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Ecosystem reconstruction during the Cambrian explosion

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Abstract. The Cambrian explosion ultimately resulted in the critical transition from microbially dominated ecosystems in the Precambrian to metazoan-dominated ecosystems in the Phanerozoic. However, the temporospatial pattern of ecosystems during the Cambrian explosion is poorly understood largely because our current knowledge is biased in metazoan evolution and redox conditions, and thus insufficient to reconstruct an ecosystem that is an integrative entirety of biotic and abiotic components. Therefore, we proposed a facies-dependent integrative approach as a working hypothesis toward a more comprehensive understanding of ecosystem evolution during the Cambrian explosion. The basis is to collect data from a rock unit with a consistent facies (or a biota) in five aspects: biodiversity, ecological network, climate, environmental trio (living, taphonomic and sedimentary conditions), and biogeochemical cycles. On the basis the temporospatial pattern can be built by tracking the spatial heterogeneity and tracing the temporal variability. Although the scenario is a general solution, not obligately applicable to the Cambrian explosion, and needs tremendous amount of work, it is a practical way, probably the only way, to understand such a global event with great complexity.

Keywords: Cambrian explosion, complexity of ecosystem, entirety of ecosystem, temporospatial pattern of ecosystem

Introduction

Eruptive occurrences of diverse metazoan lineages in the fossil record during the Ediacaran to Cambrian transition (Cloud, 1948), namely the Cambrian explosion (Brasier, 1979), have puzzled the scientific world since 1850s (Darwin, 1859, page 307). The Cambrian explosion ultimately resulted in the initial establishment of metazoan-dominated marine ecosystems comparable to present-day marine ecosystem at least in trophic level complexity (Erwin and Tweedt, 2012; Zhang and Shu, 2014). Although our knowledge on this unprecedented evolutionary event has been increasing enormously since this century (Erwin *et al.*, 2011; Erwin and Valentine, 2013; Shu *et al.*, 2014; Zhang *et al.*, 2014; Zhang and Cui, 2016; Sperling and Stockey, 2018; Erwin, 2020), its nature is still insufficiently understood. Even in the quite recent, “what caused the Cambrian explosion” was listed as one of the Science’s six unsolved mysteries (see the article “Science’s unsolved mysteries: Life, the multiverse and everything, Science has remade the world, but scientists are not finished yet” in Economist of 6th August 2015). Our current knowledge on the Cambrian explosion is heavily biased in evolution of early metazoans

(e.g. Erwin *et al.*, 2011; Erwin and Valentine, 2013) and perturbations of redox conditions (e.g. Chen *et al.*, 2015; Sperling *et al.*, 2015; Bowyer *et al.*, 2017; He *et al.*, 2019; Shield *et al.*, 2019). At this rate, we would go further from a more comprehensive understanding of the evolution of ecosystem complexity. Simply because ecosystem is a unified entirety of biotic and abiotic constituents, and all their interrelationships in a particular unit of space, which can be as small as an oasis in a desert, or as big as an ocean, spanning thousands of miles. Ecosystem itself has been evolving ever since life origin. Biotic constituents are much more than metazoans that are merely part of consumers; there are also producers and decomposers that are indispensable in any ecosystem. Abiotic constituents include the complex of environmental and climatic interactions. It is the energy flow and matter cycling that link these constituents together, forming the integrative entirety of an ecosystem. Therefore, it is essentially important to understand the Cambrian explosion in a holistic view, though the idea is not new! Here we review some crucial aspects that are easily overlooked, and propose a facies-dependent integrative approach as a working hypothesis for investigating the temporospatial pattern of ecosystem during the Cambrian explosion.

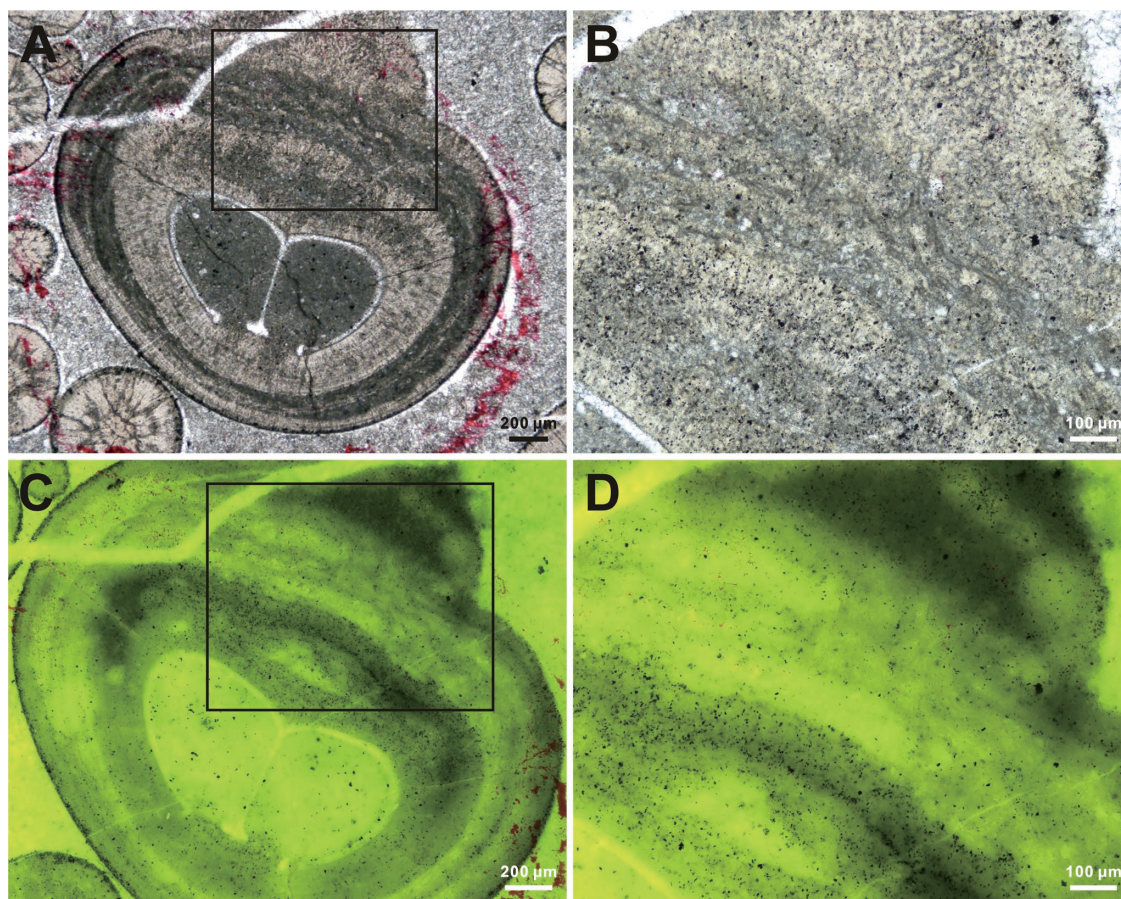


Figure 1. A cyanobacterial biofilm coated grain from the oolitic limestone of the Tianheban Formation of Cambrian Stage 4, Three Gorges Area, South China. **A**, an ooid with alternative lamination of dark and bright laminae in the cortex. **B**, close-up of the boxed area in **A**, showing calcified cyanobacterial sheaths in dark laminae. **C**, autofluorescent photograph of **A**, note that cyanobacterial laminae are brighter under blue light illumination. **D**, autofluorescent photograph of **B**, cyanobacterial sheaths darker than the matrix.

Biotic bias

Trophic relationships determine the routes of energy flow and matter cycling in an ecosystem. In modern marine environments, the trophic level that ultimately supports all others in an ecosystem consists of autotrophs, the primary producers, above which are sequentially herbivores, carnivores and tertiary consumers. Detritivores and decomposers connect all trophic levels. Therefore, primary producers and decomposers play a central role in energy flow and matter cycling, which flow through the trophic levels eventually to detritus and then cycle back to primary producers. An ecosystem is able to keep running in absence of metazoans consumers. However, it would demise without involvement of producers or decomposers.

In the geological past before the Cambrian explosion, *ca.* 88% of Earth's history, the biosphere as a super eco-

system was basically dualistic for the lack of metazoan food web, though cell-eating-cell might be ubiquitous in protists and prokaryotes. It was the Cambrian explosion that led to the formation of the Earth's ternary ecosystem with a complicated trophic structure like today, consisting of producers, decomposers and consumers. In the past two decades much attention has been paid to evolutionary, developmental, and ecological aspects of metazoans in the context of the Cambrian explosion (e.g. Erwin and Valentine, 2013; Cabej, 2020), which is absolutely necessary because it was the explosive appearances of metazoan lineages that made the critical transition in Earth's history. Paleontologists have been busy with describing metazoans from exceptionally preserved fossil Lagerstätten. Normal fossil beds are disesteemed more or less though they might represent specific ecosystem. In contrast, little has been learnt about primary producers and decomposers during the Cambrian explo-

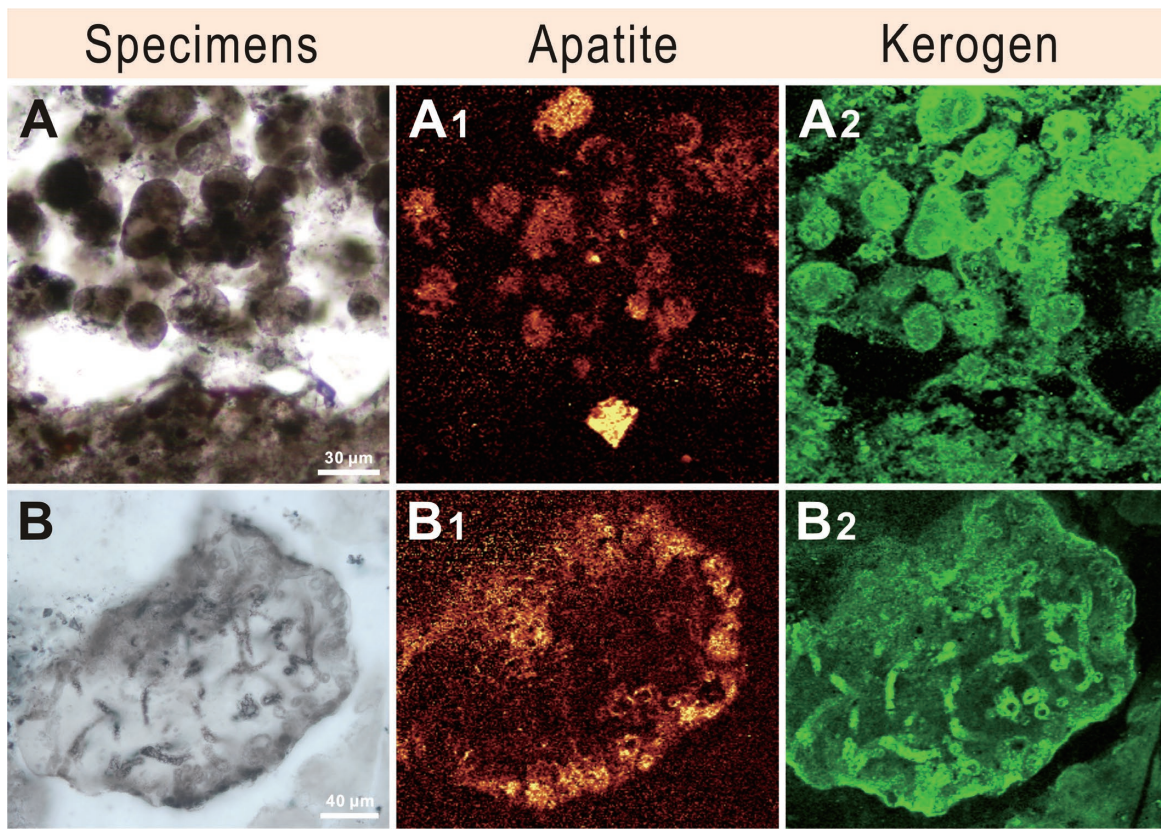


Figure 2. Spherical (A) and filamentous (B) microbial fossils from cherts of the Kuanchuanpu Formation of the Cambrian Fortunian Stage, South China. A and B, optical images. A₁ and B₁, Raman images, acquired in a window 954–974 cm^{-1} , corresponding to apatite. A₂ and B₂, Raman images, acquired in a window 1240–1680 cm^{-1} , corresponding to kerogen.

sion. They were mostly microorganisms that are easily neglected for many reasons, e.g. small size, less potential of preservation, difficulty in discovery, or less importance in metazoan sense. However, they must be flourished in all ecosystems and their fundamental roles in ecosystems are non-negligible. They drive biogeochemical cycles in many pathways and have *de facto* roles in maintaining ecosystems (Konhauser, 2007; Knoll *et al.*, 2012; Zhang, 2012). These microorganisms inhabit everywhere in an ecosystem. Remarkable preservation of cells and soft tissues occurs in Neoproterozoic to Cambrian cherts, phosphates, black shales, siliciclastic sediments and carbonates across a wide range of environmental conditions (Brasier *et al.*, 2011). Consequently the specific texture, composition, and active metabolisms of microorganisms can be recorded in rocks of various facies (e.g. cherts, phosphorites, carbonates, shales, etc.) as geological, chemical or paleobiological remains (Liu and Zhang, 2012, 2015a; Shang *et al.*, 2016; Brocks *et al.*, 2017; Cui *et al.*, 2020; Lepot, 2020), and therefore can be discovered and analyzed using traditional and *state-of-the-art* techniques to reveal their evolutionary and ecological

significance (e.g. Schopf *et al.*, 2010; Bonneville *et al.*, 2020; Cui *et al.*, 2020).

In the producers, macroscopic algae were beautifully preserved in Ediacaran to Cambrian shales (Yuan *et al.*, 2011; Hou *et al.*, 2017; Fu *et al.*, 2019) and cyanobacteria were calcified (Figure 1), phosphatized, or sealed in cherts as organic remains (Figure 2). Their contribution to primary production and other ecological aspects during the Cambrian explosion, however, remains to be evaluated. There are also many other categories of microbial primary producers (e.g. anoxygenic/oxygenic prokaryotic photoautotrophs, photoautotrophic protists and chemolithoautotrophs) in present-day ecosystems, which remain to be found in the geological past. For instance, the Fe^{2+} -oxidizing bacteria, e.g. *Acidithiobacillus ferrooxidans*, are able to grow autotrophically on pyrite mineral, and leave characteristic etching marks on mineral surface (Figure 3; Liu and Zhang, 2015b). Remarkably, such pitted marks by microbial etching have been recognized in modern and ancient sediments (Figures 3A, B; Liu and Zhang, 2011; Liu *et al.*, 2020). In contrast, paleobiological records of decomposers have been rarely reported. Recently, fungi

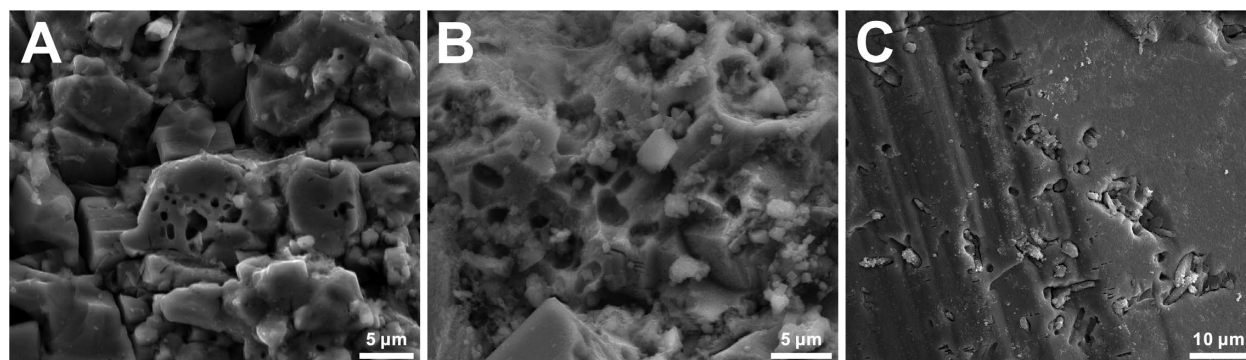


Figure 3. SEM photographs of pyrite crystals showing pitted etching marks on mineral surfaces by iron oxidizing bacteria. **A**, pyrite from the Ediacaran Doushantuo Formation, South China. **B**, pyrite from present-day sulfide deposits of the East Pacific Rise at 1.368833°N and 102.455999°E. **C**, iron-oxidizing bacterial cells of *Acidithiobacillus ferrooxidans* etching pyrite crystals in a laboratory.

that are of ecological importance were recognized from Precambrian rocks using a number of facilities (Loren *et al.*, 2019; Bonneville *et al.*, 2020), but yet remain to be recognized in the Ediacaran–Cambrian transition. Nitrate and sulfate reducers are anaerobic decomposers and critical in N and S biogeochemical cycles. Their ecological importance for the Cambrian explosion is worth great attention in the future. In short, microorganisms are composed of diverse functional groups, and their metabolic activities are recordable in sedimentary rocks as various biosignatures. Enhancement of investigation in microbial aspects would improve a more complete understanding of the Cambrian explosion.

Abiotic bias

Abiotic components include air, water, soil, minerals, sunlight, temperature, nutrients, wind, altitude, turbidity, etc. They work together to form a complex of climate and environment dynamics, which in turn are interactive with biotic components.

Marine redox is currently dominating the research of abiotic components in the context of ecosystem evolution during the Ediacaran–Cambrian transition. There is not short of global patterns of marine redox conditions. The absolute concentration of atmospheric and oceanic oxygen, however, is poorly understood (Zhang and Cui, 2016). Overwhelming evidence suggests a high degree of spatial heterogeneity and temporal volatility of Ediacaran redox condition (Lyons *et al.*, 2012; Sahoo *et al.*, 2016; Bowyer *et al.*, 2017; Wood and Erwin, 2017; Shi *et al.*, 2018). The ocean was stratified; surface water was mildly oxygenated, the deep ocean was anoxic (ferruginous); euxinic water bodies may have rimed the global ocean as “dynamic wedges” at mid-water depths (Li *et al.*, 2010). Such a heterogeneous ocean may have, at

least locally, persisted to the early Cambrian (Wang *et al.*, 2012; Feng *et al.*, 2014; Jin *et al.*, 2014; Wen *et al.*, 2014, 2015; Li *et al.*, 2017, 2018; Zhang *et al.*, 2017). Spatial heterogeneity in the ocean is not unique in the Ediacaran–Cambrian transition but a common phenomenon throughout Earth’s history. The temporal instability of the Ediacaran–Cambrian ocean redox conditions, characterized by extreme oxygen perturbations (He *et al.*, 2019) or oxygenation events in the anoxic ocean (Sahoo *et al.*, 2016; Shi *et al.*, 2018), was proposed to be able to promote morphological innovations of the Cambrian explosion, though it happened a couple of times in the subsequent Phanerozoic (Wood and Erwin, 2017). Both spatial heterogeneity and temporal instability are inferred from geochemical data in a limited number of case sections but not based on statistics of redox data over time and space. In contrast, investigations on other environmental aspects are underrepresented by a couple of studies on the oceanic temperature (Hearing *et al.*, 2018; Wotte *et al.*, 2019), rare cases on nutrient availability (Sperling and Stockey, 2018) and salinity, e.g. increasing calcium and sulfate concentrations (Brennan *et al.*, 2004; Algeo *et al.*, 2015; He *et al.*, 2019). Understanding the mechanisms, evolution and impacts of global climate and environmental systems is crucial in deciphering ecosystem evolution. However, climate change, weathering conditions and their environmental impact have been limitedly understood (e.g. Peters and Gaines, 2012; Hearing *et al.*, 2018), though each rock unit formed in a particular paleogeographical position may contain valuable climate and environmental information.

Biogeochemical cycles link biotic with abiotic components and thus are crucially important for sustaining an ecosystem. When investigating matter cycles in an ecosystem it is useful to focus on cycles of biogeochemically important elements, e.g. C, N, P, S, Fe and

so forth. Similar to marine redox investigation, currently the main focus on the biogeochemical cycles during the Ediacaran–Cambrian transition has been on global patterns based on limited data. There are studies suggesting an increase of phosphorus, nitrogen and sulfate supply during the Ediacaran–Cambrian transition (Wang *et al.*, 2018; He *et al.*, 2019; Laaksoa *et al.*, 2020). Biogeochemically unique features, however, are poorly understood. Investigations of biogeochemical cycles in specific Ediacaran or Cambrian ecosystems are generally absent.

Ecosystem complexity

Microbially dominated ecosystems appeared billions of years before the Cambrian explosion and persisted into the earliest Cambrian (Buatois *et al.*, 2014). Although the combination of paleontological and phylochronological data suggest that many photosynthesizing and non-photosynthesizing eukaryotic clades including sponges diversified in the pre-Ediacaran Proterozoic (see Erwin and Valentine, 2013 and references therein), their fossil record is not abundant and thus probably did little to alter the early microbially dominated ecosystems. The modern-style, metazoan-dominated ecosystems are essentially the outcome of the Cambrian explosion (Erwin and Tweedt, 2012; Zhang and Shu, 2014). It was supposed that the early Cambrian marine ecosystems appeared to have been as complex as many modern marine ecosystems, at least in terms of their trophic relationships (Erwin and Valentine, 2013). This judgement is mostly based on complex ecological interactions documented in Cambrian Burgess Shale-type fossil Lagerstätten such as Chengjiang (Bambach *et al.*, 2007; Dunne *et al.*, 2008; Zhao *et al.*, 2009, 2014). However, ecosystem itself has been evolving since life origin. Therefore, the ecosystem complexity was different from time to time, and places to places. The Chengjiang ecosystem merely represents a small piece of marine environment during the Cambrian Stage 3, when the Cambrian explosion reached its summit and was concluded (Paterson *et al.*, 2019), marked by the arrival of trilobites and those familiar symbols of the Cambrian (Gould, 1989).

Indeed, ecological networks expanded considerably in both size and complexity between the Ediacaran and the early Cambrian (541–509 Ma, equivalent to Cambrian stages 1–4) as measured by the number of life modes (Bambach *et al.*, 2007; Bush *et al.*, 2011), complexity of food web (Dunne *et al.*, 2008), and ecosystem engineering (Erwin and Tweedt, 2012; Mángano and Buatois, 2014). The results revealed a striking contrast in the paleoecology between the Ediacara-type macrofossil assemblages and essentially modern aspect of early Cambrian faunas. A total of 12 different life modes were recognized in

three Ediacaran macrofossil assemblages (Avalon, White Sea, and Nama) and 30 in Chengjiang and Burgess Shale biotas (Bambach *et al.*, 2007); relatively minor positive ecological feedback during the Ediacaran was followed by a substantial increase during the early Cambrian, principally through bioturbation and the appearance of a number of structural engineers (Erwin and Tweedt, 2012); a major shift in benthic ecological structure (agronomic revolution) resulted in the establishment of the Phanerozoic-style ecology during the Cambrian Stage 2 (*ca.* 529–521 Ma), which in turn drove a further diversification of deposit-feeding strategies by Cambrian Stage 3 (*ca.* 521–514 Ma), favoring an ecological spillover scenario (Mángano and Buatois, 2014); the fundamental structure of metazoan marine food webs appears to have been established by the Cambrian Stage 3 as seen in the Chengjiang biota (*ca.* 518 Ma).

Clearly, the basic structure of Phanerozoic ecosystems had been achieved by the arrival of trilobites at the Cambrian Stage 3. There is still much to learn about such evolving systems, in particular, the increase of ecosystem complexity during the first 20 million years of the Cambrian Period. The Burgess Shale-type deposits have yet been discovered. Phosphatized fossil beds in this time interval contain rich ecological information. For instance, a phosphatic grain-stone bed, immediately below an ash layer dated as *ca.* 535 Ma in age, in eastern Yunnan, South China, is rich in metazoan and microbial fossils. The early diagenetic phosphatization and siliceous cementation are responsible for the preservation of microbial remains (Zhang *et al.*, 2017). Additionally, on the rock surface, small shelly fossils are extremely abundant. Surprisingly, a giant worm-like, soft-bodied organism, *Vittatusivermis*, is present on the surface. It is preserved as elongated and flattened tubes with cross annulations, 1 cm wide and more than 20 cm long, and shows plastic deformations, which can be twisted, folded and bended. The close spatial association with trace fossils on the same surface suggests *Vittatusivermis* is one of the long expected trace maker at the earliest Cambrian (Zhang *et al.*, 2017). Ecologically, metazoans from this 535 Ma fossil bed are mostly herbivores (primary consumers), though many life modes can be recognized. Secondary and tertiary consumers (carnivores), which are well represented in Cambrian Stage 3 faunas (e.g. Chengjiang ecosystem), have not been recognized (Figure 4A). Collectively, the information from this earliest Cambrian fossil bed implies that the microbial world constituting producers and decomposers of Cambrian marine ecosystems is recordable and remains to be investigated; the ecological network recorded in this phosphatic bed is less complex than the Chengjiang ecosystem (Figure 4B).

In contrast to the increase of ecological complexity

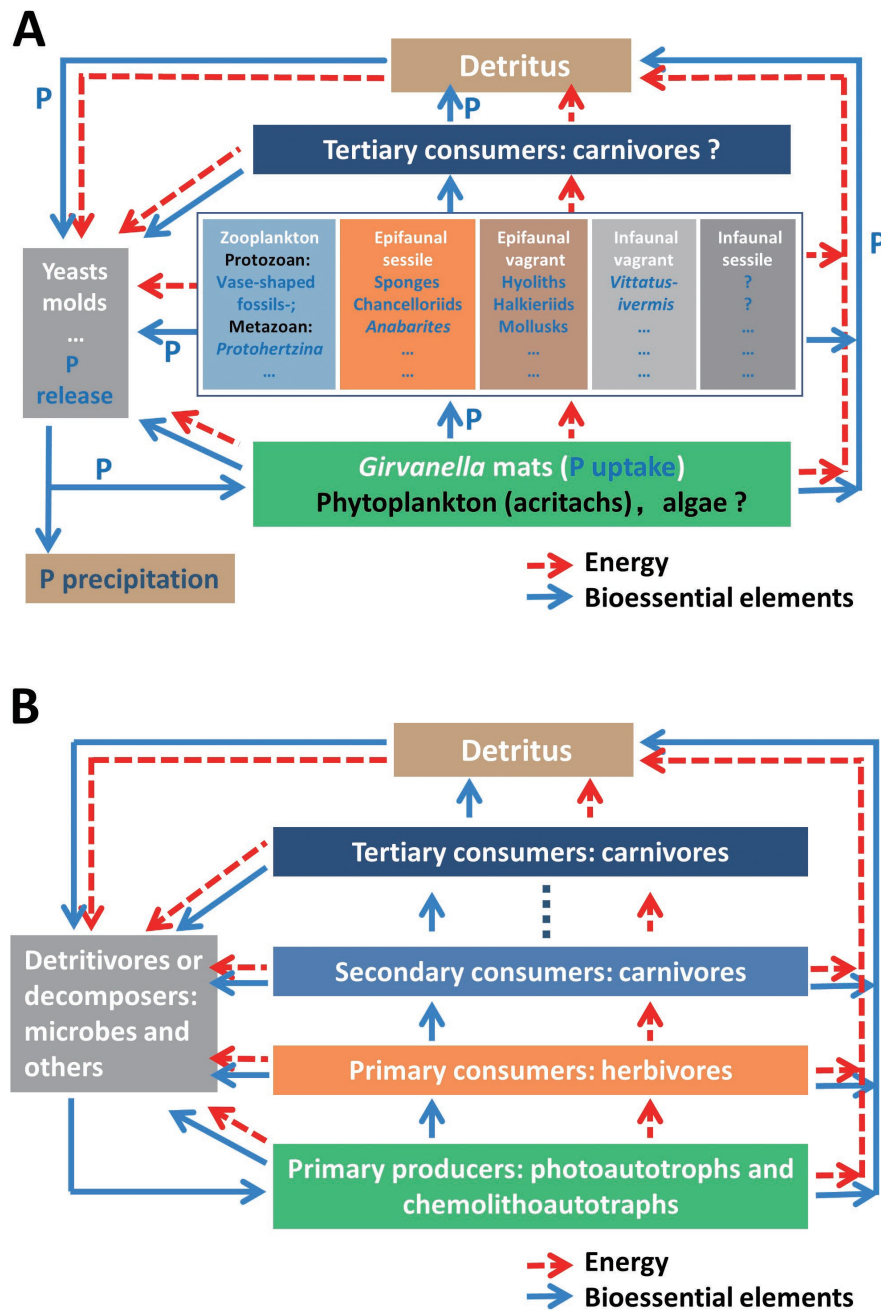


Figure 4. Hypothetical ecosystem complexity during the Fortunian Stage (A) and since the Cambrian Stage 3 (B).

over time, spatial heterogeneity of ecosystems during the Ediacaran–Cambrian transition remains to be revealed in the future. For example, the Burgess Shale-type fossil Lagerstätten in siliciclastic platform facies (Hou *et al.*, 2017; Fu *et al.*, 2019), sponge-based ecosystems in black shales of slope facies (Steiner *et al.*, 1993; Xiao *et al.*, 2005), archaeocyathan-based reef ecosystems in carbonate platform facies are all Cambrian Stage 3 in age

but markedly different from each other in biotic composition and abiotic conditions. Similarly, Ediacara-type macrofossil assemblages developed in both sandstone and carbonate facies (Chen *et al.*, 2014) are in contrast to the contemporary tube world of the Gaojiashan biota (Schiffbauer, 2016) and *Cloudina*-microbialite reef systems in carbonates. Comparative ecological studies of contemporary fossil deposits in different facies and in dif-

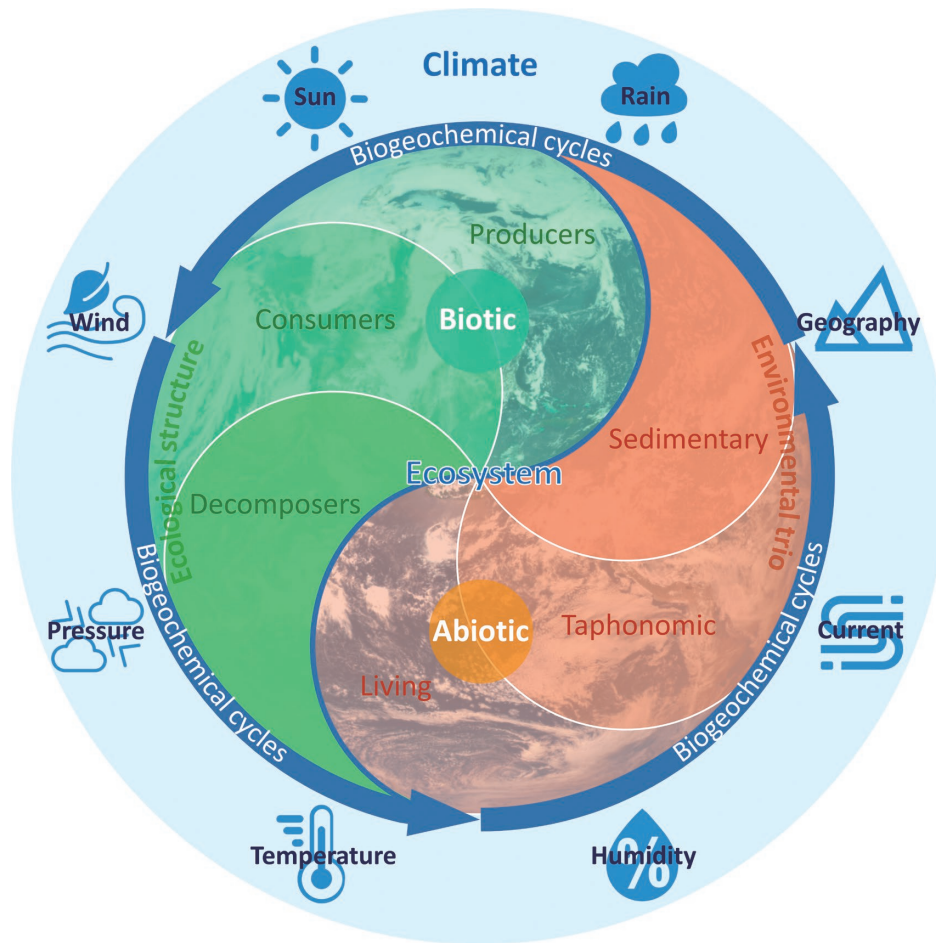


Figure 5. A working hypothesis for ecosystem reconstruction during the Cambrian explosion.

ferent regions would no doubt be a practical approach to understand the spatial pattern of ecosystems during the Ediacaran-Cambrian transition.

Facies-dependent integrative approach

A number of lines of evidence suggested that metazoans emerged before the Ediacaran (635–541 Ma) (Love *et al.*, 2009; Erwin *et al.*, 2011; dos Reis *et al.*, 2015). Sponge-grade metazoan body fossils (Yin *et al.*, 2015) and the record of bioturbation (Pecoits *et al.*, 2012) were discovered in early Ediacaran deposits prior to the Gaskiers Glaciation (582–580 Ma). However, these early metazoans might be ecologically insignificant because their fossil record is very sparse (Erwin *et al.*, 2011). Microbially dominated communities remained important through the Ediacaran and persisted into the Cambrian Fortunian Stage (541–529 Ma) (Buatois *et al.*, 2014); the substrate revolution from microbially bound matgrounds to bio-

turbated mixgrounds took place in the Cambrian Stage 2 (529–521 Ma) (Mángano and Buatois, 2014); the basic structure of present-day marine ecosystems had been achieved by the Cambrian Stage 3 (521–514 Ma), which is well documented in numerous Burgess Shale-type fossil Lagerstätten. It took metazoans more than 100 million years to take over the ocean, from their emergence in the pre-Ediacaran, through a long term development in the Ediacaran, to a major ecological burst in the early Cambrian. The critical transition toward a metazoan-dominated ecosystem occurred in the first 20 Ma interval of the Cambrian Period.

Ecosystems are differentiated in space and evolving through time. To understand the temporospatial pattern of ecosystems during the Cambrian explosion, we here propose a facies-dependent integrative approach as a working hypothesis (Figure 5). The target is a rock unit with consistent facies or a biota that can be roughly treated as an entirety of a specific ecosystem. Integrative inves-

tigations comprise five aspects: (1) revealing biodiversity, including physical fossils and chemical signatures, all biotic components; (2) building ecological structure, ecological composition, life mode, trophic level, etc.; (3) understanding environmental trio composed of living, taphonomic and sedimentary conditions; (4) collecting climate information; (5) reconstructing biogeochemical cycles. In this scenario, we firstly have an integrative understanding on specific ecosystems recorded in a rock unit with a consistent facies, secondly track the spatial heterogeneity by comparative studies of contemporary ecosystems recorded in different facies (or biotas), thirdly trace changes of ecosystems recorded in the same (similar) facies through time (the time scales can be resolved to geological stages or biozones), and finally work out the temporospatial pattern of ecosystems during the Cambrian explosion in global scale. The first step is the basis of this hypothesis but need enormous work. We have to investigate rock units one by one and there are too many! Obstacles are in two folds: (1) much attention has been paid to rock units with exceptionally preserved biotas that are minor in number; in contrast, a majority of normal rock units were far less investigated though they may have valuable ecological information; (2) previous investigations on a particular rock unit were usually less integrative, not conducted in the context of the ecosystem entirety, and thus provided incomplete information; in most cases, only metazoan diversity and redox condition were available.

This approach, neither specific for the Cambrian explosion nor novel in any sense, is nothing but a general idea which is applicable to any evolutionary event of great magnitude. Systematic investigations of each rock unit in global scales mean a tremendous amount of scientific work. However, there is no easy solution! The Cambrian explosion is a once-in-an-era happening event, which built the basic structure of modern style marine ecosystems. It is worth all hard work by generations of scientists in the world.

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Author contributions

X. Z. initiated and organized the study. C. C. reviewed the biogeochemical researches. L. C. and Y. Q reviewed microbial fossil record and prepared figures. All authors contributed to the writing of the paper.