (Grazhdankin 2004; Tarhan et al. 2015). Phototrophs in the form of macroalgae are present within some communities (Wang et al. 2014; Droser and Gehling 2015; Xiao et al. 2020) as are the dominant Avalon taxa, rangeomorphs and arboreomorphs, but in reduced diversity and abundance (Evans et al. 2018). Communities of the tubular organism *Funisia* reach extremely high densities – over 6000 specimens/m$^2$ (Suprenaut et al. 2020) likely due to reproductive spawning akin to corals (Droser and Gehling 2008). Besides the these frondose organisms, the White Sea assemblage includes mat-sticking organisms with a range of symmetries not present today, such as triradial and tetraradial (Xiao and Laflamme 2009), as well as facultative mobile organisms in their colonisation life-stage (Darroch et al. 2017; Coutts et al. 2018). Tissues diversified, with hard tissues functioning as structural supports in the form of long (up to 37cm) spicules in association with a cone (Serezhnikova and Ivantsov 2007; Clites et al. 2012). During this Ediacaran second wave, there is also a diversification of bilaterians (Evans et al. 2018), including mobile taxa (Glaessner 1959; Fedonkin and Waggoner 1997) and a corresponding increase in ichnodiversity (Mángano and Buatois 2020). Some bilaterians are interpreted to have burrowed in and out of the microbial mats (Xiao et al. 2019), underneath them (Ivantsov et al. 2019) and through them (Evans et al. 2019). It is also around 555 Ma that within substrate habitats become well occupied with erniettomorphs (Glaessner 1959; Ivantsov et al. 2016). Mat grazing by *Kimberella* (Fedonkin and Waggoner 1997), is complemented by trails of *Yorgia* and *Dickinsonia* that suggest they fed directly on the microbial mat (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Ivantsov et al. 2019). Trails that wind underneath decaying body fossils suggest the first occurrences of scavenging (Gehling and Droser 2018). The irregular morphology of *Attenborites,* in contrast to most other Ediacaran taxa, suggests that it settled out of the water column, and was pelagic (Droser et al. 2020). Thus, the White Sea assemblage records a radiation of life-habitats, feeding and mobility.

Bridging the White Sea Assemblage (558-550 Ma) and the terminal Ediacaran assemblage, the Nama (550-539Ma), is the Shibantan assemblage (551 – 543Ma) (Condon et al. 2005; Huang et al. 2020). In common with the South Australian and Russian sites, Shibantan communities include rangeomorphs, arboreomorphs, bilaterians and macroalgae, with an increased abundance of ichnofossils as well as erniettomorphs (Xiao et al. 2021). What is notably different between the White Sea and South Australia localities and the Shibantan is the abundance of trace fossils, for which the Shibantan have consistently a high proportion of trace fossils, and dominant many communities (Xiao et al. 2021), some in association with complex body fossils of bilobed, segmented bilaterians (Chen et al. 2019).

### *2.3 Advent of biomineralization: Nama assemblage and the terminal Ediacaran 550 – 539 Ma*

Crucially, the Nama assemblage is where abundant biomineralizers are first found forming metazoan reefs, (Hofmann and Mountjoy 2001; Wood et al. 2003; Cortijo et al. 2010; Warren et al. 2011; Becker-Kerber et al. 2017). These reefs capture the first evidence of macropredation in the form of drill holes in the reef-building *Cloudina* (Hua et al. 2003). Ichnodiversity captures increasing behavioural complexity in the form of more complex and 3D burrows of treptichnids (Jensen et al. 2000), as well as evidence of sediment bulldozing *Parapsammichnites* (Buatois et al. 2018). Soft-bodied organisms such as rangeomorphs and erniettomorphs lived attached to and within the substrate (Pflug 1966; Meyer et al. 2014), but mat stickers are not found and soft-bodied mobile taxa are not preserved (Boag et al. 2016). Thus, at the end of the Ediacaran, we have occupation of pelagic, erect, surficial, seminfaual and shallow infaunal habitat occupation, the full complement of feeding strategies, from suspension feeding, deposit feeding, mining, grazing and predatory modes with a range of mobility from sessile attached, to fully mobile.

## *2.4 Digging deeper, building bigger: The Terreneuvian 539 – 521 Ma*

Microbial mats persisted into the Terreneuvian, with evidence for mat grazers, scratchers and miners continuing into the Fortunian (Buatois et al. 2014). Over the 20 Myr of the Terreneuvian, the maximum depth of burrows increased dramatically (from ~ 6 to 100 cm), and a range of hitherto unrecorded behaviours and structures can be observed in the ichnofossil record including penetrative feeding traces, farming burrows and domiciles for suspension feeders (Buatois et al. 2020). Archaeocyath reefs of active suspension feeders emerged during the early Terreneuvian, c. 535 Ma, initially as small patch reefs in shallow water environments of the Siberian Platform, (Zhuravlev et al. 2015; Antcliffe et al. 2019; Gibson et al. 2023). The Terreneuvian also records the first appearance of a new group of metazoan predators – chaetognaths – into the pelagic realm (Szaniawski 1983, 2002; Vannier 2007) and the earliest evidence for durophagous predation (Bengtson 1968; Conway Morris and Bengtson 1994), while the number of predatory drillholes – and diversity of groups with them – increased (Bicknell and Paterson 2018; Vinn 2018).

## *2.5 Radiation of feeding modes and mobility: Cambrian Epoch 2 and beyond (Post 521 Ma)*

Ichnodiversity, disparity and the modes of life represented in the trace fossil record increased again in Cambrian Epoch 2, across siliciclastic and carbonate environments (Buatois et al. 2020), complemented by a huge array of morphological innovations across the sensory, trophic and movement spectra, as well as an overall increase in the maximum size of animals. Archaeocyath diversity and geographic spread increased, and meter scale reefs appear in the fossil record, with different biohermal communities and structures reflecting the latitude and depth of their location (Gandin and Debrenne 2010; Zhuravlev and Wood 2018).

The widespread appearance of sensory organs (antennae, eyes, palps) in animals from Cambrian deposits of Epoch 2 and younger, and corresponding increases in brain complexity evidenced by exceptional fossils of nervous tissues (Ma et al. 2012*a*; Tanaka et al. 2013; Cong et al. 2014; Ortega-Hernández et al. 2019, 2022; Parry and Caron 2019; Parry et al. 2021; Wolfe and Ortega-Hernández 2021) has been termed the Cambrian Information Revolution (Plotnick et al. 2010), due to the sharp increase in the ability of organisms to sense and process their environment. Eyes are best known, most abundant, and most disparate in euarthropods (Zhao et al. 2013), but originated across a range of phyla in animals occupying very different niches. The oldest eyes in the fossil record – focal apposition eyes in the trilobite *Schmidtiellus* – are from the base of Stage 3 (Schoenemann et al. 2017). Some total-group euarthropod compound eyes contained thousands to tens of thousands of lenses (Zhao et al. 2013; Paterson et al. 2020), with variation in eye morphology indicating specialisations for different depths and feeding ecologies, including mesopelagic suspension feeders (Schoenemann and Clarkson 2011; Paterson et al. 2020). Camera-type eyes have been reported in the mollusc *Nectocaris* (Smith 2013), with simpler eyes and eye spots recorded in annelids (Zhao et al. 2023*a*), chordates (Shu et al. 2003), lobopodians (Ma et al. 2012*b*) and even priapulids (Schoenemann 2006). Beyond eyes, metazoan sensory structures first recorded at this time include antennulae and antennae in total-group euarthropods (Ma et al. 2012*a*; Ortega-Hernández et al. 2018, Zhai et al. 2019*a*, *b*), and annelid palps (Eibye-Jacobsen 2004, Liu et al. 2015*a*; Nanglu and Caron 2018; Parry and Caron 2019).

The first large active swimmers are also found in Cambrian Stage 3 deposits, adding multiple trophic levels to the pelagic realm. The largest swimming animals in Cambrian oceans were stem-group euarthropods such as radiodonts, predators which could reach up to one meter in length at this time (Potin and Daley 2023; Wu et al. 2024) and stem-group chaetognaths, reaching up to about 30 cm (Park et al. 2024). Adaptations for active swimming can be seen across a range of groups, including specialised swimming flaps, fins, and streamlined fusiform bodies (Whittington and Briggs 1985; Chen et al. 1995; Shu et al. 1999; Vannier and Chen 2000; Usami 2006; Daley et al. 2009; Vannier et al. 2009; Conway Morris and Caron 2012; Smith 2013; Daley and Edgecombe 2014, Liu et al. 2015*a*; Lerosey-Aubril and Pates 2018; Izquierdo-López and Caron 2019, Pates et al. 2021*a*; Lerosey-Aubril and Ortega-Hernández 2022; Potin and Daley 2023). Closer to the seafloor, specialised walking appendages facilitated more rapid movement for vagrant epifaunal animals (Minter et al. 2011).

The Cambrian Epoch 2 also saw increased specialisation in feeding appendages across groups, in particular within euarthropods. Multisegmented appendages for raptorial predation (Briggs 1979; Daley and Budd 2010; Daley and Edgecombe 2014; Jiao et al. 2021; Potin and Daley 2023), sediment sifting and sweep feeding (Daley et al. 2013; Yang et al. 2013; Moysiuk and Caron 2019; Potin and Daley 2023) and durophagy (Pratt 1998; Haug et al. 2012), are found across a number of total-group euarthropods, complemented by robust gnathobases, gnathobase-like structures, mandibles and mandible-like structures (Harvey and Butterfield 2008, 2022; Zacaï et al. 2016, Aria and Caron 2017*a*, *b*; Cong et al. 2017, 2018; Vannier et al. 2018; Yang et al. 2018; Bicknell et al. 2021; Moysiuk and Caron 2021).

Computational fluid dynamics analyses support both active pharangeal filter feeding and passive suspension feeding in Cambrian echinoderms (Rahman et al. 2015*a*, 2020), while numerous groups display feeding apparatuses with rows of finely spaced spines, setae, cilia or comb-like elements, suitable for suspension or filter feeding. These include total-group euarthropods (Vinther et al. 2014), luolishaniids (Ma et al. 2009; Yang et al. 2015; Caron and Aria 2017; Howard et al. 2020), hemichordates (Nanglu et al. 2016, 2020*a*) and the problematica *Siphausauctum* (O'Brien and Caron 2012) and dinomischids (Ou et al. 2017, Zhao et al. 2023*b*). This time period also sees the first documentations of brood care and extended parental care in the fossil record (Caron and Vannier 2016; Fu et al. 2018; Ou et al. 2020; Ma et al. 2023), demonstrating a diversification of behavioural ecology, as well as trophic ecology.

### *2.6 Summary of organism ecology over the ECT*

A fundamental shift in organism ecology occurred over the ECT. Prior to the Ediacaran, macro-organisms were exclusively primary producers, such as algae, and all heterotrophic organisms were microbial. The earliest animals still fed, like their microbial counterparts, on microscopic life such as plankton, and DOC and POM in the water column. Key innovations such as large-body size, coupled with differentiated tissues likely enabled further diversification of feeding modes, and the expansion to grazing, scavenging and indeed predation. Coupled to this trophic diversification, was the advent of mobility, facilitating access to nutrients which were becoming increasingly concentrated on the seafloor. Yet, despite the origination of mobility and predation in the Ediacaran, it is not until Cambrian Epoch 2 that specialisations really start to intensify. The specialisations and variation in form of feeding appendages, sensory equipment, movement types and burrowing employed by a diverse range of animal groups set the Cambrian Epoch 2 apart from the Terreneuvian and Ediacaran, and lay the groundwork for the rest of the Phanerozoic.

## 3 Community ecology

### *3.1 Dominant ecological modes within communities*

The simplest way to consider the community ecology of an ecosystem is in terms of the relative abundance of ecological modes – i.e. what is the primary niche of the community, and how are niches distributed within it. The oldest Ediacaran communities, the Lantian assemblage (~600 Ma), are dominated by algae with a few putative cnidarians (Yuan et al. 2013), so would be mainly autotrophic with some possible suspension feeders (Wan et al. 2016). The majority of communities prior to 560 Ma, from Newfoundland, Canada, and

Charnwood Forest, UK (Clapham et al. 2003; Wilby et al. 2011), only have suspension feeding organisms, rendering them ecologically monotypic. Ecological diversification of relative abundance of ecological modes, starts to occur around 550 Ma, with communities from Nilpena, South Australia (Droser et al. 2019) and the White Sea, Russia (Zakrevskaya 2014) hosting communities with only suspension feeders, cf. *Funisia* beds (Droser and Gehling 2008), as well as more ecological diversity communities with algae, suspension feeders, scavengers (Gehling and Droser 2018), and microbial mat feeders (both under and on top of the mat) (Ivantsov and Malakhovskaya 2002; Droser et al. 2019; Evans et al. 2019) (Figure 3). Less is known about the period between 550 Ma and 539 Ma, as fewer communities are preserved in-situ, but the Shibantan (551 – 543 Ma) records a diversity of complex mobile animals such as *Yilingia* (Chen et al. 2019) and ichnofossils as well as a diversity of suspension feeders and macroalgae (Xiao et al. 2021). The relative abundances of Shibantan communities are not (yet) known, but from the diversity of organisms, appear ecological similar to White Sea Assemblage communities. Note, that because the feeding mode of some complex, endemic species such as *Yilingia* are unresolved, there could be as yet un-reported additional feeding complexity. As in older (~555 Ma) communities, the terminal Ediacaran (550-539 Ma) has a plethora of suspension feeding tubular organisms preserved alongside trace fossils, but in the terminal Ediacaran biomineralized forms dominate (Becker-Kerber et al. 2017, 2020; Warren et al. 2023) and the relative proportions of predators are not known (Hua et al. 2003). These suspension feeding dominated communities form two distinct community types. In Namibia, Brazil and Paraguay *Cloudina* and *Namaclathus* reefs dominate (Hofmann and Mountjoy 2001; Grotzinger et al. 2005; Warren et al. 2011; Penny et al. 2014; Becker-Kerber et al. 2017). Soft-bodied rangeomorph and erniettomorphs are also present, occupying different settings to the reefs (Pflug 1966; Narbonne et al. 1997; Grazhdankin and Seilacher 2002) and are found mainly in transported deposits (Bowyer et al. 2017).

Less is known about the Terreneuvian, due to the lack of deposits preserving exceptional soft-tissues (see §2.4), so ecological dynamics cannot be resolved until the Cambrian Epoch 2. Deposits of this age and younger, for which the Chengjiang and Burgess Shale have been studied in most detail, show a variety of different dominant ecological modes. Chengjiang communities (518 Ma), are dominated by carnivorous taxa (mainly polychaetes) (Zhao et al. 2010, 2014), similar to near-contemporaneous Sirius Passet communities (Harper et al. 2019). In contrast Burgess Shale localities (506 Ma, Figure 3) have a mixture of deposit feeding (cf. Walcott Quarry) or suspension feeding dominated communities (cf. Tulip Beds) (O'Brien and Caron 2016), though it is important to note that recent flume experiments and reanalysis of sedimentary structures suggest that organisms from the classic Walcott locality in the Burgess Shale may have been transported large distances (Bath Enright et al. 2021). When the localities are sampled at a finer scale (10 cm sample intervals) a more complex pattern emerges with four community types of suspension feeding, hunting/scavenging, deposit feeding and nektobenthic-vagrant-deposit feeding and deposit feeding (Nanglu et al. 2020*b*), with a more general Cambrian Stage 3 pattern of the four BST community types (Hou et al., 2017; Fu et al., 2019) alongside those dominated by archaeocyath reefs (Sun et al. 2020).

While the diversification of feeding modes throughout the ECT is high, the innovation of predation dominated systems does not lead to a unidirectional change in ecosystem functioning, but more a broadening of different sorts of relative abundances of ecological niches across a spectrum. This point is illustrated by the notable overlap that occurs in the ranking of Nilpena Ediacaran communities (Droser and Gehling 2015; Droser et al. 2019) with Burgess Shale Cambrian communities (Nanglu et al. 2020*b*) when ordered by proportion of suspension feeding (Figure 3).

### *3.2 Abiotic and non-trophic biotic interactions within communities*

The relative abundances of different ecological groups within each community is a result of the interactions of taxa within the community, and how they interact with the local resources/environment. The environmental impacts on organisms, and the feedback relationships between organisms and their abiotic environment, are dependant on the relative needs of the organisms and the extent of abiotic nutrients. Organisms adapt to their environment to optimise their efficiency, for example, rangeomorphs maximised their surface area to volume ratios in order to optimise nutrient/resource exchange with the water column (Narbonne 2004; Laflamme et al. 2009).  These abiotic impacts can, and most commonly do, include organisms only existing in suitable habitats – these can be very clear, such as only organisms with good cold-tolerance existing at high-latitudes, or more subtle, such as trees having higher densities in regions of higher soil nutrients.  These habitat associations and influences can be detected through a variety of different methods.  In the Ediacaran, spatial point process analyses have been used to detect increased densities where taxa (or pairs of taxa) exhibit higher densities in areas of good quality patchy habitat (Baddeley and Turner 2005; Illian et al. 2008; Wiegand and Moloney 2013; Mitchell et al. 2019). Furthermore, these increased densities or aggregations can be statistically distinguished from other aggregation processes such as dispersal limitation and reproductive processes and facilitation. These methods have shown that environmental, or niche, influences are limited from 572-560 Ma (Mitchell and Kenchington 2018; Mitchell et al. 2019), and increase from 560-550 Ma (Mitchell et al. 2020). Preferential settlement (Boan et al. 2023) with community composition corresponding to different microbial mat maturity/complexity (Droser et al. 2022), demonstrates the importance of local environment to communities.  In the terminal Ediacaran (555 Ma -551 Ma), the reef builders *Cloudina*, *Corumbellina* and *Namacalathus* show clear associations with biolaminites such stromatolites and thrombolites (Hofmann and Mountjoy 2001; Grotzinger et al. 2005; Warren et al. 2011; Cai et al. 2014), reflecting either biotic interactions and/or mutual habitat associations.

The importance of local habitat patchiness increases into the Cambrian, as can be seen through the trace fossil record, through an increase in sediment bulldozing into the Fortunian as sediment feeders diversified (Mángano and Buatois 2014; Buatois et al. 2018) and where the complexity of interactions of ichnotaxa with patchiness increases (Mitchell et al. 2022). As the depth and complexity of burrowing increased into Cambrian Stage 2, with the onset of mix-ground ecology, and suspension feeding from within the sediment (Mángano and Buatois 2014), these subtle differences of substrate local patchiness likely decreased in importance, since large-scale and more significant habitat variations took over, and the benthic realm became more akin to the modern, with other factors becoming a first order process of habitat variation, over subtle differences in microbial mat or sediment variations.

Biotic interactions, that is the interactions between two taxa consist of interactions such as competition, facilitation and mutualisms and trophic interactions.  For the oldest Ediacaran communities, there is limited evidence of competition for resources, with only rare intra and inter-specific competition (Mitchell and Butterfield 2018; Mitchell and Kenchington 2018). As the extent of intra and interspecific competition increases throughout the Ediacaran (Droser et al. 2017), coupled to an increase in relative importance of niche/environment interactions (Mitchell et al. 2020; Droser et al. 2022) so does the complexity of interactions, with facilitation first detected in the terminal Ediacaran in terms of preferred settling near favourable fluid dynamic flow (Gibson et al. 2021).

Complexity of types of ecological interactions increases in the Cambrian, with symbiosis (Vinn 2017), parasitism (Peel 2015; Li et al. 2020; De Baets et al. 2021; Chen et al. 2022), mutualisms and commensalism (Topper et al. 2014; Peel 2015; Nanglu and Caron 2021), and epibionts (Zhang et al. 2009; Topper et al. 2015) all present. Yet, in terms of observed competition within Cambrian ecosystems, there is only limited evidence of its impact. Competitive exclusion is extremely rare in Phanerozoic benthic marine ecosystems (Klompmaker and Finnegan 2018), likely due to the higher levels of bioturbation, predation and disturbance preventing ecosystems from reaching carrying capacity (Stanley 2008*a*; Klompmaker and Finnegan 2018). An exception is possible in the case of archaeocyath reefs. Distorted specimens likely resulted from competition for space (Zhuravlev and Wood 1995), in an ecosystem lacking known predators and – due to its biomineralized nature – less prone to environmental disturbance. Though even then both niche and neutral processes appear to have played a role in these early sponge reef ecosystems (Zhuravlev et al. 2015).

### *3.3 Trophic interactions*

Trophic interactions, namely the interactions that occur between an organism and its food source, have been suggested to be a key driver of the Cambrian Explosion, with predators and their prey driving the morphological changes and diversity seen during the Cambrian (Bengtson 2002). Trophic complexity started relatively simply (Figure 4), with early Ediacaran organisms feeding primarily/exclusively on plankton and POM/POC from the water column (Laflamme et al. 2009; Butterfield 2022). New trophic links formed between organisms and the microbial mat, with *Dickinsonia* and *Yorgia* feeding on it (Ivantsov and Malakhovskaya 2002; Sperling and Vinther 2010; Ivantsov 2011; Evans et al. 2019; Ivantsov et al. 2019; Ivantsov and Zakrevskaya 2021; Bobrovskiy et al. 2022), and with the origination of the first scavengers (Gehling and Droser 2018) (Figure 4). There is no evidence of pelagic macroscopic predation until the terminal Ediacaran (Hua et al. 2003). Further insights into the extent of resource niche overlap found that the majority of 560 – 572 Ma Ediacaran communities had shared niches, so likely food sources, niche complexity increased with complex/partitioned niches within communities during 560 – 550 Ma, then decreased with simpler/shared niches in the 550 – 540 Ma (Darroch et al. 2018*a*). These data likely reflect an increase in trophic complexity around 555 Ma, potentially followed by a decrease in the terminal Ediacaran.

These matground dominated dynamics persisted into the early Cambrian (Fortunian), with a shift in trophic dynamics starting in Cambrian Age 2, with similar style of trophic dynamics to the modern present in Age 3 (Cambrian Epoch 2) (Zhang et al. 2021*a*) (Figure 4). There is a distinct shift in the importance of biotic interactions within Cambrian food webs from Age 3 and younger, i.e. with trophic interactions, where we see a sharp increase in the functional morphology of feeding apparatuses, predatory apparatuses and defensive tools (§2.6). Initially it was thought these trophic chains were relatively short, with only primary predators (Vannier and Chen 2005), but more recent work has suggested that there can be relatively long trophic chains of 4-5 species long (Hu et al. 2007; Dunne et al. 2008). Such complex chains are not necessarily present in all Cambrian ecosystems, such as those dominated by suspension feeders or detritovores cf. (O'Brien and Caron 2016) (Figure 3) .

All these trophic interactions translate into relative complex trophic networks (or food webs), with food webs of the Burgess Shale and Chengjiang displaying similar topologies in terms of distributions of feeding links as modern ones (Dunne et al. 2008). These Cambrian food webs show a dependence of their structure on the number of taxa and feeding links, which is found in modern webs modelled by simple "niche models". However, the Chengjiang web has long paths (feeding chains) and more feeding loops than modern webs. One cause of this is that the prey species with the most predator links have many more predators than expected from modern webs, perhaps due to a lack of specialised defence mechanisms. Both Burgess Shale and Chengjiang food webs show a higher variation in the number of trophic links per taxa than is seen in the modern. These results are thought to suggest that as ecosystems evolved after the Cambrian, the trophic structure became more constrained (Dunne et al. 2008).

### *3.4 Ecosystem resilience and complexity*

In order for ecosystems and the organisms within them to persist over geological time-scales, these ecosystems must be stable, i.e. have resilience. Ecosystem stability is strongly correlated to taxonomic and functional diversity, because more diverse systems have a better capacity to cope with biotic and abiotic changes and fluctuations through feedbacks within the network of interactions (abiotic, biotic and trophic) within the community (May 1974; Tilman 1994; McCann 2000). These feedbacks and redundancy mean that the more complex an ecosystem is, the more stable it is (Ruiter et al. 1995; Neutel et al. 2007), in contrast to theoretical (random) networks, where complex networks are less stable (May 1974, 2019).

Ecological complexity is most simply measured in terms of taxonomic diversity – with more diversity corresponding to more stable ecosystems (Ives and Carpenter 2007). However, ecological stability is not as straightforward as just taxonomic diversity stabilising the ecosystems. If there is a single species which is crucial for ecosystem function/stability, then the system is vulnerable (Paine 1969; Jain and Krishna 2002). As such, communities in which many species occupy similar niches tend to be more stable, so that if a specialist predator, or pathogen, or habitat changes, other species can fill in that ecological role (Petchey and Gaston 2006). The capacity for ecosystems to have this redundancy is most simply measured using evenness (Shannon 1948), that is the distribution of relative abundances of taxa within an community. If the community is very skewed, and so has a few very high abundance taxa, and many rarer taxa, the system is likely much more sensitive to perturbations compared with communities that are more even (Hillebrand et al. 2008).

Over the ECT, some Ediacaran communities exhibit relative high evenness, corresponding to many relatively abundant taxa and complex niches, alongside simpler, more monospecific communities (Darroch et al. 2018*a*). As such, it is likely that Ediacaran ecosystems were not all equally resilient. The stabilising mechanisms for this resilience can vary, with systems stabilised primarily through primary production availability (bottom-up), and other systems stabilized by predators (top-down). Due to the lack of higher predators, and short trophic links (Figure 4), Ediacaran ecosystems were stabilised from the bottom-up, so dependent on abiotic resources, and environmental factors. The lack of resource competition suggests that such resources are not limited (Mitchell and Kenchington 2018; Mitchell et al. 2019), making these Ediacaran systems relatively stable.  This bottom-up stability likely persists until Cambrian Ages 2 and 3, when some (but not all,§3.1) systems exhibit many trophic levels, which could potentially lead to top-down stabilising mechanism.  However, longer feeding chains seen in the Chengjiang are sufficiently long that species may be functional separated from each other, potentially destabilising the systems (Dunne et al. 2008). The potential (relative) lack of stability in the Cambrian was also possibly present within Burgess Shale communities, where the Tulip Bed and Walcott Quarry communities have high abundances of a few dominant taxa, with many rarer taxa (O'Brien and Caron 2016).

# 4 Macroecology

Determining the processes that shape community-level ecological metrics such as diversity and community composition is enhanced through comparisons with other communities, enabling the teasing apart of the relative importance of different temporal and environmental drivers, and how they interact with the organisms at a community level.

## *4.1 Beta diversity*

Beta diversity is a measure of how much variation there is between communities (Anderson et al. 2011), with high diversity indicating little species overlap and thus different species in different communities, and low beta diversity indicating high levels of overlap and thus similar species are found across different communities.  Regions that exhibit high beta diversity are more stochastic, that is the community compositions are not the systematic result of adaptions to their local environment, and biotic interactions, but instead colonization and dispersal dynamics, for example as seen at modern hydrothermal vents (Giguère and Tunnicliffe 2021). If biotic interactions and environmental filtering are strong drivers of community composition, within a given environment we would expect the same community compositions to emerge, and so beta diversity would be low, for example in shallow water reefs (Harborne et al. 2006). As such, quantifying beta diversity can help inform the key factors underlying community composition and development.

Ediacaran beta diversity is significantly higher than the Cambrian and the rest of the Phanerozoic. This beta diversity increase has been suggested to be due to the rarity of mobile taxa which may have increased the patchiness of communities (Finnegan et al. 2019). Strong dispersal limitation, such as produced via asexual stoloniferous reproduction (Mitchell et al. 2015), provides a complementary cause for community patchiness.  Competitive communities can also increase beta diversity (Stanley 2008*b*), but the rarity and weakness of resource competition within Avalonian Ediacaran communities suggests that  that niche processes and biotic interactions shape the communities less than in extant systems (Na and Kiessling 2015; Finnegan et al. 2019).  As such, high Ediacaran beta diversity may result from similar processes as in hydrothermal vent systems. These vent systems often exhibit high beta diversity (Giguère and Tunnicliffe 2021) due to the stochastic nature of the creation suitable habitat (the vents). Thus the identity of organisms that reach and colonise the new habitat first are more stochastic than most extent benthic systems. Over the ECT, patterns of beta diversity do not necessarily follow those of alpha diversity. Alpha diversity increases from the Ediacaran through to Cambrian Age 3 (Figure 2), yet beta diversity decreases into the Fortunian before increasing again through Cambrian Ages 2 and 3. Middle-level beta diversity later in the Cambrian suggests an increase in the influence of these niche and biotic interactions throughout (Zhao et al. 2014).  In these first three stages of the Cambrian, alpha-beta diversity dynamics is consistent with a low-competition dynamics, i.e. little pressure on resources, (Hautmann 2014). New species appear either in previously unexploited niches, or communities have more species within a single niche, potentially due to predation exerting a top-down control (Na and Kiessling 2015).  Beta diversity increases from the Cambrian to the Devonian as resources reduce, increasing competition and constricting niches (Na and Kiessling 2015; Penny and Kröger 2019).  These beta diversity patterns suggest that stochasticity is key to Ediacaran communities, with limited niche and biotic interactions. Niches constrict and biotic interactions increase throughout the Cambrian, feasibly as a result of predation and top-down control.

### *4.2 Biogeography*

Biogeographical patterns require sufficient sample sizes to resolve, which means that inferences over the ECT are limited. Within the Ediacaran detailed biogeographical analyses are limited to differences between high and low palaeolatitudes, due to the number and geographical placement of localities (Boddy et al. 2021). The frondomorph group, which includes rangeomorphs and arboreomorphs, radiated from high to low palaeolatitudes, in contrast to algal and protist groups, which showed no palaeolatitudual differences (Boddy et al. 2021). Further palaeolatitudual differences are found with the bilaterian group which radiates from low to high latitudes, unlike algal, tubular, soft-bodied and biomineralizing taxa (Boddy et al. 2021), showing Ediacaran biogeographic differences with taxa distributions through time, even at this coarse spatial scale. The drivers behind these two patterns are not yet resolved, but the frondomorph high to low radiation is likely due to evolutionary processes with a deep water, high latitude, origination (Griffiths et al. 2023), while the bilaterian palaeolatitude signal could be a reflection of high rates of diversification at the tropics leading to quicker evolution at these lower latitudes (Mittelbach et al. 2007).

In the Cambrian, the presence and strength of biogeographical biodiversity patterns increased, showing increase in provinciality, or bioregions, coupled to a decrease in geographic ranges (Hendricks et al. 2008; Na et al. 2023). This increase in biogeographical patterns has been suggested to relate to several factors, including the geographical differences in origination of groups (Lieberman 2002, 2008; Lieberman and Meert 2004), changes from low-competition to high competition models with a change from wide to lower geographical ranges (Na and Kiessling 2015), differences within groups, relating to dispersal abilities (e.g. with soft-bodied, pelagic soft-bodied Cambrian arthropods showing greater geographical ranges than trilobites (Hendricks et al. 2008) and more broadly to biogeographic differentiation at regional and local scales (Na et al. 2023). However, in some cases, for example the trilobites, their origination within the Cambrian (Paterson et al. 2019) does not correlate with the breakup of Pannotia, tens of millions of years earlier  leaving many patterns still to be explained.

### *4.3 Metacommunity ecology*

The many different types of ECT communities (§3.1) could be due to evolutionary/temporal environmental filtering, and/or the result of different biotic interactions. Cluster analyses based on community composition, can shed led on these drivers because if environment dominates, we expect the groups of communities that share similar composition to have lived in similar environments. If the communities represent a progressive evolution, then the community groups of similar geological ages should cluster together (Anderson 1971). Once different groups of communities, or metacommunities, have been established, the metacommunity structure within these groups can shed further light on the driving forces within them, elucidating differences in environmental and biotic drivers, and the relative importance of stochasticity between metacommunities (Leibold et al. 2004).

The three classic assemblages of the Ediacaran – Avalon, White Sea and Nama, were first proposed by Waggoner in 2003, where they occupied distinct temporal, environmental as well as species-specific assemblages (Waggoner 2003), with a direct reading suggesting an evolutionary radiation from deep water, high latitude sites.  Since then the number of sites has increased dramatically from 15 in Waggoner's initial analyses to 127, with more overlap between environments and time, yet these three key assemblages (or biozones) remain robust, using a variety of different clustering and network approaches (Boag et al. 2016; Muscente et al. 2019; Boddy et al. 2021), so are likely fundamental to the Ediacaran. Because the environmental and temporal range of the Ediacaran localities are largely (but not totally) non-overlapping, determining the extent to which the differences between the oldest, Avalon assemblage, and the much more diverse White Sea assemblage are evolutionary or environmental, is not possible to establish (Grazhdankin 2004; Boag et al. 2016). As work on other sites, such as the Lantian, Shibantan and Corumbá localities increases, it possible that additional assemblages may emerge such as with the Shibantan (Xiao et al. 2021) with the potential of overlapping temporal and species ranges of the new data to enabling a teasing apart of environmental versus evolutionary trends.

Ediacaran diversity increases between the Avalon and White Sea, then decreases between the White Sea and Nama, which at a global scale is not due to sampling differences (Muscente et al. 2019; Boddy et al. 2021). This diversity decrease has been suggested to be caused by a catastrophic mass extinction (Darroch et al. 2018*b*, 2023*a*; Zhuravlev and Wood 2018; Muscente et al. 2019; Evans et al. 2022), change in taphonomic window (Laflamme et al. 2013) or a biotic replacement model, whereby Phanerozoic-type animals out competed Ediacaran-type animals, driving them extinct (Darroch et al. 2015), potentially through "wormworld" fauna (Schiffbauer et al. 2016). This diversity decrease is robust to sampling differences on a global scale (Muscente et al. 2019), but there are however palaeolatitudinal differences in sampling biases, with low latitude diversity not significantly different from the number of low latitude localities, and high latitude decoupled with only weak significance (Boddy et al. 2021). This suggests that some (but not all) of the drop in diversity in the terminal Ediacaran may be an artefact of sampling biases. Further differences in diversity could be due to internal restructuring: analyses of the metacommunity structure between the three large assemblages suggest diversity differences between the White Sea and Nama assemblages are more likely due to internal ecological restructuring because there is an increase in turnover, a maintenance/increase in significant pairwise taxa associations, and an increase in depth specialization which are all inconsistent with a catastrophic mass extinction (Eden et al. 2022). As such, biological (within organism) and ecological complexity likely increased throughout the Ediacaran.

In the Cambrian, the palaeocommunity data from contemporaneous Cambrian sites within different palaeoenvironments enables the teasing apart of niche partitioning (Na et al. 2023). However,  Lagerstätten with soft-bodied preservation that are sufficiently sampled to be able to make ecological inferences are relatively constrained to a ~20 Myr between 518 and 499 Ma, which limits the ability to infer evolutionary or temporal trends from the data. In addition, the vast majority of these Lagerstätten are found in the palaeotropics.  None-the-less, in some cases temporal trends are observable, such as with echinoderms where the differences in their presence between the Chengjiang and Burgess Shale localities could be evolutionary (O'Brien and Caron 2016). Temporal trends can also be detected at a fine-scale resolution through collection of data from narrow sample intervals of Burgess Shale communities (10cm, ~600 yr). These reveal periods of relative ecological stability, followed by a turnover in community composition, suggesting periodic environmental disturbances and then recolonization (Caron and Jackson 2008), with similar community composition between successive sample intervals. Temporal trends also changed Burgess Shale community compositions, with the youngest communities (Tulip Bed) lacking hemichordates and annelids, which are abundant in the older localities. One such suggestion for these changes is competitive exclusion within a niche, for example of sponges by hyoliths and hemichorates (Nanglu et al. 2016, 2020*b*; Moysiuk et al. 2017).

The relative effects of environmental filtering (i.e. different taxa living within different environments) varies in the Cambrian. In the House Range (Utah), the higher diversity of pelagic animals in the Marjum Formation compared to the slightly older Wheeler Formation was suggested to be due to the deepening of the environment in the Marjum Pass area of the Great Basin and/or changing regional ocean circulation (Pates et al. 2021*b*). Older Chengjiang communities (518 Ma) also show evidence of environmental filtering with a gradient from lower diversity near to higher diversity off-shore (Zhao et al. 2012), and a high facies-control on community compositions (Sun et al. 2020) but such signals are not present in Burgess Shale data (O'Brien and Caron 2016).

Other differences between  the Chengjiang and Burgess Shale localities include differences in specialisation. In contrast to Chengjiang taxa, dominant Burgess Shale taxa show broad stratigraphic and geographic ranges, with the four different community types not split by locality nor environment, but instead varying at a local and regional scale (Nanglu et al. 2020*b*).  The reoccurrence of the abundant taxa at within Walcott Quarry communities suggests that these abundant taxa are likely environmental and/or geographic generalists with the majority of abundant Walcott Quarry taxa also present in Tulip Beds, albeit as rare taxa (e.g. *Marella*) (Caron and Jackson 2008).  There are signals of localisation because many of the taxa from the Walcott Quarry and Tulip Beds occur only on a single horizon, suggesting that some taxa are adapted to their local environment, but not as well adapted to the wider regional environment (O'Brien and Caron 2016). Note, that some of these differences could be taphonomic or due to transportation since the mobile detritivores that dominate Walcott Quarry communities may have escaped from the small burial events at the Tulip Beds (O'Brien and Caron 2016), and fossils from the classic Burgess Shale quarry may have undergone significant transport (Bath-Enright et al. 2022).  While these patterns suggest recolonization from a species pool of taxa with good dispersal and/or colonization ability was important, i.e. community composition was still relatively stochastic, (as suggested by the beta diversity patterns (Na and Kiessling 2015)),  the dispersal/recolonization cannot account for all the community differences found – with priapulids and sponges abundant throughout most Cambrian localities, but not at Marble Canyon suggesting some temporal or environmental filtering (Nanglu et al. 2020*b*).

There are differences in ecological dominance between Chengjiang and Burgess Shale communities, with Chengjiang dominated by carnivorous taxa (Zhao et al. 2014) in contrast to deposit and suspension feeding ecological dominance in Burgess Shale localities (O'Brien and Caron 2016). A comparable signal is seen in the large swimming radiodonts, with raptorial amplectobeluids and anomalocaridids dominant in Chengjiang but sediment sifting hurdiids more diverse in the Burgess Shale and Great Basin (Wu et al. 2022). Again, these could be the result of environmental differences, rather than temporal or geographical, but to resolve the underlying drivers of these differences requires a series of community-level samples from sites spanning a broad temporal range but limited geographically. Thus data from Chengjiang and the Burgess Shale could be complemented with similar high resolution studies from Kaili or the Great Basin respectively.

### *4.4 Stochastic to deterministic trends*

Metacommunity comparisons reveal patterns of change across the ECT. In the Ediacaran, such metacommunity analyses have shown a pattern increasing specialisation not only of organisms, but of communities (Eden et al. 2022). The oldest Ediacaran assemblage, the Avalon, is populated by generalists, with little environmental influence. In the White Sea assemblage there is increased metacommunity variation, with metacommunity structure dependent on environment and biogeographical differences in the pairwise interactions of taxa. The terminal Ediacaran assemblage, the Nama, shows strong niche segregation (Eden et al. 2022). Patterns of increasing specialisation and habitat segregation are also seen in early Cambrian ichnotaxa, which start out as generalists in the Fortunian, but then increase in specialisation leading to habitat segregation in the Cambrian Stage 2 (Meek et al. 2023). However, the overarching change over the ECT from stochasticity populated by generalists to more deterministic, with more specialists, is not necessarily a unidirectional process. Cambrian archaeocyaths sponge reef communities on the Siberian Platform (525–514 Ma) show changes between individually-driven metacommunity structure to within-community interactions and metacommunity complex as reef habitat expands, and then a subsequent reduction in metacommunity complexity as reef habitat reduces (Zhuravlev et al. 2022). Coupled to diversity patterns in and between different Cambrian clades (Servais et al. 2023), these patterns demonstrate that while ecological complexity increases, it is not a simple linear process, but instead was likely pulsed and multidirectional (Zhuravlev and Wood 2018), and heterogeneous environmentally and geographically.

## 5 Ecosystem engineering

Interactions and feedbacks within and between ecosystems can not only stabilise, but also drive ecological dynamics through ecosystem engineering, whereby taxa change their local environment in a way that makes it more habitable for other organisms. The precise definition of ecosystem engineering is much debated: on one side, every living organism changes its environment (Jones et al. 1994), but on the other side it is not useful to discuss ecosystem engineering in terms of ecosystem changes that do not significantly change and improve the environment for other organisms (Reichman and Seabloom 2002). As such, we will define ecosystem engineering when organisms are impacted their environment in sufficient quantities, that there are observable (positive) impacts on other organisms (cf. Hastings et al. 2007).

There are four main Ecosystem Engineering mechanisms that have been suggested to contribute to the ECT diversification 1) Savannah Hypothesis, 2) Reefs, 3) Vertical substrate bioturbation and 4) Aquatic Bioturbation. The Savannah hypothesis is the oldest form of metazoan ecosystem engineering, whereby early bilaterian evolution is driven by the search for patchy food sources on the seafloor which come from the decaying remains of sessile organisms (Plotnick et al. 2010; Budd and Jensen 2017). This mechanism persists until Cambrian Stage 3 when multiple different processes, namely pervasive burrowing, detritivores and scavenging means that such patchy resources do not remain in the sediment for long enough to be evolutionary drivers. This hypothesis is consistent with data from Ediacaran community ecology. These show an increase in the amount of interactions that Ediacaran organisms had with their environment (Mitchell et al. 2020), increased scavenging

(Evans et al. 2019), increases in ichnodisparity (Mángano and Buatois 2014) and the extent to which trace fossil interact with increased complexity with substrate patchiness (Mitchell et al. 2022).

The second group of ECT ecosystem engineers are reefs which dramatically changed their environment through the creation of hard substrate and complex 3D space. Through this they created more niches, which in modern systems is highly correlated with diversity as reef animals use coral structures for food, protection from predation, habitat and nurseries (Bozec et al. 2013; Brandl et al. 2019). However, when these opportunities within reefs started to be fully utilised is not clear cut. The Ediacaran reefs of *Cloudina*, *Corumbella* and *Namacalathus* demonstrate significant ability to build large structures, but there is no direct evidence of facilitative ecological interactions of other animals with these Ediacaran reefs (Warren et al. 2017; Wood et al. 2017), although the extent to which this could be a preservational artefact is not clear since soft-bodied Ediacaran organisms are not easily preserved within such carbonate settings (Hall et al. 2013). Archaeocyath reefs are abundant from the early Cambrian, yet again the evidence of direct facilitation of diversity and habitat creation is missing. A second potential ecosystem engineering effect of archaeocyath reefs is to increase nutrient flux to the benthos through increased fluid flow over the reefs which then creates capacity for an increase in diversity of scavengers and detritoves as well as increasing the capacity for higher trophic levels of predators (Manzuk et al. 2023). The reduction in diversification after the extinction of archaeocyaths, suggests that these reefs may have contributed to diversification over the ECT (Figure 2, and Fig. 1; Na and Kiessling 2015).The first demonstration of colonization of biotic hard substrates isn’t until Cambrian Stage 4, when brachiopods form the Guanshan Biota are the first to host epibionts (Chen et al. 2022). While the presence of reefs correlates with increasing diversity (Reaka-Kudla et al. 1996; Small et al. 1998), it is not until the terminal Cambrian that there is a significant correlation between taxonomic diversity origination in reefs (Kiessling et al. 2010). As such, while reefs substantially changed their environment, the evidence that organisms utilised their structures as ecosystem engineers is not in evidence until the terminal Cambrian, so the impact of such reefs ecosystem engineering on the ECT diversity patterns is not clear.

Thirdly, the substrate was significantly changed through the ECT by increases in bioturbation, also known as the Agronomic revolution or Cambrian substrate revolution (Seilacher 1994; Bottjer et al. 2000). The impact of the first tracemakers on the physical environment was initially minimal, with horizontal trails such as *Helminthoidichnites* and *Dickinsonia* trails on or below microbial mats ~555Ma (Ivantsov and Malakhovskaya 2002; Buatois et al. 2014; Evans et al. 2020; Ivantsov and Zakrevskaya 2021). These horizonal trails increased in density and complexity in the Shibantan and Nama assemblages (Cribb et al. 2019; Linnemann et al. 2019), with increased capacity to bulldoze cf. *Parapsammichnites*, or move sediments (Buatois et al. 2018), and increased depth penetration cf. treptichnids (Mángano and Buatois 2020). Matground coverage persisted into the Fortunian (Buatois et al. 2014), indicating that sediment disturbance was insufficient to impact mat growth, but crucially the development of vertical burrows cf. *Treptichnus pedum*, and more complex structures cf. *Oldhamia*, enabled more efficient feeding on the mats and sediments (Mángano and Buatois 2020). Ichnodiversity and bioturbating ecosystem engineers increased the most between the terminal Ediacaran and Fortunian within the ECT and Ordovician (Buatois et al. 2020), but the most significant changes in benthic-pelagic coupling occurred during Cambrian Age 2 (529–521 Ma), with the colonization of the substrate by deep suspension feeding burrowers cf. *Skolithos*. Suspension feeding changed the benthic and pelagic environment, by increasing organic carbon fluxes and geochemical recycling to the water column, expanding the surface area of the water-substrate interface through their burrows, thus ventilating the substrate, and bringing sediment up from deep to the water interface (Mángano and Buatois 2020) and through the oxygenation of the sediment increasing niche space (Mángano and Buatois 2014), although the realised impacts of these during the ECT may be minimal (Cribb et al. 2023). Detritovores and deposit feeders further churn up the surface substrate, further enhancing geochemical fluxes (McIlroy and Logan 1999; Mazurek 2014; Herbers et al. 2016; Stachacz 2016; Gougeon et al. 2018).

Finally, animals changed the water column by mixing the stratified oceans of the Ediacaran through movement of the water by filter feeding (Lenton et al. 2014; Chen et al. 2022) and swimming (Butterfield 2009, 2018). Biogenically induced aquatic bioturbation would have started with stromatolites, and macroalgae, changing fluid dynamics through their physical presence as they grew. As yet there is no evidence that these changes in fluid flow led to a feedback inducing further changes. Thus the first evidence that animals start to contribute to disturbing the fluid flow, and leading to changing in the occupation of vertical niches within the water column, comes from the Ediacaran ~572 Ma (Ghisalberti et al. 2014). Mobility in the form of horizontal trace makers, and mat stickers would not have likely impacted the fluid flow since the physical changes were limited vertically. Planktonic pelagic macro-animals, such as *Attenborites* and jellyfish, also likely did not contribute to significant differences of fluid flow because they only had limited ability to swim against the current. Therefore, the largest impact on water-column fluid dynamics comes from filtering feeding, as it increases in abundance both within and top on the substrate, increasing benthic-pelagic coupling (Mángano and Buatois 2014). Today, the largest impact of animals comes from swimming, especially with the marine pump and diel vertical migration, whereby the vertical migration of zooplankton from the depths to the surface at night to feed is the largest (in terms of biomass) migration on this planet with planktivores following the zooplankton, and predators following them (Barnes 1988; Cisewski et al. 2010). Indeed, the feeding migrations of large marine animals, such as whales contributes a substantial amount to oceanic mixing, and the biological pump removing carbon from the atmosphere and bringing it into the deep sea (Berger 2007; Cotte et al. 2011; Lavery et al. 2012). However, with advent of active swimming by macroscopic zooplankton in Cambrian Age 3 (Vannier 2007), nutrients and geochemical mixing would have massively increased vertically, as well as with larger organisms, and larger dispersal ranges, also horizontally, thus increasing the habitability of the water column, and thus opening up new pelagic niches (Butterfield 2011, 2018).

While the four types of different ecosystem engineering processes are not independent, and taken together these animals fundamentally changed the biosphere over the ECT cf. (Butterfield 2011). Importantly the strong positive feedbacks of these ecosystem engineering processes do not appear to have been fully realised immediately following the respective innovations. Indeed it may not have been until the Ordovician that full ecosystem-engineering feedbacks started, albeit with small effects (Erwin and Tweedt 2012).

## 6 Conclusions

Over the last fifty years we have seen a significant change in our understanding of the early evolution of animals with the taxonomic resolution of pre-Cambrian animals in the Ediacaran (Chen et al. 2013; Bobrovskiy et al. 2018; Evans et al. 2020; Dunn et al. 2021, 2022), and the use of phylogenetic analyses to enable to recognition of Ediacaran and Cambrian taxa as stem-group representatives of modern classes and phyla (Daley et al. 2009; Legg et al. 2013; Smith and Caron 2015; Park et al. 2024; Rahman and Zamora 2024). But key for the increase in our capacity to understand the drivers underlying the ECT is our changed approach to put individual specimens and taxa in context of the environment in which they lived. After all, it is the interactions that organisms experienced in their daily lives with each other and their environment, i.e. their community ecology (§3), that led to the morphological diversification (§2) and macroecology (§4-5) and evolutionary patterns (§1.1) that we see over the ECT.

Throughout the ECT, we not only see a diversification in the types of ecological interactions that exist, namely trophic, habitat modifications and biotic interactions, but also an increase in the number and type of these different interactions. There is a remarkable consistency of patterns across different ecological scales, with organism, community and macroecological patterns all showing a pattern of relative stochasticity, starting in the Ediacaran with low levels of biotic interactions such as competition (Mitchell and Kenchington 2018; Mitchell et al. 2019; Dunn et al. 2022), which then changes with an increase in morphological and ecological diversity (Shen et al. 2008; Bush et al. 2011) at the organism level, increases in niche interactions (Gehling and Droser 2018; Mitchell et al. 2020; Boan et al. 2023) throughout the Ediacaran and into the Cambrian (Bush et al. 2011; Muscente et al. 2019; Buatois et al. 2020, Nanglu et al. 2020*b*). These patterns are also captured at the macroecological scale (Na and Kiessling 2015; Eden et al. 2022; Meek et al. 2023), demonstrating the build-up of these micro to macro ecological interactions.

By Cambrian Epoch 2, the ecosystem structure in many aspects, is similar to that of marine systems today. However, while many of these the key ecological processes, such as predation, habitat modification, facilitation, symbiosis, mutualisms and commensalism are present (Figure 4), there are time-delays between the origins of such processes and the time when they have an observed impact on other organisms – for example reef production predates the advent of reef/hard substrate habitation by ~ 40 million years, and complex trophic structures emerged around 30 million years after the advent of predation. As such, while the key building blocks of ecosystem structure were in place by the end of the Cambrian, it takes evolutionary time-scales for the impact of them to be realised.

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## Declaration of Competing Interests

The authors declare no competing interests.

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## Author contributions.

E.G.M. conceptualised this manuscript, and both authors contributed to the writing of his paper

## Figure and Table Captions

**Figure 1**: *Iconic ECT organisms known in 1975. A. Mistaken Point E surface (~564 Ma), Newfoundland, Canada showing Charniodiscus spinous, Charniodiscus arboreus, Beothukis mistakensis and Fractofusus misrai  B. Charnia masoni holotype (LEIUG 2328), Bed Bed (~560 Ma) Charnwood Forest, UK. Image Credit: British Geological Survey. C. Dickinsonia costa (left) and Parvancorina minchami (right) (~550 Ma), South Australia Museum, D. Cyclomedusa disc (~560 Ma), Charnwood Forest. A, C, D: Image Credits: Emily G. Mitchell E. Stem-group chordate Pikaia gracilens Walcott, 1911, Burgess Shale, Canada (Cambrian: Wuliuan). USNM PAL 83940B.*

*Image courtesy of the Smithsonian Institution (CC0 license) (EZID:http://n2t.net/ark:/65665/m37ec4e117-c554-4a97-b352-5deb01b3081f). F. Stem-group mollusc Wiwaxia corrugata Walcott, 1911, Burgess Shale, Canada (Cambrian: Wuliuan). USNM PAL 198745. Image credit: Mark Florence. Image courtesy of the Smithsonian Institution (EZID: http://n2t.net/ark:/65665/m3038e2e32-c309-4da5-b28e-3f8cfdc8c941). G. Stem-group euarthropod Opabinia regalis Walcott, 1912, Burgess Shale, Canada (Cambrian: Wuliuan). USNM PAL 57683. Image credit: Han Zeng. Image courtesy of the Smithsonian Institution (EZID: http://n2t.net/ark:/65665/m31c224d68-28cb-465b-b42e-e565c31a44d1). H. Total-group ecdysozoan Aysheaia prolata Walcott, 1911, Burgess Shale, Canada (Cambrian: Wuliuan). USNM PAL365608. Image credit: Javier Ortega-Hernández. Scale bars for A-H, 10 mm.*

***Figure 2**. Key Ediacaran (pink) and Cambrian (green) Lagerstätten with their genera diversity in 1975 and 2024, and the total diversity from the PBDB (Na and Kiessling 2015) (black line).*

***Figure 3:** The relative proportions of feeding type in Ediacaran (green) from Nilpena, South Australia (Droser and Gehling 2015; Droser et al. 2019) and Cambrian (blue) from the Burgess Shale (Nanglu et al. 2020*b*). Feeding types are Suspension feeding (yellow), Deposit Feeding (blue) Grazing (Orange), Primary production (Green), Hunters and Scavengers (Red) and Unknown in Grey. The top plot is temporal ordered, and the bottom plot has been ordered by relative proportion of suspension feeders from left to right. Note that while there is a trend of Ediacaran on the left to Cambrian on the right, there is a significant overlap between them.*

***Figure 4:** Ecological networks across the ECT, with four time periods illustrated (from left to right, 565 Ma, 550 Ma, 539—521 Ma, 521 Ma). Suspension feeding communities and simple trophic interactions (white arrows) are present 565 Ma. An increase in*

*Habitat modification (yellow arrows) in the form of grazing and scavenging appear 550 Ma. In the Terreneuvian (539 -- 521 Ma), the active pumping of archaeocyaths and swimming of chaetognaths increase aquatic bioturbation (blue arrows), archaeocyath reefs modify the substrate, and vertical as well as horizontal bioturbation complexity and depth increase dramatically. In the Cambrian Epoch 2 (521 Ma), there is a further increase in trophic interactions, aquatic bioturbation, and vertical bioturbation, as well as symbiotic interactions and epibionts (red arrows). Reconstruction by Franz Anthony.*