

Environmental drivers of evolving biological complexity on Earth

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Abstract

The first-order features of Earth’s biosphere have undergone fundamental transformations over time, in parallel with major changes in the chemistry of Earth’s ocean-atmosphere system. In particular, major changes in the availability of oxygen and nutrients in Earth surface environments have potentially played a significant role in constraining the timing and dynamics of major advances in biological complexity. However, there are still fundamental unanswered questions about the cause-and-effect relationships between Earth system change and the development of biological complexity, and these remain among the most compelling challenges in evolutionary science and astrobiology. We argue here that understanding the environmental context of major changes in biotic and ecosystem complexity is critical for fully understanding the factors that favor (or inhibit) the emergence and expansion of complex life. To illustrate this, we propose two case studies emphasizing the complex interconnectedness between biogeochemical cycles, evolutionary ecology, and biological innovation – (1) the role of marine nutrient abundance in shaping early eukaryotic ecosystems, and (2) the impact of oxygen on the ecology of the earliest metazoan (animal) life. We suggest that the Early Cells to Multicellularity (ECM) Research Coordination Network (RCN) is uniquely positioned to push forward the science of biological complexity, by bringing together researchers with diverse backgrounds across organismal biology, evolutionary ecology, and Earth system science and by explicitly attempting to understand the factors involved in fostering biological complexity in the broadest possible context.

1. Introduction and Relevance

Understanding the factors that may foster or inhibit the emergence and expansion of biological complexity is central to the field of astrobiology. Indeed, two of the seven overarching research directions outlined in the Astrobiology Strategy 2015 are explicitly targeted at this issue – *Early Life and Increasing Complexity* and *Co-evolution of Life and the Physical Environment* [Hays et al., 2015]. This is a broad and challenging problem, requiring diverse insights from cellular and molecular biology [King et al., 2003; Ratcliff et al., 2015], physiology and organismal biology [Knoll, 2011; Sperling et al., 2015], evolutionary and ecological theory [Adami et al., 2000], paleontology [Knoll et al., 2006; Erwin et al., 2011], and biogeochemistry [Love et al., 2009; Lyons et al., 2012]. We argue here that

one major component of this effort must be forging a more robust and nuanced understanding of the environmental backdrop of major advances in biological complexity on Earth (**Fig. 1**). This is highlighted in two potential avenues of interdisciplinary work aimed at understanding the rise of biological complexity on Earth – (1) the impact of nutrients on early marine ecology, and (2) the impact of oxygen on early animal life.

2. Marine nutrient levels and early eukaryotic ecosystems

The evolution of the eukaryotic cell represents one of the most significant advances in biological complexity in Earth’s history, a dramatic shift in the architectural and genomic complexity of life. The eukaryotic cell is thought to have evolved relatively early – nearly 2,000 million years ago (Ma; **Fig. 1**). The most ancient putatively eukaryotic fossils are found in the latest Paleoproterozoic [*Lamb et al.*, 2009], while the oldest definitively eukaryotic microfossils occur in the latest Paleoproterozoic and Mesoproterozoic (~1,800-1,500 Ma) [*Javaux et al.*, 2004]. However, eukaryotic organisms do not become a significant component of surface ocean ecosystems until much later in Earth’s history, with no evidence for an important role for eukaryotic algae in primary production or of significant trophic structure in eukaryotic ecosystems until after ~800 Ma [*Knoll*, 2014; *Brocks et al.*, 2017; *Zumberge et al.*, In press]. The microfossil and molecular biomarker records point to the possibility of a macroevolutionary lag [c.f., *Erwin*, 2015] of as much as 1 billion years between the emergence of the eukaryotic cell and the expansion of eukaryotes into their current role as a major constituent of Earth’s biosphere. We suggest that the following key facets of this problem deserve further exploration:

- i. How have marine nutrient levels (foremost phosphorus and nitrogen) evolved over time on Earth?
- ii. Is there a temporal correspondence between changes in ocean-atmosphere chemistry and major changes in marine ecology (e.g., the rise of eukaryotes and subsequent radiation of animals)?
- iii. How do carbon and nutrients cycle through modern ecosystems that are early ocean analogues?

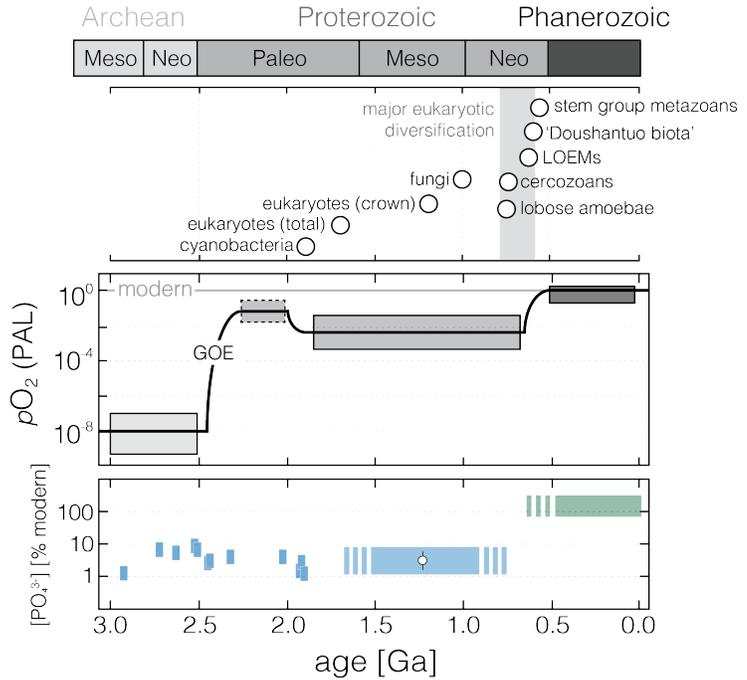


Figure 1. Summary of major events in the evolution of Earth’s biosphere over the last 3 billion years (*top*), along with trajectories for atmospheric O₂ abundance relative to the present atmospheric level (PAL, *middle*) and marine nutrient availability (*bottom*). Major events in biological evolution are after *Lyons et al.* [2012] and *Knoll* [2014], while atmospheric pO₂ and marine nutrient abundances are following *Reinhard et al.* [2017]; [2020].

- iv. What other environmental factors (e.g., ocean-atmosphere O_2 abundance) have controlled the availability of key nutrients for early eukaryotic ecosystems?

Answering these and other critical questions in the evolutionary history of eukaryotic life will require an interdisciplinary approach that combines, paleoenvironmental and paleoecological reconstruction (stable isotope tracers, chemical sedimentology, micropaleontology, organic geochemistry), field and lab studies of the physiology and environmental tolerances of modern basal eukaryotic organisms, and predictive theoretical models that couple ocean biogeochemistry and marine ecological function (**Fig. 2**).

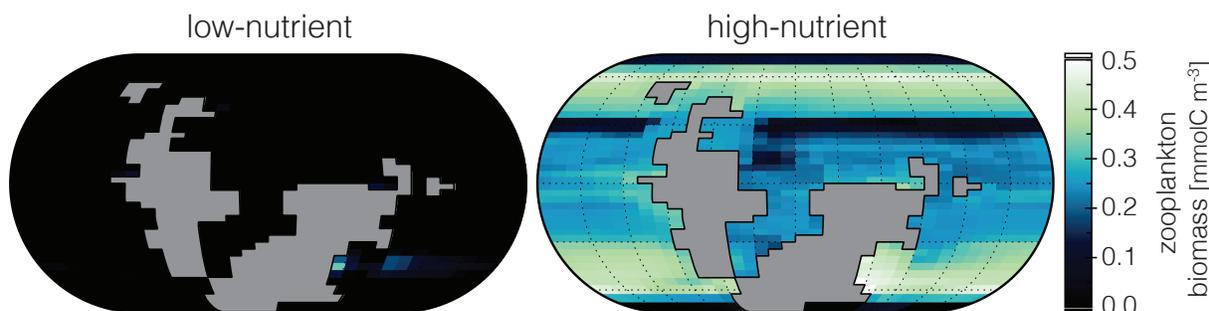


Figure 2. Trait-based zooplankton ecology in an Earth system model with late Proterozoic climate and continental configuration. Shown are biomass distributions for large (190 μm) zooplankton in the surface ocean under low-nutrient (10% of modern levels; *left*) and high-nutrient (modern levels; *right*) conditions. After *Reinhard et al.* [2020].

3. Ocean oxygenation and the early evolution of animal life

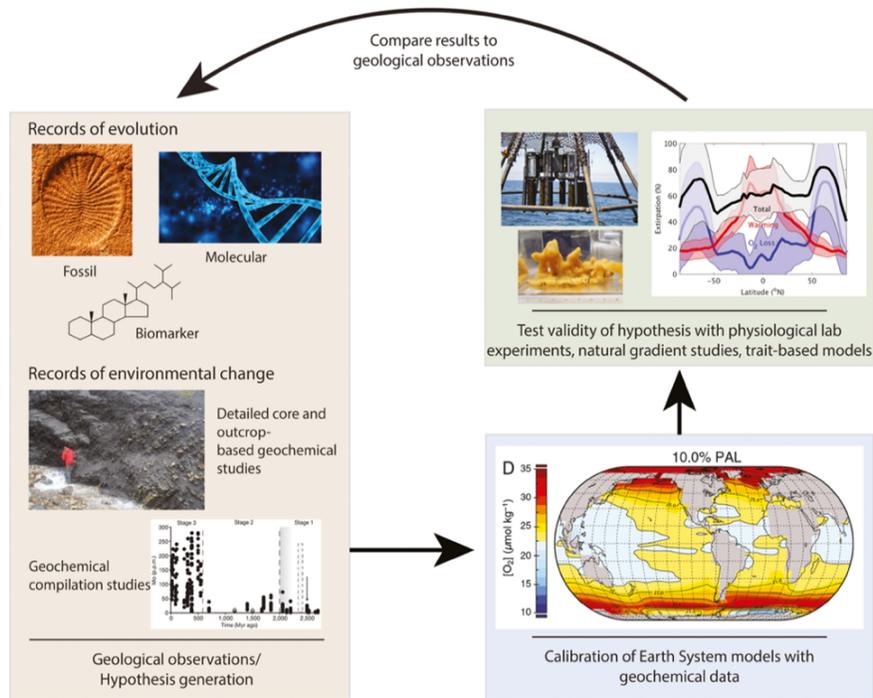
Understanding the environmental factors structuring the evolution and ecology of the earliest animal life speaks to the history of complexity on Earth, but can also potentially provide broader insight into the conditions likely to foster (or inhibit) the emergence and long-term viability of complex life elsewhere [e.g., *Schwieterman et al.*, 2019]. As a result, this is a question that lies at the core of NASA’s goal to understand the “rules” of biological complexity [*Hays et al.*, 2015]. However, the role of changing environmental conditions – and in particular atmospheric O_2 – in structuring the evolution and early ecology of metazoan (animal) life is intensely debated [e.g., *Cole et al.*, 2020]. Fully understanding this relationship requires information from Earth’s geochemical and fossil records [*Erwin et al.*, 2011; *Droser et al.*, 2017], knowledge about the physiological links between environmental O_2 and other potentially synergistic factors [*Sperling and Stockey*, 2018], and an understanding of the biological novelties required for different styles of complex multicellularity [*Ratcliff et al.*, 2015]. We suggest the following key questions are central to a full elucidation of the factors shaping the evolution of complex animal multicellularity:

- i. Are there O_2 “thresholds” for basal metazoan organisms that can impact either individual or species-level survivorship? How do these relate to environmental O_2 availability through time?
- ii. What are the synergistic effects between O_2 , temperature, pH, aqueous CO_2 , and nutrients on metazoan physiology?
- iii. How have these potential synergistic effects evolved over time as a function of ocean-atmosphere chemistry?

- iv. How do the impacts of environmental parameters change through life history and as a function of ecology?
- v. How do environmental constraints impact metazoan development?
- vi. What role (if any) does time-dependent variability in environmental conditions play in fostering or inhibiting the emergence of animal multicellularity?
- vii. What is the timing and spatial pattern of ocean oxygenation?

We argue that answering these questions demands an interdisciplinary approach, drawing together: (1) paleontological and molecular records of evolutionary change; (2) geochemical/geologic records of shifting environmental conditions; (3) developing more robust correlations between these records; (4) the development, calibration, and application of spatially explicit Earth system and trait-based ecological models; and (5) exploration of metazoan physiology in the lab, in the field, and *in silico* (Fig. 3).

Figure 3. Idealized workflow for understanding the environmental context of early metazoan (animal) evolution. More robust records of environmental change and hypotheses of biotic response are produced from Earth’s rock record. Geochemical and sedimentological data can link these to the development and calibration of Earth system models and trait-based ecological models. Insights from theory can be iterated with lab- and field-based exploration of organismal physiology, all of which can be used to refine hypotheses for explaining observations from Earth’s rock record. From *Cole et al.* [2020].



4. Moving forward

Understanding the factors governing the emergence of biological complexity on Earth is central to the goals of the NASA Astrobiology Program [*Hays et al.*, 2015]. While a wide range of fundamental questions remain in this effort, we suggest that elucidating the role of the environment is critical for fully understanding the evolution of complexity on Earth. In turn, constraining the role of environmental drivers in evolving complexity requires coordinated research across diverse scientific disciplines including evolutionary biology, paleontology, ecology, organismal physiology, geochemistry, sedimentology, and Earth system modeling, rendering the Early Cells to Multicellularity (ECM) Research Coordination Network (RCN) uniquely positioned to push forward the science of biological complexity.

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