


REVIEW

On the co-evolution of surface oxygen levels and animals

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Abstract

Few topics in geobiology have been as extensively debated as the role of Earth's oxygenation in controlling when and why animals emerged and diversified. All currently described animals require oxygen for at least a portion of their life cycle. Therefore, the transition to an oxygenated planet was a prerequisite for the emergence of animals. Yet, our understanding of Earth's oxygenation and the environmental requirements of animal habitability and ecological success is currently limited; estimates for the timing of the appearance of environments sufficiently oxygenated to support ecologically stable populations of animals span a wide range, from billions of years to only a few million years before animals appear in the fossil record. In this light, the extent to which oxygen played an important role in controlling when animals appeared remains a topic of debate. When animals originated and when they diversified are separate questions, meaning either one or both of these phenomena could have been decoupled from oxygenation. Here, we present views from across this interpretive spectrum—in a point-counterpoint format—regarding crucial aspects of the potential links between animals and surface oxygen levels. We highlight areas where the standard discourse on this topic requires a change of course and note that several traditional arguments in this “life versus environment” debate are poorly founded. We also identify a clear need for basic research across a range of fields to disentangle the relationships between oxygen availability and emergence and diversification of animal life.

KEYWORDS

animals, evolution, oxygen, precambrian

1 | INTRODUCTION

Both fossil and molecular records tracking major evolutionary events are converging on a relatively coherent timeline for the history of life on our planet (Knoll & Nowak, 2017). Likewise, empirical records and biogeochemical modeling are providing an increasingly well-constrained view of ecosystem evolution in deep time. There

has also been a flood of recent work reconstructing environmental evolution—foremost the history of surface oxygen levels. The most significant advances in these fields have come in the Precambrian (>541 million years ago, or Ma), which is attributable at least in part to few meaningful constraints on Precambrian environmental conditions. These advances provide an impetus for continuously revisiting the role of environmental factors in controlling the timing and dynamics of the switch from bacteria-and-archaea-dominated ecosystems to ecosystems with more macroscopic life—ecosystems with

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animals and other multicellular eukaryotes. Particular focus has been given to the role, if any, that surface oxygenation played in driving the origin and early diversification of animals.

The range of views on the links between oxygen and animals runs the gamut from oxygen controlling the timing of the emergence and diversification of animals to surface oxygen levels playing no role at all. It has also been proposed that rising surface oxygen levels were a consequence of increased metazoan diversity and abundance. This range of views indicates either that there are too few constraints to make this a tractable question or that different authors are talking past or parallel to each other. As with many historical events, the actual dynamics are likely to have involved a complex pattern of cause and effect. Although increasing oxygen levels have long been invoked as a driver for the diversification of animals, the dynamic has become more nuanced by developments in geochemistry and in our understanding of both the tempo of the Ediacaran–Cambrian radiation and the nature of feedbacks between environmental change and evolutionary response.

Here, we use a point-counterpoint format to sharpen the distinction between two end-member opinions: (a) Environmental oxygenation was a primary driver of early animal evolution; and (b) environmental oxygenation played an insignificant or marginal role in early animal evolution. Our hope is to focus attention on unresolved and under-constrained aspects of the larger question. We do not claim to speak for all those thinking about environmental controls on metazoan evolution, or even that we all agree on every statement in this paper—we only claim to hold a wide range of views on this topic. In spite of our diversity of views, however, we agree that several ideas consistently appearing in the literature are outdated or are no longer supported by empirical or theoretical studies. Therefore, in the spirit of the long-running series in the Sunday *Washington Post*, we begin by outlining six persistent myths about surface oxygen levels and animals that we hope will be abandoned.

2 | MYTHS ABOUT OXYGEN AND THE RISE OF ANIMALS

2.1 | Myth no. 1 The biological events of the late Neoproterozoic and Cambrian are largely about skeletonization, or all about animals

The extraordinary explosion of durably skeletonized fossils in lower Cambrian rocks puzzled Charles Darwin (Darwin, 1859). But the extent of the biological transformation in the late Ediacaran and Cambrian encompasses more than just hard parts, and more than just animals. The discovery of the Burgess Shale fossils in 1909 and the Chengjiang biota in 1985 greatly expanded the breadth of diversity associated with the Cambrian Explosion, establishing that soft-bodied metazoan lineages exhibit similar disparity as lineages with hard parts. The trace fossil record confirms that this diversification of larger-bodied animals roughly coincided with the appearance of durably skeletonized forms, suggesting that to fully understand the

dynamics of this event we need to look beyond just the increase in hard parts. Interestingly, there is increasing evidence that burrowing (including bed penetrative burrowing) and calcification are actually late Ediacaran not early Cambrian phenomena (Tarhan, Droser, Cole, & Gehling, 2018).

Just as the story of Cambrian animals is not all about skeletons, the broader picture is not all about animals. Protists and other organic-walled microfossils underwent a series of dynamic changes after ca. 800 Ma. The record of organic-walled microfossils (acritarchs), a polyphyletic assemblage of eukaryotic phytoplankton and other groups, possibly including some animal embryos, suggests an increase in diversity and disparity in the late Neoproterozoic and Cambrian (Huntley, Xiao, & Kowalewski, 2006; Nowak, Servais, Monnet, Molyneux, & Vandembroucke, 2015). Regarding photosynthetic clades, Brocks et al. (2017) used biomarker evidence to track an ecological “rise of algae” during the interval between the Sturtian and Marinoan glaciations (ca. 657–645 Ma). Although our view of late Ediacaran and early Cambrian biotic diversity is still being refined, what will not change is clear evidence for major shifts in ecosystem structure and complexity through the Ediacaran and early Cambrian, coincident with a record of increasingly diverse animals (Darroch, Smith, Laflamme, & Erwin, 2018; Tarhan et al., 2018; Wood et al., 2019). And in that light, late Neoproterozoic and Cambrian biotic transitions are largely not about skeletonization, or all about animals.

2.2 | Myth no. 2 Long intervals of stable redox conditions occurred through the Proterozoic

Some redox scenarios postulated long periods of relatively stable conditions. For example, the “Canfield ocean” featured anoxic and euxinic (sulfide-rich) deep-ocean conditions through the Proterozoic, relieved only by a relatively unidirectional rise in oxygen during the late Ediacaran (Canfield, 1998). Broader stratigraphic and geographic coverage, including onshore–offshore transects, as well as new redox proxies have provided a more nuanced view of Proterozoic redox with much less stability (Diamond & Lyons, 2018; Doyle, Poulton, Newton, Podkovyrov, & Bekker, 2018; He et al., 2019; Li, Cheng, et al., 2018; Li, Zhang, et al., 2018; Planavsky, Cole, et al., 2018; Planavsky, Slack, et al., 2018; Sperling et al., 2014; Tang, Shi, Wang, & Jiang, 2016). Any attempts to model Proterozoic redox conditions are similarly left with the conclusion that the marine redox landscape was patchy and complicated (Reinhard, Planavsky, Olson, Lyons, & Erwin, 2016).

The defining characteristic of the Proterozoic ocean rather appears to be the lack of a strong redox buffer (Planavsky, Cole, et al., 2018; Planavsky, Slack, et al., 2018), in stark contrast to the strongly ferruginous (anoxic and iron-rich) Archean oceans and the largely oxic modern oceans. Although Proterozoic oceans were dominantly reducing, conditions varied spatially and temporally—there were almost certainly regions that were ferruginous, euxinic, and oxic throughout the Eon. This is an important modification from a strict reading of Canfield’s transformative 1998 paper (Canfield, 1998).

Indeed, a strict reading of Canfield (1998) is no longer tenable; but the Proterozoic ocean does appear to have been a distinct redox state—just not one that was globally sulfidic.

2.3 | Myth no. 3 Geochemical proxies agree on a single narrative for the evolution of oxygen levels

One of the challenges for a paleontologist is that as soon as one has mastered the intricacies and limitations of one proxy for oxygen levels (for either local or global deep ocean or shallow oceans) geochemists introduce another system. While geochemists commonly embrace the idea that the periodic table is a playground to explore, few paleontologists relish this notion. The earliest proxies were often interpreted as representing a “global” signal for redox conditions. As more sedimentary sections were studied and proxies were introduced, it became increasingly apparent that there was likely to be considerable local and even regional variation in oxygen levels. The ideal is a proxy for oxygen levels in the shallow marine settings where most marine organisms live. But almost by definition, such a proxy would only provide a local or regional signal. Moreover, geochemical proxies differ in what they actually measure; for example, the ease with which individual trace metals are reduced is not equivalent, nor is their susceptibility to various reductants. Many redox proxies are best archived in deeper water sediments—settings likely decoupled from near-surface environments of interest prior to the ventilation of the oceans. Thus, the search for a “single” narrative of oxygen history from 800 to 500 Ma is a chimera. Further, currently proposed views of Proterozoic redox evolution are likely irreconcilable. Critical reevaluations of datasets and the way in which they have been interpreted, and the grounding of proxy signals in the modern marine system, will be essential next steps in creating a coherent narrative about Proterozoic redox evolution.

2.4 | Myth no. 4 Collagen places minimum constraints on the amount of oxygen required for the evolution of animals

The various collagen proteins are found across all animals where they play a critical role in the extracellular matrix. In sponges, collagen is required for cell adhesion and support. Oxygen is required for the synthesis of an altered amino acid found in collagen—hydroxyproline—and this led Towe (1970) to argue that collagen synthesis placed limits on the levels of available oxygen. Mills and Canfield (2014) carefully reviewed this controversy, showing that Towe was principally concerned with the oxygen levels required for fossilizable animals, rather than the origin of animals, and in any case the minimum oxygen level required for collagen synthesis remains undefined. As presented by Towe, collagen synthesis is likely possible at oxygen levels far below the O_2 half-saturation constant of proline hydroxylase, the enzyme catalyzing the oxygen-requiring step of collagen synthesis (Mills & Canfield, 2014; Sperling, Frieder, et al.,

2013; Sperling, Halverson, et al., 2013). Thus, at present there is no evidence that collagen synthesis was a limiting factor in the earliest evolution of animals. Although some oxygen is likely needed for collagen synthesis, the prevailing myth is that the O_2 requirement for collagen synthesis is well constrained and is as high as originally suggested (Runnegar, 1982a).

2.5 | Myth no. 5 Environmental and evolutionary changes were geologically instantaneous

Several decades ago, before the advent of better intercontinental correlations and high-resolution geochronology, the basal Cambrian appearance of fossils was easily interpreted as an explosive phenomenon. Since the early 1990s, however, increasingly high-resolution fossil, stratigraphic, geochemical, and geochronologic data have shown that the appearance of animals in the fossil record (which is not necessarily the same thing as the origin of the representative clades) was a more prolonged affair, with sponge biomarkers and at least one bilaterian (*Kimberella*, likely a stem lophotrochozoan) appearing during the Ediacaran (reviewed by Sperling & Stockey, 2018) and a diversity of tubular fossils appearing in the latest Ediacaran alongside the appearance of more charismatic members of the Ediacara biota like *Dickinsonia* (Droser, Tarhan, & Gehling, 2017; Schifftbauer et al., 2016; Tarhan et al., 2018). Various bilaterian clades staggered in through the first several stages of the Cambrian, although most major clades were recorded by Stage 3 (521–514 Ma). The explosiveness of the “Cambrian Explosion” is really an issue of temporal granularity. It is “explosive” with respect to the preceding ~3 billion years of the stratigraphic record that does not contain large, complex multicellular fossils, but also it clearly unfolded over millions to tens of millions of years. Similarly, as discussed later in this paper, redox proxies show a complicated and temporally expanded pattern of change through the Neoproterozoic and Cambrian.

2.6 | Myth no. 6 Evolution is always opportunistic (empty niches drive evolution)

One of the common implicit assumptions is that evolution is intrinsically opportunistic, capitalizing on environmental and ecological opportunities. In this view, the ancestral metazoan lineage was poised to explode into the diversity of animal life as soon as oxygen levels (or, in other scenarios, some other environmental change) reached a critical threshold. In earlier scenarios, pre-metazoan lineages diverged before this threshold was achieved, and thus, the generation of metazoan multicellularity may have occurred independently in different clades (Cloud, 1978; Nursall, 1962).

Evolution certainly can be opportunistic, and selection can respond remarkably fast to new opportunities (witness the diversity of dogs, for example; Stroud & Losos, 2016). But such rapid response often depends upon the extent of genetic variation present in the population. Evolutionary opportunism was a key intellectual feature

of architects of the Modern Synthesis such as Ernst Mayr and George Gaylord Simpson, who believed that existing genetic variation and mutation were sufficient to respond to ecological opportunity (Dobzhansky, 1937; Haldane, 1927; Mayr, 1942; Simpson, 1944). Potentiating genetic mutations may be required for evolutionary novelties, however (Blount, Barrick, Davidson, & Lenski, 2012; Stern & Orgogozo, 2008), and the ubiquity of macroevolutionary lags further demonstrates that we cannot assume that evolution will rapidly capitalize on opportunity (Erwin, 2015).

3 | POINT-COUNTERPOINT ARGUMENTS

In the following section, we present eleven key points regarding the relationship between oxygen and animals in the form of questions. Each question is argued from a “yes” and a “no” perspective (with variable ordering of the “yes” and “no” responses depending on the point being argued), discussing both agreements and disagreements in the literature, as well as highlighting critical gaps in our knowledge and avenues on which we may usefully move forward. Most arguments build on the narrative that Proterozoic atmospheric oxygen was in fact lower than the Modern (discussed in Point 3); substantial revision to this framework would force re-evaluation of many answers.

3.1 | Is there a minimum O₂ threshold for the origin of animals/animal multicellularity?

Yes: Anaerobic energy metabolism is widespread in eukaryotes (Müller et al., 2012). However, despite various claims, no animal has been convincingly or definitively shown to complete their life cycle under anoxia (Fenchel & Finlay, 1995; Mentel, Tielens, & Martin, 2016), suggesting that life cycle completion in the total absence of oxygen is either wholly incompatible with metazoan ecology and physiology, or is an extremely rare and derived metazoan trait. Therefore, some amount of oxygen is needed to complete the life cycle of all currently known animals. Just what this amount is, however, and how often or for how long it needs to be met remain undefined for animals in the broadest sense (Mills & Canfield, 2014). Importantly, this absolute oxygen requirement does not preclude certain animals from living anaerobically under anoxic, and even euxinic, conditions for extended periods of their life cycle (Mentel et al., 2016; Müller et al., 2012) (*for redox terminology, see Box 1*).

The absence of strictly anaerobic animals could either result from an absolute physiological oxygen requirement, or from ecological exclusion. In other words, animals may require higher oxygen concentrations, or perhaps need to be exposed to oxygen more frequently, than microbial eukaryotes, or anoxic environments may simply be unsupportive of the long-term persistence of colonial and multicellular life. Having interconnected tissues is one of the most obvious factors that could drive higher minimum oxygen requirements than those present in single-celled eukaryotes (i.e., could require aerobic respiration). However, there are no solid estimates (from empirical observations

or from physiological modeling) on how or if basic connective tissues would alter minimum oxygen requirements. Alternatively, multicellularity may not have a selective advantage under anoxia if the increased fitness from multicellularity comes largely from escaping phagotrophy (Knoll, 2014; Knoll & Lahr, 2016), which is less common, albeit present, in anoxic settings (Fenchel & Finlay, 1995). Animals appear to be obligate or facultative aerobes, in contrast to strict anaerobes (and thus have an oxygen limit at some level), but the factors driving the need for increased oxygen are not well resolved.

No: While animals appear to have an absolute oxygen requirement (see “yes” above), it is unclear if this oxygen requirement is higher than those of their unicellular and colonial eukaryotic ancestors—and this is the critical distinction when attempting to determine if the origin of animals could have been limited by oxygen availability. The last common ancestor of living eukaryotes (or the last eukaryotic common ancestor, LECA) was almost certainly aerobic—whether it was an obligate aerobe (Sagan, 1967), or a facultative aerobe (Martin & Müller, 1998; Müller et al., 2012). The same conclusion equally applies to the metazoan last common ancestor (LCA) (Mentel, Röttger, Leys, Tielens, & Martin, 2014; Müller et al., 2012). Thus, at least some surface environments must have remained sufficiently oxygenated to support aerobic eukaryotes since LECA appeared (Butterfield, 2018).

The first multicellular stem-group metazoans and the metazoan LCA likely possessed body plans with the majority of metabolically active cells in direct contact with seawater—an organization these early animals would have shared with their immediate unicellular and colonial ancestors (Runnegar, 1982b; Sperling, Frieder, et al., 2013; Sperling, Halverson, et al., 2013; Sperling, Knoll, & Girguis, 2015). Furthermore, colonies of flagellated cells have the potential to bypass diffusive O₂ transport through the collective and coordinated beating of their surface flagella (Goldstein, 2015; Roper, Dayel, Pepper, & Koehl, 2013; Short et al., 2006; Solari, Kessler, & Goldstein, 2007), leading to gas-exchange rates surpassing those of their strictly unicellular, diffusion-limited counterparts (Butterfield, 2018; Mills & Canfield, 2017). Since fossil evidence for eukaryotic multicellularity potentially dates back to the late Paleoproterozoic and early Mesoproterozoic (Bengtson, Sallstedt, Belivanova, & Whitehouse, 2017; Javaux & Knoll, 2017; Zhu et al., 2016), there is no obvious reason for thinking that Mesoproterozoic environments were sufficiently oxygenated to support (facultative) aerobic and colonial microbial eukaryotes, yet were insufficiently oxygenated to support the earliest multicellular animals. In the absence of more compelling evidence, the minimum O₂ threshold for the first multicellular animals has conceivably been met since the origin of LECA, and perhaps even farther back in the Proterozoic (Butterfield, 2018).

3.2 | Would traditional estimates of proterozoic oxygen have been prohibitive to crown-group animals (sponges/bilaterians)?

No: The evolution of estimates for atmospheric oxygen levels is summarized in Figure 1, but is broadly considered to be ~1%–40%

Box 1 Redox terminology

One historical aspect that has caused confusion between fields is simply the use of different oxygen units in different fields across geobiology. Oceanographers and ecologists have generally used concentration units (e.g., $\mu\text{mol/kg}$, ml/L , which will depend on the solubility of oxygen in a specific water mass based on its temperature and salinity), physiologists commonly use units related to partial pressure (the driving force for the diffusion of oxygen into an organism, e.g., mmHg , kPa), and geologists and ancient Earth system modelers often compare ancient atmospheric oxygen levels to modern levels as a percentage of Present Atmospheric Levels (PAL). These modeled ancient atmospheres would then equilibrate with ancient oceans, with the same basic gas laws as today, but with concentrations dependent on the ancient temperature/salinity. Sedimentary geochemists and paleontologists, who provide the empirical data which guide the efforts of Earth system modelers, mainly use a series of terms (explained below) that describe the oxygen concentration of an ancient environment based on its redox geochemistry or fossils preserved in the rock record. In this paper, we generally use the following redox terminology:

Anoxic: No oxygen present.

Euxinic: Anoxic, with free sulfide present (iron-limited).

Ferruginous: Anoxic, no sulfide (iron-replete).

Suboxic: The very featheredge of low oxygen before anoxia. In the modern ocean, only very small or chemosymbiotic animals can live in these environments.

Dysoxic: Low O_2 . Animals are present, but ecology is impacted by low oxygen.

Oxic: Similar to the modern surface ocean.

The actual oxygen concentrations tied to these latter three terms will vary between classification schemes, but here we present the traditional (Tyson & Pearson, 1991) classification (Figure B1). Note the modern global change community has introduced an additional series of terms for low-oxygen states (e.g., hypoxia)—for more discussion of oxygen nomenclature, see Canfield and Thamdrup (2009), Hofmann, Peltzer, Walz, and Brewer (2011), and Sperling et al. (2015).

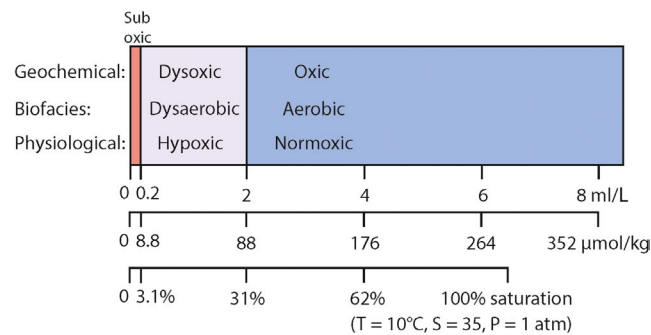


Figure B1 This is the traditional classification from Tyson and Pearson (1991). This scale shows two oxygen concentration units ($\mu\text{mol/kg}$ and ml/L) and how these numbers relate to different percent saturations (equivalent to % PAL) at a given temperature and salinity. It should be noted, however, that the scale for saturation will expand and contract depending on changes in temperature and salinity. That is, with a decrease in salinity or temperature 100% saturation would be equivalent to a higher concentration of oxygen in the water.

PAL during the Proterozoic (Holland, 2006; Kump, 2008). Some extant animals—including both bilaterians and non-bilaterians—can live in modern oxygen minimum zones (OMZs) under oxygen concentrations corresponding to 1%–10% PAL (Sperling, Frieder, et al., 2013; Sperling, Halverson, et al., 2013; Sperling et al., 2015) (Box 1). Further, sponges can maintain normal transcription down to, and perhaps even below, 0.25% PAL (equivalent to $0.5 \mu\text{M O}_2$ at 26°C and a salinity of 32) (Mills, Francis, Vargas, et al., 2018), and can live in environments featuring ~1%–3% PAL ($3\text{--}8 \mu\text{M O}_2$ at $\sim 7^\circ\text{C}$ and a salinity of ~ 34) (Mosch et al., 2012), as well as environments

characterized by seasonal anoxia (Bell & Barnes, 2000) (*for redox terminology and conversion between units*, see Box 1). Facultative anaerobiosis is widespread and conserved across crown-group metazoans, suggesting that these pathways were present in the metazoan LCA (Mentel et al., 2014; Müller et al., 2012), even if the exact evolutionary pathway by which animals gained these capacities is unclear (Ku et al., 2015; Martin, 2017; Müller et al., 2012; Stairs et al., 2018). This means that not only can multiple animal phyla live under O_2 concentrations corresponding to 1%–10% PAL, but they can also survive extended anoxia and euxinia (Müller et al., 2012). The traditional

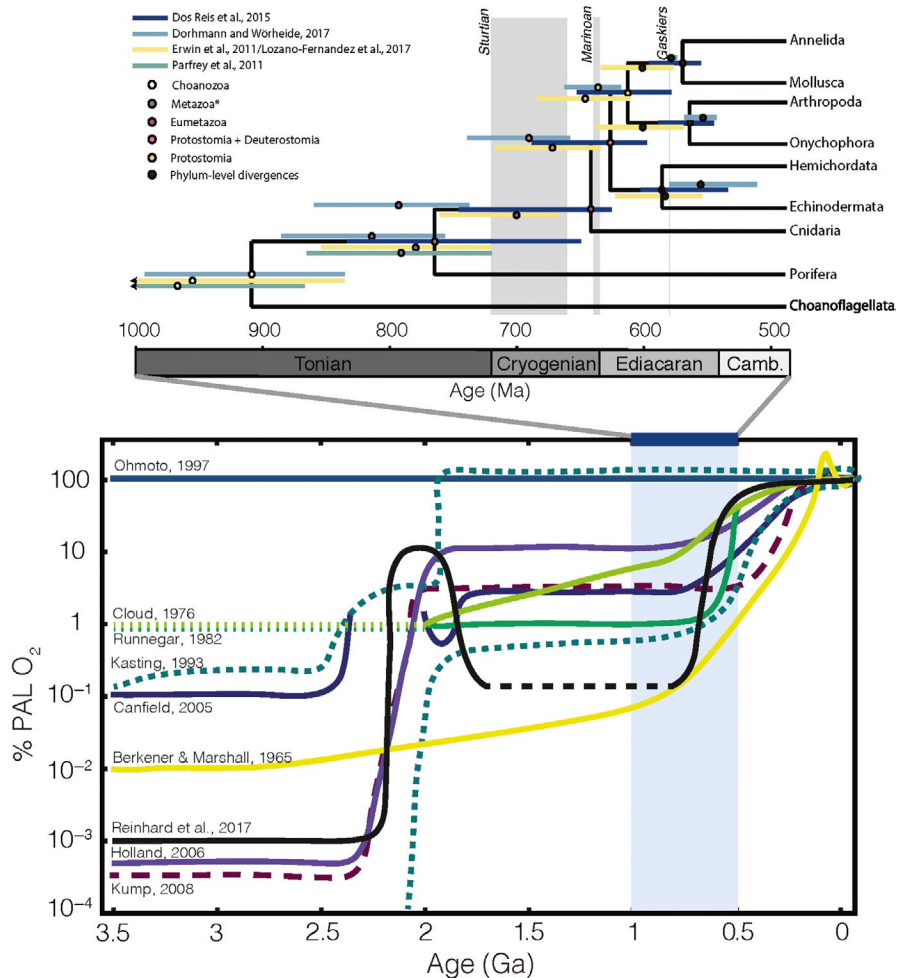


FIGURE 1 A summary of our evolving understanding of atmospheric oxygen levels through Earth's history over the last 50+ years relative to estimates for the timing of early animal evolution. The top panel (adapted from Sperling & Stockey, 2018) shows 95% confidence intervals (colored bars) on molecular clock estimates of the divergence of the earliest multicellular animals from four recent studies. The bottom panel summarizes the estimates of atmospheric oxygen levels through time from nine studies spanning the last half century. The dashed lines representing the Cloud (1976) and Runnegar (1982b) estimates are projected back in time, as both authors do not indicate specific pO_2 values prior to 2.0 Ga. The Kasting (1993) estimate is represented by the two dotted lines indicating upper and lower bounds on the proposed pO_2 levels

estimates of mid-Proterozoic pO_2 of 1%–10% PAL very clearly do not represent a fundamental impasse to modern animals. Further, there is no strong evidence that the morphological and metabolic traits needed to adapt to these dynamic and low-oxygen conditions would have been absent from, or unavailable to, stem-group metazoans and the metazoan LCA (Mills & Canfield, 2014) or early bilaterians (Sperling, Frieder, et al., 2013; Sperling, Halverson, et al., 2013).

Yes: It has been commonly argued that because some animals can thrive under low-oxygen conditions today, they could have similarly thrived in an Earth system with dramatically lower atmospheric oxygen levels than those of the modern. However, most metazoans thriving in modern low-oxygen settings do so as a result of gradual adaptation to these conditions (Lamont & Gage, 2000). Most modern OMZs are also at bathyal depths, which are relatively cold—the organisms are not tasked with facing low O_2 (= low supply) and warm temperatures (= high demand, due to effects on metabolism; Pörtner, 2012). A shallow-water setting with low O_2 resulting from marine waters equilibrating with a low O_2 atmosphere is simply a fundamentally different evolutionary landscape from a well-oxygenated ocean/atmosphere system with small pockets of low oxygen resulting from high organic carbon respiration (e.g., OMZs). More importantly, members of basal metazoan clades have a benthic life stage, and benthic anoxia is expected to be widespread through the

oceans at atmospheric pO_2 values of 1%–10% PAL (Reinhard et al., 2016). Therefore, the presence of a wide range of metazoans in low oxygen concentrations today does not necessarily imply that animals would have had stable populations (i.e., lineages that persist over geological time) in pervasively low-oxygen oceans.

More broadly, we need to move beyond a threshold approach based on minimum metazoan oxygen requirements and consider the oxygen stress animals would have experienced throughout their life cycle in an ocean with a spatially variable redox landscape. With that in mind, it is possible that oxygen dynamics around a mean O_2 value above 1% PAL significantly shaped ecosystem structure and may have even been prohibitive of crown-group animals. In addition, O_2 availability must be considered together with other environmental factors that could exacerbate the metabolic impacts of low-oxygen conditions—most notably temperature.

3.3 | Do recent geochemical proxies rule out traditional pO_2 estimates from 1900 to 800 Ma?

No: Traditional estimates of Proterozoic atmospheric oxygen levels were ~1%–40% PAL (Holland, 2006; Kump, 2008) (Figure 1). Multiple lines of recent geochemical evidence support a mid-Proterozoic

marine redox landscape that is difficult to reconcile with oxygen levels higher or lower than these traditional estimates. There are no direct atmospheric oxygen estimates for the mid-Proterozoic, so atmospheric reconstructions rely on linking marine and atmospheric oxygen levels. This effort builds from the principle that the surface oceans are largely in equilibrium with the atmosphere (despite some disequilibrium from oxygen production). Reports of mid-Proterozoic basin scale ocean oxygenation exist (Planavsky, Slack, et al., 2018; Sperling et al., 2014; Wang et al., 2018) which, barring very low levels of primary productivity, are most easily interpreted as intervals with oxygen above 1% PAL. On the other end of traditional estimates, there is general agreement that marine anoxia was more widespread than in the modern and the oceans were likely not fully ventilated until the Phanerozoic (or at least the Neoproterozoic) (Ozaki & Tajika, 2013; reviewed by Lyons, Reinhard, & Planavsky, 2014), suggesting lower than modern atmospheric oxygen levels. Therefore, although mid-Proterozoic atmospheric oxygen levels are poorly constrained, geochemical evidence is still broadly consistent with pO_2 estimates of ~1%–10% PAL. This conclusion is not dependent on controversial (strongly debated) proxies and proxy records (see discussion below; e.g., Large et al., 2018; Yeung, 2017; Zhang et al., 2016).

Yes: Over the past decade several geochemical approaches have suggested that oxygen was significantly lower than traditional estimates. Iron retention in paleosols has historically been the most commonly cited constraint on minimum pO_2 from 1,800 to 800 Ma—which most modeling attempts found corresponded to a minimum oxygen level of roughly 1% PAL (Zbinden, Holland, Feakes, & Dobos, 1988). However, more recent efforts revealed that most definitive mid-Proterozoic paleosols are characterized by iron loss, not retention, which in the traditional framework suggests a pO_2 of <1% PAL (Mitchell & Sheldon, 2016; Planavsky, Cole, et al., 2018). Several mid-Proterozoic sedimentary units have authigenic Cr enrichments with limited Cr isotope fractionations—indicative of either limited Cr oxidation (a pO_2 of ~0.1%) or quantitative reduction of any Cr oxidized in the critical zone (which means available surface Fe(II)—a potent Cr reductant—and a pO_2 of <1% PAL) (Cole et al., 2016; Crowe et al., 2013; Planavsky et al., 2014). There are instances of partial iron oxidation in shallow-water mid-Proterozoic settings (Lin, Tang, Shi, Zhou, & Huang, 2019)—a compelling indicator of low-oxygen conditions (Canfield, 2005). Similarly, modeling of Ce oxidation kinetics across marine bathymetric sequences from ca. 1.9 and ca. 1.45 Ga benthic carbonates suggests a pO_2 of 0.1%–1% PAL (Bellefroid et al., 2018; Bellefroid, Planavsky, Hood, Halverson, & Spokas, 2019). Finally, recent work on rare oxygen isotopes ($\Delta^{17}O$) recorded in ca. 1.4 Ga terrestrial sulfates may also suggest a pO_2 of <1.5% PAL (Crockford et al., 2018; Planavsky, Cole, et al., 2018). The rare oxygen isotope work is particularly exciting, given that this method allows measurement of an atmospheric signature that is directly related to atmospheric oxygen levels.

Finally, several recent claims of atmospheric oxygen levels closer to traditional estimates in the mid-Proterozoic have garnered substantial controversy. The robustness of both the quantitative and

empirical frameworks for a number of these studies have been questioned (e.g., Planavsky et al., 2016; Zhang et al., 2016; although it is important to note that aspects of studies suggesting lower than traditional pO_2 have also been questioned). Thus, additional work is needed to make a sound case for mid-Proterozoic atmospheric oxygen concentrations close to traditional estimates. However, even if the Proterozoic episodically experienced oxygen levels well above 1% PAL, this does not negate evidence for, or predominance of, lower atmospheric oxygen levels (see Myth 2), or indicate that intervals of lower atmospheric oxygen did not have a major effect on contemporaneous ecosystems. In fact, with lower pO_2 (<1% PAL) and limited buffering of the global oxygen reservoir, rapid and large magnitude changes in pO_2 are expected (i.e., a doubling of pO_2 would only require a small shift in redox balance) (Planavsky, Cole, et al., 2018; Planavsky et al., 2014).

3.4 | Was there an organic-rich neoproterozoic “soup” with high bacterial concentrations and dissolved organic matter?

Yes: Since deep-ocean anoxia was a prevalent feature of Proterozoic oceans, labile dissolved organic matter (DOM) should have been more readily preserved in the water column. Furthermore, before the proliferation of relatively large and fast-sinking eukaryotic cells, as well as the advent of fecal-pellet-producing zooplankton, export production would have been reduced at a given nutrient inventory, thereby encouraging deep-ocean anoxia and the preservation of marine DOM (Logan, Hayes, Hieshima, & Summons, 1995). Oxidation and rainout of this predicted marine DOC pool has been used to explain anomalously negative Neoproterozoic carbonate carbon isotope values, which may have occurred during surface oxidation events (Fike, Grotzinger, Pratt, & Summons, 2006; Rothman, Hayes, & Summons, 2003). Specifically, there are large negative carbon isotope excursions reaching values lighter than the mantle input (most famously the Shuram carbon isotope excursion [ca. 570 Ma]). If these are capturing marine DIC values, they require massive input of isotopically negative carbon. Other Neoproterozoic carbon isotope excursions also exhibit decoupling of carbonate and organic carbon. Rainout of DOC, which would not track marine DIC values because it accumulated over an extended period of time, provides a process that can explain this anomalous decoupling. However, based on the arguments below, direct geochemical evidence for a large Neoproterozoic DOC pool has become a “Myth.” Therefore, persistent arguments for a Neoproterozoic “soup” come from biological and oceanographic reasoning. First, fractal body plans are common among Ediacaran (570–543 Ma) rangeomorphs—which, despite exceptional preservation, do not show any obvious feeding structures, suggesting a dependency on dissolved organics for nutrition. These fractal body plans were arguably adapted to maximize the uptake of DOC from this presumably large Neoproterozoic DOC reservoir (Laflamme, Xiao, & Kowalewski, 2009), although it may have been the lability

of DOC at depth that mattered rather than the size of the reservoir (Sperling, Peterson, & Laflamme, 2011). Combined with arguments for slowly sinking organic matter (Butterfield, 2009, 2009, 2018) discussed above, this has been leveraged as evidence in favor of a Proterozoic “soup.”

No: Both model (Derry, 2014; Laakso & Schrag, 2014, 2017, 2019; Ozaki, Reinhard, & Tajika, 2019) and new empirical (Crockford et al., 2018; Reinhard et al., 2017) evidence indicates that low-oxygen Earth states must have had dramatically lower primary productivity than in modern oceans. Most recent estimates suggest low-oxygen (<1% PAL) Earth states would have had rates of marine primary productivity <10% of modern levels (Ozaki et al., 2019), and this dramatically lower productivity would have severely curtailed DOC production. Further, there are a wide range of pathways through which DOC is destroyed in the modern oceans that would have also operated in a largely anoxic ocean—including photochemical degradation, as well as on- and off-axis hydrothermally mediated (thermal) degradation (Hawkes et al., 2015) and scavenging (via iron oxides; Tarhan et al., 2018). Finally, DOC concentrations commonly decrease in anoxic waters, potentially as a result of the relative inefficiency of anaerobic growth (e.g., Black Sea; Ducklow, Hansell, & Morgan, 2007). Alternatively, the stability of the marine DOC reservoir may instead be controlled largely by the metabolic costs of consuming a dilute substrate pool (Arrieta et al., 2015; Dittmar, 2015), which would imply that it is difficult to sustain a marine DOC reservoir significantly larger than that in the modern oceans.

With respect to geochemical data, there is no sound empirical evidence for a large DOC reservoir. The Shuram carbon isotope excursion—if it is recording marine DIC values—can be easily explained via modest changes to atmospheric O₂ and net pyrite burial in the sedimentary rock cycle without any need for a large DOC reservoir (Miyazaki, Planavsky, Bolton, & Reinhard, 2018). Decoupling of carbonate and organic carbon isotope values is also not sound evidence for a large DOC reservoir (cf. Rothman et al., 2003)—C isotope decoupling is found on the modern Bahama Bank (the canonical modern shallow-water carbon analogue) and it is not linked to “DOC rainout” (*contra* Oehlert & Swart, 2014; Rothman et al., 2003). Further, the only Neoproterozoic successions in which carbon isotope decoupling is observed either contain <0.5% TOC, which can easily be explained by detrital (petrogenic) OC transport (Johnston, Macdonald, Gill, Hoffman, & Schrag, 2012), or may be the result of mixing between different pools of organic matter (Lee, Love, Fischer, Grotzinger, & Halverson, 2015). Detrital organic matter transport is ubiquitous even on the high-oxygen modern Earth (Derry, 2014) and would have been even more common with lower atmospheric oxygen levels (Daines, Mills, & Lenton, 2017). Finally, the fractal structure of rangeomorph Ediacaran organisms only implies that these organisms were maximizing their surface area, which would be beneficial if consuming DOC or respiring at low oxygen levels—and it therefore cannot be used to argue for high DOC oceans.

3.5 | Did anything interesting biologically happen at 800 Ma?

Yes: Evidence from body fossils, biomarkers, and molecular clock analyses all suggests important evolutionary and ecological transitions between ca. 800 and 720 Ma. Compilations of Proterozoic global species richness based on organic-walled microfossils consistently suggest an increase ca. 800–750 Ma (Knoll, 1994; Vidal & Moczyłowska-Vidal, 1997; Xiao & Tang, 2018), and compilations of within-assemblage diversity (WAD) show the same pattern of increase ca. 800 Ma (Knoll, Javaux, Hewitt, & Cohen, 2006). A more recent higher resolution analysis focused on the period from 1,000 to 635 Ma suggests a more complex pattern in Tonian organic-walled microfossil diversity, with a peak ca. 780–770 Ma (Riedman & Sadler, 2018). This shift near 800 Ma is then followed by a decline through the last ~40 myrs of the Tonian to levels lower than those of the latest Mesoproterozoic (Riedman & Sadler, 2018), indicating that while there was a transition it may have been more complex than originally suggested.

Eukaryotic innovations that are interpreted to reflect changes in microbial food webs also first appear in the fossil record between 800 and 720 Ma (Knoll, 2014; Porter, 2011). Apatitic-scale microfossils in ca. 811 Ma carbonates and cherts from the Fifteenmile Group, Yukon, may provide the earliest evidence for controlled biomineralization (Cohen, Strauss, Rooney, Sharma, & Tosca, 2017), and vase-shaped microfossils (VSMs) found in nearly a dozen units around the world between 790 and 730 Ma (Riedman, Porter, & Calver, 2018) provide the earliest evidence for tests (microscopic shells). These protective structures, encircling otherwise naked cells, may have evolved as a defense against predation. This is consistent with the discovery of microscopic drill holes of various shapes and sizes in VSMs and organic-walled microfossils ca. 780–730 Ma indicating that eukaryovory (i.e., the predatory mode whereby nutrients are obtained from relatively large eukaryotic prey) (Leander, 2004) had evolved by that time (Knoll & Lahr, 2016; Porter, 2016). Lastly, in terms of the rock record, the first robust sedimentary steranes—which are indicative of eukaryotes being a major component of the local biological pump—appear in ca. 800–730 Ma rocks from the Amadeus Basin in Australia, the Chuar Group in the United States, and the Visingsö Group in Sweden (Brocks, 2018; Brocks et al., 2016).

Recent molecular clock estimates converge on a pre-Cryogenian (>720 Ma) origin of crown-group metazoans, with mean estimates ranging from ca. 855 to 650 Ma (Dohrmann & Wörheide, 2017; dos Reis et al., 2015; Erwin et al., 2011; Lartillot, Lepage, & Blanquart, 2009). Appealing to parsimony, the metazoan LCA exhibited complex multicellularity, while the LCA of metazoans and their sister group, the choanoflagellates, was likely unicellular, and potentially colonial (Mills & Canfield, 2017; see also Brunet & King, 2017) with temporal cellular differentiation (Sogabe et al., 2019). Using these predicted ancestral states, obligate animal multicellularity with temporal and spatial differentiation most likely evolved

between the Metazoa + choanoflagellate group, recently estimated to ca. 925–906 Ma (Dohrmann & Wörheide, 2017), and the origin of crown-group Metazoa, sometime around 800 Ma (compiled in Mills, Francis, & Canfield, 2018; Sperling & Stockey, 2018) (Figure 1). Therefore, according to the most recent molecular clock estimates, the origin of metazoan multicellularity occurred sometime between 925 and 800 Ma (Dohrmann & Wörheide, 2017).

No: We know too little about the Mesoproterozoic and Tonian fossil record to be able to say whether anything important happened ca. 800 Ma. Paleontological sampling of the >800 Ma interval, in particular, is poor; of the 40 geologic units used by Cohen and Macdonald (2015) to estimate within-assemblage eukaryote diversity patterns through the Proterozoic, 30 had a mean age between 860 and 720 Ma while only three had a mean age between 860 and 1,000 Ma. Thus, it is possible (or even likely) that the ca. 800 Ma peak in diversity is driven entirely by sampling. In fact, a spate of recent paleontological studies from rocks 1700–800 Ma suggest higher eukaryotic diversity during this earlier interval than previously known (Agić, Moczyłowska, & Yin, 2017; Baludikay, Storme, François, Baudet, & Javaux, 2016; Beghin et al., 2017; Loron, Rainbird, Turner, Greenman, & Javaux, 2019; Miao, Moczyłowska, Zhu, & Zhu, 2019). Recent discovery of complex eukaryotic fossils in previously unexplored 1,000 to 900 Ma rocks in Arctic Canada bolster the case that diversity trends can change with new work in Tonian successions (Loron, François, et al., 2019). Another potential contributor to a spurious ca. 800 Ma diversity peak is the fact that while the 800–720 Ma interval includes a number of complementary preservational windows (shale-hosted, chert-hosted, and carbonate-hosted fossil assemblages), nearly all of the pre-800 Ma body fossil record comes from shales, limiting our view of diversity to only those organisms that lived and could be preserved in siliciclastic settings (Cohen & Macdonald, 2015).

Further, while the robust preservation, abundance, and widespread occurrence of the VSMs provides some confidence that their first appearance between ca. 790 and 750 Ma reflects the evolution of tests in this group, the apatitic-scale microfossil (ASM) record is much sparser. As a result, we can have little confidence that their first appearance in the Fifteenmile Group ca. 811 Ma (Cohen et al., 2017), is close to the origin of this innovation. Additionally, evidence for early biomineralization largely boils down to preservation of structure at a micrometer-to-submicrometer scale. However, since cases of exceptional (even subcellular level) preservation abound in the fossil record (Briggs, 2003) and mineral saturation states can increase exponentially at an interface (e.g., carbonate fluorapatite saturation at the organic interface) it is difficult to ever determine primary mineralogy with very sparse occurrences (e.g., early Neoproterozoic apatite scales from a single locality). Therefore, the case for early Neoproterozoic biomineralization is intriguing but should not, at this point, be viewed as conclusive. Similarly, many of the drill holes recently reported from Chuar microfossils are so tiny as to escape notice under conventional microscopy; closer inspection may reveal much older fossils with evidence of drilling (cf. Loron, Rainbird, Turner, Greenman, & Javaux, 2018, who recently reported possible predatory holes in

ca. 1150–900 Ma Shaler Group fossils). Finally, molecular clock estimates, as most acknowledge, are plagued by large uncertainties. The optimistic view above based on “most likely” estimates is that the origin of animal multicellularity can be pinned between 925 and 800 Ma; the pessimistic view incorporating the most extreme results across all possible sensitivity tests and full confidence intervals suggest animal multicellularity evolved between 1,200 Ma and 650 Ma. Therefore, it is hard to rely on molecular reconstruction to precisely date key biotic innovations.

3.6 | Did anything geochemically interesting happen at 800 Ma?

Yes: Evidence from a wide range of geochemical proxies has been used to argue for first-order shift in both nutrient cycling and surface redox conditions at ca. 800 Ma (Cole et al., 2016; Isson et al., 2018; Liu et al., 2016; Lu et al., 2017; Partin et al., 2013; Planavsky et al., 2014; Reinhard et al., 2013; Reinhard et al., 2017). Additionally, some of these studies provide statistically based evidence to this effect, including a significant shift in the phosphorite record (the appearance of the first continuously phosphoritic stratigraphic interval greater than 50 m; Reinhard et al., 2017), a significant shift in the $\delta^{53}\text{Cr}$ record ca. 800 Ma interpreted as an increase in atmospheric oxygen levels (Figure 2; note change-point test), and a significant difference in pre- and post-800 Ma in the $\delta^{66}\text{Zn}$ record interpreted as the onset of more eukaryote-rich ecosystems (Isson et al., 2018). Other evidence for a major geochemical transition at ca. 800 Ma unfortunately lacks a firm statistical basis. In an effort to address this lingering issue, we have compiled data from the literature for U, V, Mo and P concentrations, I/Ca, Zn/Fe, Ce anomalies (Ce/Ce*), $\delta^{66}\text{Zn}$, and $\delta^{53}\text{Cr}$ records to provide a quantitative exploration of proposed trends and patterns in these records (see Box 2).

In sum, much of the Neoproterozoic is marked by a series of statistically significant geochemical shifts. And, while the onset of these transitions does appear to be close to 800 Ma, major transitions in various proxy records continue across the Ediacaran–Cambrian boundary and beyond, in the same way, perhaps, that the animal record was a much more prolonged and gradual affair than the traditional idea of the “Cambrian explosion” (see Section 2.5). Finally, it should be noted that each geochemical proxy has individual nuances; the sensitivities of redox-sensitive metals vary substantially—I/Ca tracks shallow-water redox conditions while others track deeper waters or are capable of picking up atmospheric signatures. It follows then that a more extended range of change points for each system should be expected, though the onset of these transitions may very well have been ca. 800 Ma.

No: There are two separate and equally critical pieces to this question; first, do geochemical records reflect true first-order changes in the surface environment, and second, did these shifts occur near 800 Ma? Despite some evidence for robust shifts in some proxy records (see Box 2; Figure 2), which are frequently pinned to “ca. 800 Ma,” the paucity of data restricts the conclusions

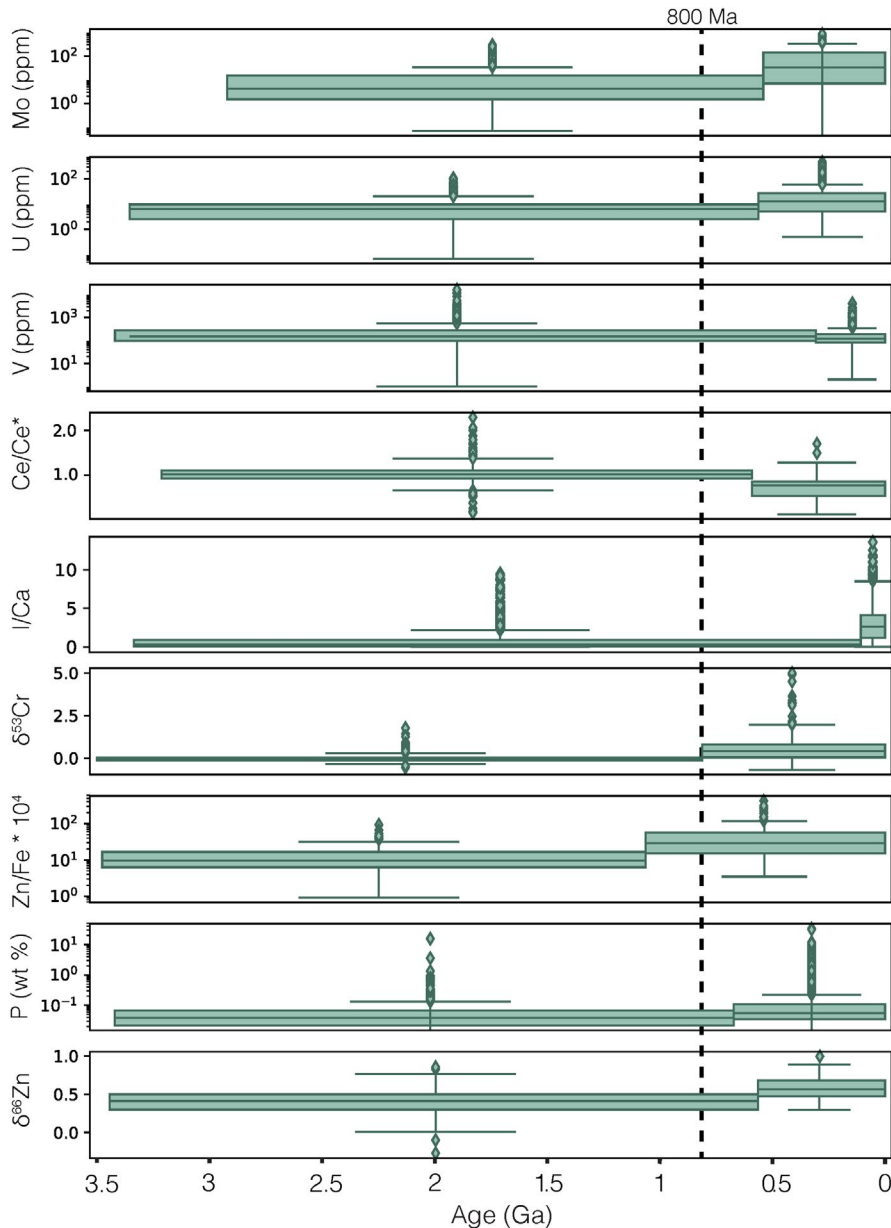


FIGURE 2 Geochemical records of Mo, U, V, Ce/Ce*, I/Ca, $\delta^{53}\text{Cr}$, Zn/Fe, P, and $\delta^{66}\text{Zn}$ divided into two bins using a change-point analysis (see Section 5; Box 2). Binned data are plotted as box-and-whisker plots where the three quartiles are represented within the box and the whiskers each extend to 1.5 interquartile ranges of the upper and lower quartiles, respectively. Any data falling outside those ranges are considered outliers and plotted as points. Residual errors (re) are from the change-point analyses (data compiled from the following: Canfield et al., 2018; Hardisty et al., 2017 and references therein; Isson et al., 2018; Liu et al., 2016; Lu et al., 2018; Partin et al., 2013; Planavsky, Cole, et al., 2018 and references therein; Reinhard et al., 2013, 2017; Scott et al., 2008; Wallace et al., 2017 and references therein)

that can be drawn. As with the fossil record discussed above, few formations document the interval between ca. 1,000 and 700 Ma, and even fewer between 1,000 and 800 Ma. In many compilations, only a handful of formations fall within this 300 million-year window. No amount of statistical analyses can overcome the limitations of our current rock record sampling within this interval, and improved sampling coverage must be an avenue for future work.

Moreover, the sparsity of the record is amplified by exceptionally poor age constraints on many of these critical formations—in particular, those frequently invoked as evidence of the first major shifts in a given proxy record. Examples include the Upper Carbonate Member of the Wynniatt Formation, which has been dated at ca. $761 \text{ Ma} \pm 41 \text{ Ma}$ (van Acken, Thomson, Rainbird, & Creaser, 2013) or the Simla Group of Northern India, which has been dated at ca. 839 ± 139 (Singh, Trivedi, & Krishnaswami, 1999). As a result, it is nearly impossible to claim a robust geochemical shift near 800 Ma.

Although age constraints through this interval are improving (Gibson et al., 2017; Rooney et al., 2018), at this point, major environmental changes should be thought of as transitions occurring over a time span perhaps roughly the length of the Mesozoic.

3.7 | Are existing models for translating redox proxies into biologically relevant data too coarse?

No: There are quantitative estimates of key parameters from geochemical proxies that can be used to calibrate spatially resolved models and output the most critical environmental data. Historically there was limited effort linking geochemical data, ocean models, and ecosystems to explore the role that environmental factors played in controlling the rise of animals. However, in recent years there has been an upswing in interest in modeling Proterozoic

Box 2 Change-point analyses of geochemical data

In an effort to assess geochemical shifts free of bias, a change-point test was used for each dataset to identify the single point that marks the most significant change in the mean (see Section 5). That is, rather than asking “is there a significant difference between data before and after 800 Ma?,” we ask “where does the most important shift occur within the dataset?” Once divided, raw data in each bin were used to construct box-and-whisker plots, representing the mean, quartiles, and outliers (Figure 2; see Section 5). Additionally, a *t* test was applied to each pair of bins, and all were found to be statistically significant (*p*-values < 10⁻⁵). Using this approach, we find the following results.

First, for five of the datasets, change points fall just prior to the Ediacaran–Cambrian boundary (ranging from 526 to 631 Ma for Mo, U, P, δ⁶⁶Zn, and Ce/Ce*). In contrast, two datasets have older change points; δ⁵³Cr (change point = 800 Ma), and Zn/Fe (change point = 1,100 Ma), while two have significantly younger change points; V (change point = 305 Ma; however, the large residual error indicates this is a less important shift relative to other proxies), and I/Ca (change point = 94 Ma; see Lu et al., 2018) (Figure 2). These findings may be the results of a number of factors; for example, Mo and U records could be tied most closely to a shift in shale total organic carbon (TOC) values (Sperling & Stockey, 2018). The Ce/Ce* record is marked by a change point preceding the statistically significant and likely more important transition to modern seawater values identified by Wallace et al. (2017) in the Late Devonian. The I/Ca record currently is marked by a change point at 94 Ma; however, prior to the publication of data in Lu et al. (2018), this record had a change point at 825 Ma, demonstrating the difficulty of uncovering robust temporal trends in small datasets, or failure to reexamine geochemical records as they grow. Finally, the change point identified in the δ⁵³Cr record (Cole et al., 2016; Planavsky, Cole, et al., 2018) matches well with prior analyses that chose to bin the data pre- and post-800 Ma.

marine environments and a jump in the complexity of models being utilized. For instance, the intermediate-complexity Earth system model cGENIE has been utilized by several groups to explore marine redox structure leading up to and during the rise and diversification of metazoans (Reinhard et al., 2016), and more recently to explore the potential impacts of marine nutrient levels on eukaryotic trophic ecology (Reinhard et al., accepted). As an alternative approach, estimates of marine physical dynamics at various climate states from higher resolution GCMs have been coupled with marine biogeochemical models (Bellefroid et al., 2018). This method allows for stochastic approaches to quantify unavoidable uncertainties when modeling Proterozoic environments. Therefore, it is possible

to explore how oxygen levels (or sulfide concentrations) would have varied in the Proterozoic oceans in a modeling framework with a realistic representation of ocean circulation on essentially any spatial scale. These model outputs can be compared to regional redox reconstructions from the rock record or the models can be forced with surface oxygen estimates. The model outputs can then be coupled with species extinction–origination models (Saupe et al., 2019) or with trait-based ecophysiological models (Penn, Deutsch, Payne, & Sperling, 2018). Therefore, a case can be made that existing modeling frameworks do not present fundamental limitations on our ability to quantitatively explore the impact of environmental factors on early animal evolution.

There has also been significant recent work toward inverting geochemical constraints for environmental conditions—providing insights that are useful in their own right and supplying critical inputs for modeling efforts discussed above. While making quantitative ties between oxygen levels and geochemical proxy data introduces additional error, progress has been made recently to hone some of these constraints. For example, developments in weathering models exploring the mobility of iron in paleosols (Mitchell & Sheldon, 2010, 2016) have revised interpretations of earlier work and suggest the Proterozoic soils were characterized by iron loss (consistent with *p*O₂ ≤ 1%; Planavsky, Cole, et al., 2018; Planavsky, Slack, et al., 2018). These results are also consistent with approaches based on a lack of fractionation in the Cr isotope system (Crowe et al., 2013; Planavsky et al., 2014). Recent developments in the interpretation of rare oxygen isotope data are similarly narrowing our constraints on atmospheric *p*O₂ (Crockford et al., 2018; Planavsky, Cole, et al., 2018). In parallel, open-system biogeochemical models are helping to refine our understanding of the potential solution space of internally consistent Earth system states, allowing us to make predictions about nutrient inventories, ocean redox structure, and atmospheric composition. Though there is significant progress to be made in refining, applying, and coupling currently available modeling frameworks and inversions of geochemical data, many existing and emerging tools are primed to provide new insights into the significance of environmental forcing as better empirical records become available.

Yes: As discussed above, early animals likely needed very low levels of oxygen—which means that small amounts of error in reconstructions and linked modeling approaches make a large difference for whether or not oxygen levels would influence metazoan evolution. The difference between 1% and 0.1% PAL is critical for metazoans (across this range of oxygen levels in modern OMZs there is a shift from low-diversity animal assemblages to no animals), but this difference is within error of all reports of “low” mid-Proterozoic atmospheric oxygen (e.g., Planavsky, Cole, et al., 2018). Further, most marine elemental or isotopic redox proxies calculate the proportion of anoxic or euxinic seafloor with considerable uncertainty (for instance, a recent U isotope study by Zhang et al., 2019, estimated anoxic seafloor area prior to the Shuram carbon isotope excursion to be between 25% and 100%—an enormous range). Even if these proxies had less error they would not provide a full view of the water column redox landscape. Indeed, as we more rigorously interrogate

the variables involved in “proxy to oxygen” inversions, the errors associated with these estimates are only likely to increase. The use of stochastic analyses and added complexity to quantify error on trace metal and trace metal isotope mass balances or kinetic weathering models does provide a way forward in that without proper quantification of error it is impossible to answer this question in the first place. However, it may be that the result—using our current understanding of these geochemical proxies—is that we are not currently equipped to discern this level of paleoenvironmental detail from the rock record. Calibrating Earth system models with geochemical data is clearly an exciting research direction, but the realism with which 3-D models can take an input value (i.e., proportion of euxinic seafloor \pm error) and reproduce the distribution of suboxic/dysoxic water masses has yet to be demonstrated. And it is these water masses that are the ecologically critical question.

3.8 | Does animal monophyly suggest that the origin of animals was dictated strictly by internal factors?

Yes: Perhaps the biggest challenge to an environmentally driven origin of animals is animal monophyly (Butterfield, 2009, 2009, 2018; Erwin & Valentine, 2013; Lane, 2015; Maynard Smith & Szathmáry, 1997). Animal monophyly alone suggests that the origin of animals was primarily dictated by the acquisition of specific genomic, cytological, and/or developmental novelties, otherwise there are no obvious reasons why other eukaryotic lineages did not develop animal-grade architectures (Erwin, 1993). Invoking an environmental trigger hypothesis for the *origin* of animals (rather than the subsequent *diversification* of multiple animal clades) must reconcile animal monophyly, which is overwhelmingly supported by modern phylogenetic analyses (Dunn, Giribet, Edgecombe, & Hejnol, 2014).

While complex multicellularity has evolved at least six times (Knoll, 2011), animals represent the only living instance of complex multicellularity evolving from wall-less microbial eukaryotes capable of phagocytosis (Mills & Canfield, 2017; Mills, Francis, & Canfield, 2018). It is possible that some evolutionary events destroy the conditions needed for them to evolve in other lineages (reviewed in Bains & Schulze-Makuch, 2016). However, brown algae evolved complex multicellularity in a world already populated with multicellular red algae and embryophytes, including seagrasses (Mills, Francis, & Canfield, 2018), and fungi have evolved complex multicellularity numerous times (Nagy, Kovács, & Krizsán, 2018). Yet, other wall-less unicellular flagellates—cytologically and functionally comparable to the unicellular ancestors of animals (Mills & Canfield, 2017; Mills, Francis, & Canfield, 2018)—have not independently evolved phagocytic complex multicellularity since the origin of Metazoa; this re-emphasizes the singular nature of metazoan multicellularity.

No: A polyphyletic origin of animals (Cloud, 1978; Hanson, 1977; Nursall, 1962) can be salvaged if the metazoan LCA was unicellular (meaning complex multicellularity evolved multiple times within crown-group metazoans), or if multiple eukaryotic lineages evolved

animal-grade multicellularity, but have all gone extinct except for metazoans (Mills, Francis, & Canfield, 2018). Despite these alternative scenarios, a single, monophyletic origin of animals remains the simplest hypothesis, consistent with all available evidence (Mills, Francis, & Canfield, 2018).

Animal monophyly does not necessarily imply that the environment did not play a role in controlling when animals emerged. Rather, the critical issue is whether environmental and ecological changes generated the conditions needed for the successful acquisition (or phenotypic expression) of metazoan characteristics (Scenario D in figure 2 of Mills, Francis, & Canfield, 2018). In this scenario, a single eukaryotic lineage possessed the cytological and genomic features necessary for achieving animal multicellularity, yet was unable to express complex multicellularity until after some suite of environmental and ecological changes occurred (Mills, Francis, & Canfield, 2018). Testing this particular scenario against the phylogenetically indistinguishable null hypothesis will require a better understanding of the physiological and ecological requirements of the metazoan LCA and when these requirements were first met by the environment (Mills & Canfield, 2014).

3.9 | Could other environmental factors have been more important than oxygen in driving the origin and diversification of animals?

Yes: Studies of biotic response to modern global change offers an obvious answer: temperature (Deutsch, Ferrel, Seibel, Pörtner, & Huey, 2015; Pörtner, 2012). An upper thermal limit of 50°C for animals is fairly well established (Ravaux et al., 2013), above which protein stability is compromised. However, this level is only ~10°C lower than for unicellular eukaryotes (Rothschild & Mancinelli, 2001). Given the long fossil record of eukaryotes pre-dating animals, there is a possibility that before 800 Ma temperatures were limited to a narrow zone below the eukaryote thermal limit and above the animal thermal limit, and animals were restricted at the level of basic protein stability (Schwartzman, 2002), but this requires a very constrained and likely unfeasible climate system. More likely, temperature played an important role through its effects on oxygen demand. An animal's oxygen demand increases at both higher and lower temperatures than its temperature optima due to effects on oxygen supply and ventilation costs in the cold spectrum and effects on metabolic rate in the warm spectrum (Boag, Stockey, Elder, Hull, & Sperling, 2018; Pörtner, 2012). In other words, animals die at higher temperatures not because of any direct effect of temperature, but because their metabolic rates are so high they are literally suffocating. This also means an organism does not have a static oxygen tolerance, but its tolerance is temperature-related through effects on both supply and demand. The synergistic effects of O₂ and temperature are only starting to be explored with respect to early animal evolution (Boag et al., 2018; Reinhard et al., 2016), and temperature estimates for the Proterozoic are scarce or unreliable. These are obvious areas for future research.

Primary productivity—that is, food supply—is another factor we are beginning to realize cannot be decoupled from atmospheric oxygen levels. Multiple modeling studies have demonstrated that the main, if not only, knob to turn in maintaining low and stable oxygen levels in the Earth system is primary productivity (Laakso & Schrag, 2019; Ozaki et al., 2019, and references therein). This work suggests that low Proterozoic oxygen levels (<10% PAL)—if they existed—would most likely have been coupled with low marine primary productivity and ultimately low food supply and energy flow to ecosystems. A Neoproterozoic Oxygenation Event would then likely have been coupled to increasing food supply. Of note, a recent review of animal ecology across natural gradients in food supply on abyssal plains demonstrated that increased food supply is associated with increases in diversity, animal biomass, sediment mixed-layer depth, and specialist predator types (Sperling & Stockey, 2018). These are many of the same ecological changes that are seen across modern oxygen gradients in oxygen minimum zones (OMZs; Rhoads & Morse, 1971; Sperling, Frieder, et al., 2013; Sperling, Halverson, et al., 2013), which are often invoked as *prima facie* evidence that oxygen changes could have driven the Cambrian radiation (Reinhard et al., accepted).

To the extent that any of these ecological responses are related to energy supply, the similarity in responses makes sense: Aerobic respiration requires sufficient oxygen and organic carbon, and OMZs are food-rich but oxygen-poor while abyssal plains are oxygen-rich but food-poor. Given this similarity in ecological responses across natural gradients in food and oxygen, and the links between these parameters in the Earth system, it is clear that changing food supply could potentially have held equal rank with oxygen in driving the early radiation of animals and the Cambrian radiation (Brocks, 2018; Sperling & Stockey, 2018).

No: No one argues that other environmental factors (temperature, pH, food supply, etc.) are not important. But the question is whether any other environmental parameter was *more* important during the Neoproterozoic and Cambrian. Returning again to the modern ocean, mega-analyses of the whole ocean do indeed demonstrate that energy matters: Kinetic energy (temperature) in the shallow ocean and chemical energy (food) in the deep ocean are best correlated with diversity (Tittensor et al., 2010; Woolley et al., 2016). Oxygen has a statistically significant but relatively minor correlation with diversity. Such studies, however, use oceanographic data available on a relatively coarse 0.5–1° latitude/longitude grid. In modern OMZs, where oxygen concentrations actually approach levels generally considered for the late Proterozoic, oxygen can drop from ~25% of surface ocean levels to <0.5% over very short distances (several minutes latitude/longitude, e.g., Palma et al., 2005). When *in situ* oxygen measurements and biological data from OMZs are used rather than the coarse-gridded data, a different pattern emerges. Oxygen is found to be the best predictor of diversity, with low oxygen associated with low diversity, and critically, the response to oxygen change is strongly non-linear (Sperling, Frieder, & Levin, 2016). For macrofauna, the biodiversity response is strongest at O₂ levels less than ~8% of surface ocean levels, which is a threshold also seen for

carnivore species richness (Sperling et al., 2015). In essence, based on ecological patterns in the modern ocean, a change in oxygen in the range predicted for the Neoproterozoic could have resulted in a dramatic response in early animal communities. No such linkage has yet to be demonstrated for pH, temperature, or any other environmental variable.

3.10 | Could the rise in oxygen have been driven by animals, rather than vice versa?

Yes: Metazoans can fundamentally transform the redox balance of modern marine settings. Filter feeders (e.g., sponges and oysters) clarify waters, and the loss of these species results in a shift to more turbid waters with higher water column organic carbon contents (POC and DOC contents). Chesapeake Bay, Long Island Sound and Florida Bay all provide examples where filter feeders lead to a marked drop in suspended carbon concentrations (Butterfield, 2009, 2009, 2018). High suspended carbon concentrations will result in more rapid oxygen drawdown in surface waters (dramatically shallowing the e-folding depth of remineralization). Similarly, high rates of primary productivity and shallow e-folding depth of remineralization will result in the shoaling of an OMZ, potentially leading to extensive shallow-water anoxia. These effects in surface waters can result in deep-water anoxia, as bottom waters are supplied directly from strong downwelling of surface waters. Therefore, by changing the nature of the biological pump, animals can dramatically alter the marine redox landscape at a given atmospheric oxygen level. Animals could also directly drive shifts in atmospheric oxygen concentrations by promoting organic carbon burial. Fecal pellets can be orders of magnitude larger than protistan cells and could therefore potentially increase particle settling rates, the shuttling of organic matter to the sediment pile, and ultimately organic carbon burial, thus driving a rise in surface oxygen levels.

No: As stressed above, mechanistic models (Ozaki et al., 2019) and mass-balance exercises (Derry, 2014; Laakso & Schrag, 2014, 2017) reconstructing stable low-oxygen states require dramatically less marine primary productivity than in modern oceans. Empirical evidence for low mid-Proterozoic primary productivity (Crockford et al., 2018) supports these results. Size-structured marine ecosystem models embedded within a GCM suggest animals (and even large protists) would have played only a minor role in ecosystems at these reconstructed primary productivity levels (Reinhard et al., accepted). In this light, metazoans simply would not have had the scope to alter biogeochemical cycles in a low-oxygen Earth system. This is consistent with the lack of evidence for eukaryotes in the biomarker record until ca. 800 Ma (Brocks, 2018; Isson et al., 2018; Nguyen et al., 2019). As noted above, constraints on productivity may have also been a key factor inhibiting the rise of metazoans. Additionally, the idea that animals would drive increased organic carbon burial—and thus oxygenation—is not empirically grounded. The dogma that animals, by producing fecal pellets, would promote enhanced organic carbon

burial (Logan et al., 1995) ignores observations that modern meta-zoans commonly drive particle disaggregation (Dilling & Alldredge, 2000; Steinberg, Silver, & Pilska, 1997; Stemmann, Jackson, & Ianson, 2004) and that even cyanobacterial cells aggregate (Deng, Monks, & Neuer, 2015). Therefore, although modeling the evolution of the efficiency of the biological pump is an obvious area of future research, it is unlikely that animals either have the mechanistic capacity to mediate oxygenation or that their activities on a low-oxygen planet would have been of a sufficiently large scale to drive substantial oxygenation.

3.11 | Assuming a causal link between large body size and rising oxygen, do we see evidence of such a correlation?

No: After billions of years where the fossil record was dominated by microscopic life, the first large, complex multicellular organisms appear following the Gaskiers glaciation at ca. 571 Ma (Pu et al., 2016; the “Avalon” Ediacara biota), and large three-dimensional animals and bilaterian trace fossils appear ca. 555 Ma (Martin et al., 2000; the “White Sea” Ediacara biota). Is this increase in body size correlated with geochemical evidence for increased oxygen levels? The answer is perhaps very different from the one most researchers would have given a decade ago. While a link between oxygen and animal evolution was posited long before, three papers in the mid-2000s seemingly provided geochemical “smoking guns” for oxygenation near the Ediacaran–Cambrian boundary. First, Fike et al. (2006) analyzed carbon and sulfur isotope systematics in the Ediacaran Nafun Group of Oman, and interpreted the “Shuram” carbon isotope excursion as representing the oxidation of a large reservoir of organic carbon suspended in the deep ocean during the mid- to late Ediacaran. Next, Canfield, Poulton, and Narbonne (2007) investigated iron speciation geochemistry of the Ediacaran succession on the Avalon Peninsula, Newfoundland, and in the mid-Ediacaran found evidence for deep-water oxygenation following the Gaskiers glaciation and just prior to the appearance of the Avalon biota. Finally, Scott et al. (2008) studied molybdenum contents in euxinic black shales—which can track the global seafloor redox landscape—and found evidence for a decrease in euxinic conditions in the late Ediacaran. Following these papers, a majority of geochemists have accepted the narrative linking oxygen and the appearance of large animals (although see Butterfield, 2009, 2009, for a different, contemporaneous, perspective).

The geochemical data in these three papers are considered robust, but additional sampling and new intellectual frameworks for interpreting isotopic data have made the picture murkier. Regarding carbon and sulfur isotope data from carbonates, it is now recognized that (a) local oceanographic and diagenetic controls play a major role on the resulting signals and (b) isotopic data cannot be simply read in a mass-balance framework relating burial of oxidized and reduced species (Ahm et al., 2019; Fike, Bradley, & Rose, 2015; Miyazaki et al., 2018). The Avalon Peninsula succession may have become more

oxygenated in the mid-Ediacaran, but new iron speciation data from other successions, as well as recent reports of banded iron formations in the Cambrian (Li, Cheng, et al., 2018; Li, Zhang, et al., 2018), demonstrate this was likely a regional phenomenon and that widespread deep-water anoxia persisted into the Paleozoic (Sperling et al., 2015). Consistent with this picture, new uranium isotope data from carbonates demonstrate extensive (if sporadic) anoxia in the late Ediacaran and early Cambrian (Tostevin et al., 2019; Wei et al., 2018; Zhang et al., 2018)—the ocean clearly did not become fully oxygenated after the Gaskiers glaciation. Redox-sensitive trace metal abundances in anoxic shales still provide one of our strongest sources of evidence for a “state change” in ocean redox associated with the appearance of larger animals, but as with the iron record, additional data have pointed toward a noisier record of both oxygenation and deoxygenation than originally posited (Sahoo et al., 2016). Overall, the clear story that emerged a decade ago has become cloudier.

Yes: Even if new data provide a cloudier picture and the field is re-learning how to interpret isotopic records, it is apparent that *something* changed with respect to oxygen and redox in the mid- to late Ediacaran and early Cambrian. These intervals are marked by some of the largest carbon isotope excursions in the geologic record (Fike et al., 2006; Maloof et al., 2010). The carbon cycle is still intimately linked to the oxygen cycle through organic carbon burial, and even accounting for local effects or questions about the directionality of change, there is little chance oxygen levels were static. Similar logic can be applied to redox proxies based on trace metal abundances or isotopes: Although there may not have been a single “state change” cleanly separating the pre-Ediacaran from the Phanerozoic, it is abundantly clear that global marine redox did change (see question in Section 3.5; Figure 2). If so, it is possible that larger size or more complex animal ecologies evolved during brief oxygenated intervals (Sahoo et al., 2016) and/or that poorly oxygenated intervals allowed the surviving small, thin animals with streamlined gene regulatory networks to rapidly generate evolutionary novelties (Wood & Erwin, 2018). In recent redox work designed to test this idea, Wei et al. (2018) found periods of intense marine anoxia in the early Cambrian immediately before jumps in fossil appearances. During multiple global redox transitions animal size and complexity could potentially have ratcheted up. Such evolutionary scenarios linking redox and animal evolution are far more complex than the traditional narrative, but are still very much on the table.

4 | CONCLUSIONS AND FUTURE DIRECTIONS

Oxygen did not cause animals to evolve (Knoll & Carroll, 1999). The critical question is whether there was environmental exclusion of animal-grade multicellularity through most of Earth's history (e.g., until the end Proterozoic) and if animals appeared and diversified roughly in step with shifts in surface oxygen levels. Although an animal lifestyle could have evolved multiple times through the Precambrian, there is little compelling evidence that this happened, and therefore,

it is reasonable to assume that animal-like complex multicellularity is an evolutionary singularity. Based on modern observations, animals appear to require oxygen—so Earth's oxygenation (i.e., the evolution of biological oxygen production), in the most basic sense, “paved the way” for the rise of animals. Or put differently, on Earth, animals could not have evolved until after the evolution of cyanobacteria and aerobic respiration. But nor could animals have evolved until the genomic and developmental capacity existed, which does not appear to have been until about 1 billion years ago. Nonetheless, there could have been a substantial gap between when there were environments in which animals *could* have existed—estimates for the evolution of oxygenic photosynthesis are commonly >3.0 Ga—and when they actually appeared. Assuming the environment was permissible for metazoan evolutionary novelties, the late appearance of animals can be explained in terms of evolutionary contingency and tinkering, rather than any kind of environmental control. However, in other reconstructions, environmental factors (oxygen, temperature, and sulfide levels) would have prevented the presence of stable metazoan populations, and complex multicellular organisms may have evolved only shortly after the onset of conditions in which they could have thrived.

Deciphering whether oxygen played a proximal role in eukaryotic diversification (including animal origins and diversification) provides one of the best means to grapple with the question of why biotic complexity (of which metazoans and multitrophic-level ecosystems are a key part) developed when it did. Because we only know of one planet on which life emerged, reconstructing the factors that shaped the history of life on Earth provides one of the only ways to explore how common complexity is likely to be in the universe. If animal-grade complex multicellularity necessarily requires billions of years to evolve—and it was the appearance of these biological innovations that essentially ended the Proterozoic Earth system—it begs the question of what exactly controls the evolutionary appearance of novel body plans (Peterson & Mueller, 2013). Alternatively, if animals were environmentally excluded for most of the Proterozoic, it begs the question of how the Earth system broke out of this relatively inhospitable state to ultimately permit the evolutionary origin and subsequent diversification of animals and other complex multicellular life. As long as we fail to understand what ultimately controlled the evolution of animal-like multicellularity in Earth history, whether it was internally or externally dictated, we are in no position to estimate the likelihood of similarly complex life arising elsewhere in the universe (Bains & Schulze-Makuch, 2016; Ward & Brownlee, 2000). One can make a case that understanding the links between oxygen and the early evolution of animals is central to some of the most fundamental unresolved questions in the natural sciences.

There are some obvious future research goals that can push the “life versus environment” debate forward (Figure 3). There is general agreement that we need better estimates of the oxygen requirements of a wide range of animals throughout their life histories. There is a particular need for estimates of oxygen utilization during the reproduction and life cycle completion of non-bilaterian animals, such as sponges and ctenophores. To better understand metazoan physiology, energy metabolism, and multicellularity, a broader

perspective of eukaryotic evolution also needs to be embraced by geobiologists. Seminal researchers like Lynn Margulis and Preston Cloud commonly considered eukaryotic evolution in the context of Earth history and environmental evolution—and modern evolutionary biologists like Bill Martin still do. Despite the emphasis on animals by the geobiological community, animals represent only a single and relatively recent branch of the eukaryotic tree. However, modern geobiologists are beginning to re-embrace a more holistic view and the importance of the evolutionary history and biospheric role of microbial eukaryotes. Whatever factors make animal evolution unique can only be appreciated by such a comparative approach.

There is no consensus in the community about ancient surface oxygen levels, which means that we need to work toward resolving disagreements. Although the answer commonly offered for this problem is new proxies, the greatest impact will likely come from better understanding of currently utilized proxies and putting geochemical records into a more robust statistical framework. Quantitative frameworks for proxies are continuously being updated and conclusions must similarly be updated. Equally, we will need to revisit and reevaluate the fidelity of the rock record over the next decade. Instead of trying to fit all of the conclusions from previous work into a “coherent narrative,” we must as a community encourage and support work revisiting previously proposed conclusions—not all data are equal and published data must not be regarded as unassailable. Much of the recent surge in Proterozoic redox work has been pursued without petrography or thorough screening for diagenetic alteration. Therefore, much of this work will need to be revisited and in the future samples need to be archived in museums in order to foster more rigorous reproducibility standards. Work on the Precambrian biomarker record provides a cautionary tale highlighting the need to constantly revisit sedimentary records—over the past decade there was a realization that most of the biomarker record was heavily influenced by contamination (Brocks, 2018; French et al., 2015). Similarly, we will likely find that diagenetic alteration has strongly influenced many redox records.

Greater integration between different fields is an equally important goal. For some fields this would represent a shift in approach or guiding questions. Geochemists have focused on whether the environment could exclude metazoans. An equally fruitful question to ask might be: What is the problem to which animals are the solution? In other words, we could ask if it is possible, combining our understanding of environmental and ecosystem evolution and modern biogeochemical processes, to explore why the unicellular ancestors of animals evolved multicellularity or bilaterality (e.g., escaping predation, more efficient feeding and reproduction). This is a problem typically tackled by evolutionary and theoretical biologists, with geochemists and geologists often left out of the conversation. Therefore—as with most interdisciplinary fields and questions—the obvious path forward is for more interdisciplinary work. Given that truly interdisciplinary work is easier to propose than accomplish, we will likely not end our debate on the factors shaping the coevolution of surface oxygen levels and animals anytime soon. Nonetheless, the paths forward are becoming clearer and there is consensus that

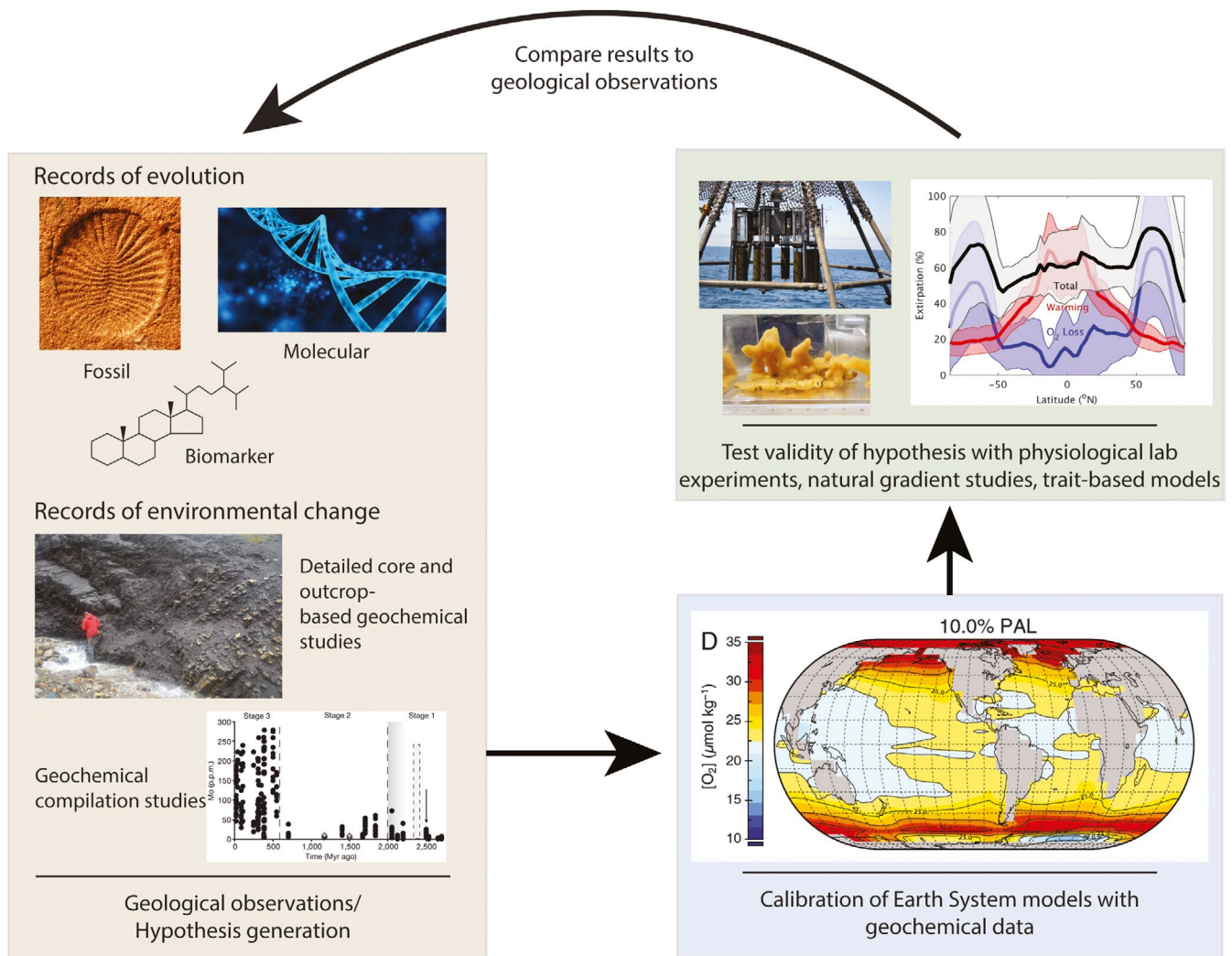


FIGURE 3 Much previous work on the relationship between early animal evolution and oxygen levels focused on correlation between records of evolution and records of environmental change (left panel). The idealized geobiological workflow depicted here provides the opportunity to test these relationships on a deeper level. First, hypotheses relating environmental change and biotic response are generated from geological/biological observations. Second, available geochemical data are used to calibrate Earth system models consistent with those data. As discussed in the text, this is critical because the outputs of many current geochemical redox proxies (i.e., the proportion of euxinic seafloor) are in some ways not directly useful to questions of early animal evolution—because no animals can tolerate complete anoxia, it is the degree and spatial distribution of dysoxia in the shallow ocean that matters. The model of the ancient Earth system is then evaluated against insights from laboratory physiological experiments, natural environmental gradient studies, trait-based ecophysiological models, or species origination–extinction models to test the validity of the hypothesis. Ultimately, we compare these results back to the rock and fossil records and generate new hypotheses. Mo compilation from Scott et al. (2008); Earth system model from Reinhard et al. (2016); *Halichondria panacea* sponge photo from Mills et al. (2014); ecophysiological model from Penn et al. (2018)

untangling the role that environment played in shaping the history of the life on our planet is a fundamental question.

5 | METHODS

5.1 | Change-point analyses

Once assembled from the literature, we utilized a change-point search algorithm (Killick, Fearnhead, & Eckley, 2012) in MATLAB called findchangepts (MathWorks, 2018a) to identify a single

change point (i.e., the point in the data where the mean on either side of that point are the most different) and the residual error in each dataset. Because this algorithm treats data sequentially, and most geochemical data from one formation are assigned a single age, data were initially grouped by age and a mean for that age was calculated and utilized in the analysis. The ages were rounded to 1 million years in order to minimize outsized influence from Cenozoic data with high-resolution age constraints. Once identified, the change point was used to define two bins for each dataset. The raw (ungrouped and averaged) data were then used to make box-and-whisker plots where the three quartiles are

represented within the box and the whiskers each extend to 1.5 interquartile ranges of the upper and lower quartiles, respectively. Any data falling outside those ranges are considered outliers and plotted as points.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

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