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Evolution of the structure and impact of Earth's early biosphere

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We provide a new perspective on how the structure of Earth's biosphere and its capacity to alter geochemical cycles have changed over its >3.5 billion-year history. We review evidence that oxygenic photosynthesis evolved relatively early in Earth's history, but contend that marine primary productivity was low, surface oxygen was scarce, and marine anoxia was prevalent for the majority of Earth's history. Anoxygenic phototrophs were likely a key part of the marine biosphere in these low-oxygen oceans, and nutrient uptake by these organisms

was one factor limiting the extent of marine oxygenic photosynthesis. This marine biosphere—which is fundamentally different from that of today's oceans—likely persisted up until, and potentially even during, the early diversification of eukaryotic algae and animals. We also highlight potential issues with the commonly held idea that early animals and algae fundamentally altered marine nutrient cycling and transformed the marine biological pump. We further argue—in contrast to the standard view—that following the widespread emergence of continental landmasses terrestrial primary productivity was a significant mode of biological carbon fixation, even before the rise of land plants.

Introduction

There is clear evidence that life evolved early in Earth's history and has persisted for well over 3.5 billion years[1–3], but we are still trying to piece together a basic history of biology on our planet. There has been a recent surge of work on the impact of Earth's biosphere on planetary processes driven, in part, by increased interest in developing a predictive framework for what dictates how planetary bodies evolve with or without life. As far as we know, Earth is the only planet where all surface environments have been transformed by life. Earth's atmosphere, climate, water cycle, and upper lithospheric compositions are all decidedly different from those expected on an abiotic planet[4]. More comprehensive knowledge of how the size and structure of Earth's biosphere have shaped our planet can inform predictions for the likelihood that planets beyond our solar system are habitable and could—like Earth—be detectably transformed by life. In the coming decades, it is likely that developing observational techniques[5] will permit us to remotely explore the atmospheric composition of Earth-like planets. A solid knowledge of how our biosphere has reshaped Earth's surface and atmosphere and what features constitute robust biosignatures will be essential for interpreting these data[5]. Atmospheres integrate almost all planetary-scale processes, both biotic and abiotic, and are possible to observe from afar. Much recent focus has, therefore, been on the mechanisms that drive development of atmospheric biosignatures.

The most heated debates about Earth's atmospheric evolution, historically, have focused on when and why Earth's atmosphere became well oxygenated[6,7]. It is now generally accepted that Earth has undergone a protracted, several-billon-year oxygenation[6], but there is no sign of emerging consensus about what role biotic innovations and the evolution of solid Earth processes played in key steps in this oxygenation. It is clear that atmospheric oxygen levels were low in the Archean, generally higher in the Proterozoic, and higher still across much of the Phanerozoic (Figure 1). There is also general agreement that this progressive rise in oxygen levels was essential for the rise of many lineages of eukaryotic life, including animals[6,8]. However, there is still debate about nearly all aspects of the history of this oxygenation, including the timing, pace, and impact on the biosphere. For example, there is now agreement that oxygen first rose to appreciable levels between 2.4 and 2.3 Ga[9], but the trigger for this event, either a shift tectonic processes[10] or the onset of biological oxygen production by cyanobacteria[11], or removal of previous brakes on cyanobacterial proliferation[12], remains contested. There is agreement that carbon dioxide levels have gradually decreased through time, maintaining a clement climate, with noteworthy but short-lived climate extremes. However, there remains no coherent view of the role that the biosphere played in driving climate shifts[13,14].

Debate stems, in part, from poor constraints on the timing of many key biotic novelties (the formation of newly individuated characters and features) and innovations (when these novelties began to alter and shape the structure or function of ecological networks)[15]. Even the timing of the evolution of 'highly influential novelties'—new metabolisms or basic cell types[15]—remains a strongly debated aspect of the history of life on Earth. Similarly, there is growing appreciation that rates of biological carbon fixation have increased through Earth's history, but constraints on rates of biospheric productivity through Earth's history are limited and accompanied by large error estimates[16]. Nonetheless, the timeline and history of life on Earth is coming into better focus. Recent efforts have revisited when particular groups of organisms appeared on Earth and have sought to constrain when and how they first began to shape Earth's surface environments and global biogeochemical cycles—a level of emergence we refer to here as "biotic scope".

Here, we present a new view of the evolution of the structure and scope of life on our planet. We discuss the planetary-scale evolution of Earth's biosphere in terms of the impact of key biotic innovations on global biogeochemical cycles. We argue for the relatively early evolution of oxygenic photosynthesis and a persistent dominance of a marine biosphere characterized by anoxygenic phototrophs and chemotrophs. We also challenge the standard view that the rise of eukaryotes to ecological prominence fundamentally altered marine nutrient cycling. We argue that although the emergence of plants had a major impact on the global carbon cycle, terrestrial primary productivity was appreciable or even dominant, well before the emergence of land plants. Collectively, this represents an alternative view of the co-evolution of Earth and life that is grounded in current empirical records and mechanistic models. However, we highlight that there are many aspects about this view that remain poorly constrained.

Early oxygen

The evolution of oxygenic photosynthesis, potentially as far back as 3.8 billion years ago (Ga)[1,17], enabled a dramatic increase in the size and complexity of Earth's biosphere (Figure 2)[18]. This evolutionary singularity was the first step in Earth's progressive oxygenation and subsequently allowed organisms to colonize essentially all Earth surface environments. Photosynthesis is the only process that releases appreciable oxygen to Earth's surface and leads to the accumulation of free O_2, which is required by animals and other complex life forms for respiration and the biosynthesis of key macromolecules[4]. The buildup of oxygen also allowed for the formation of an ozone layer, drastically reducing the harmful effects of UV radiation. There has been continuous debate as to whether the evolution of oxygenic photosynthesis immediately triggered a switch to a more oxygenated atmosphere at the end of the Archean, or whether there was a protracted and delayed increase in atmospheric oxygen levels[19–21]. Current estimates for the timing of the onset of oxygenic photosynthesis span over a billion years of Earth's history, ranging from prior to 3.8 Ga[22] (the age of the oldest sedimentary rocks) to 2.4–2.3 Ga[11]. The latter date is coincident with the first permanent rise of atmospheric oxygen, the "Great Oxidation Event" or GOE and thus represents the absolute youngest age for the onset of oxygenic photosynthesis[9].

While controversial, a wealth of inorganic geochemical information now suggests appreciable traces of oxygen in Earth's surface environments hundreds of millions, or perhaps more than a billion years, before the GOE[21,23–27]. Some of the earliest such evidence comes from Mo isotopes[23] and Mo and other metal elemental distributions in sedimentary rocks[24,25] deposited in the Neoarchean, more than 100 Myr prior to the currently accepted date of ~2.4 Ga for the GOE[9]. Evidence for an even earlier rise of oxygenic photosynthesis comes from the distributions and isotope values of Cr, U, and Mo in 3.0 Ga paleosols and IFs from the Pongola Supergroup[21,26,27]. This interpretation is further supported by broadly contemporaneous sulfur isotope systematics that point toward extensive oxidative sulfur cycling[28]. While a comprehensive review of all evidence for pre-GOE oxygen is beyond the scope of this review, it is worth noting that there are a number of other examples between the Mesoarchean and the GOE, and a few, albeit more controversial, examples before 3.0 Ga[29,30]. Previous geochemical evidence of free oxygen has been controversial, however, and tracking early oxygen production by inorganic means has been hindered by concerns similar to those that plagued biomarker work, which was previously the most widely touted evidence of early oxygen[31,32]. There are concerns about whether geochemical records uniquely fingerprint biological oxygen production and if geochemical records are truly recording paleoenvironmental signals. For instance, signals of early oxygen could instead be tied to secondary oxidation during surface weathering under today's oxygen-rich atmosphere[33]. In short, despite great effort, it has proven difficult to ensure that geochemical signatures diagnostically reveal the presence of oxygenic phototrophs[34,35] in past environments.

The most recent debate about when oxygenic photosynthesis evolved has focused on whether or not manganese (Mn) oxides in the pre-GOE rock record can be uniquely ascribed to Mn(II) oxidation with free oxygen produced through oxygenic photosynthesis[21,36]. There was, without question, significant Mn(II) oxidation in the Archean[37], but it is less clear whether oxidation required molecular oxygen. Recent work[19] suggested there could have been extensive anaerobic Mn(III,IV) oxide production, challenging earlier views that oxidative geochemical signals reflect the antiquity of oxygenic photosynthesis. Thermodynamic and basic mass balance considerations, however, question the relevance of these new findings to Archean oceans, and the recent discovery of anoxic microbial Mn(II) oxidation is potentially no more significant than the longstanding observation of photochemical Mn(II) oxidation[38]. Photochemical Mn(II) oxidation has been generally regarded as an essentially inconsequential process in the Archean oceans, as Fe cycling ultimately dictates the fate of Mn oxides in early marine settings[38]. Further, it is not clear if recent work on anoxygenic photosynthesis dependent Mn oxidation[19]—based on enrichment cultures from a sulfidic lake—is relevant to the Archean oceans. Given the lack of any known high-potential photosynthetic reaction center in the photosynthetic microorganisms in the enrichment culture (e.g., green sulfur bacterium *Chlorobium* sp.), oxidation of manganese using elemental sulfur is the only thermodynamically feasible Mn oxidation pathway. However, under reasonable Archean conditions (e.g., pH = 7[132], [Mn] = 100μM[133], HS^- and S^0 = 10μM[47]) the free energy of this reaction is likely not high enough to support microbial metabolism (ΔG = -18 kJ/mol for birnessite formation and 71 kJ/mol for pyrolusite formation[39–42]). These energy yields are both below the commonly reported minimum requirement of about -15 to -20 kJ/mol for anaerobic microbial metabolisms[135]. In the very likely case that $[HS^-] > [S^0]$, energy yields from these reactions are even lower.

Pinpointing when oxygenic photosynthesis evolved is one of the most important questions about the history of Earth's biosphere. Although there is currently no consensus within the community as to when this novelty arose, there is a clear path towards resolution—researchers pushing for the early (pre-GOE) rise of oxygenic photosynthesis need to continue to carefully consider anoxic oxidation pathways and the effects of secondary alteration on oxidation proxies[33]. At the same time, researchers skeptical of the early rise of oxygenic photosynthesis need to make efforts to ensure that their own observations are placed into a framework that is consistent with the geologic record. In the context of the most recent debate[19], we argue that simple consideration of thermodynamics and mass fluxes can be extremely powerful. With that in mind, we argue that recent challenges to an early rise for biological oxygen production still fall well short of providing the cogent argument necessary for overturning the current paradigm of an early (>3.0 Ga) rise of oxygenic photosynthesis.

Anoxygenic photosynthesis

The rise of oxygenic photosynthesis was, without question, a major event in Earth's history, but anoxygenic (i.e., non-oxygen producing) phototrophic microbes likely played a key role in fueling the biosphere and driving planetary evolution throughout most of Earth's ~3 billion-year early history[20,43–45]. Phylogenetic analyses almost unanimously show that anoxygenic photosynthesis evolved prior to oxygenic photosynthesis (e.g., [46,47]; however see also[48]), and thus likely had exclusive and unfettered access to the photosynthetic niche for hundreds of millions of years prior to the emergence of oxygenic photosynthesis[20,43–45]. Models suggest that the emergence of anoxygenic photosynthesis would have energized the biosphere, leading to global productivity far greater than an exclusively chemosynthetic biosphere[44,49]. Nonetheless early in Earth's history this anoxygenic photosynthetic biosphere would have been primarily responsible for interacting with geophysical processes to regulate atmospheric composition and climate (Figure 2a)[20,45,50] and anoxygenic photosynthetic likely played a key role in regulating global biogeochemical cycles untiil the ocean became fully oxygenated[20,49].

Anoxygenic photosynthesis in the marine realm is driven by a suite of inorganic and organic electron donors that, together with bio-essential nutrient elements like nitrogen and phosphorus, limit rates of photosynthesis[45]. Extant anoxygenic phototrophs are able to grow photosynthetically with Fe(II), H_2, and H_2S, as well as some organic compounds such as acetate and pyruvate[44,45] as electron donors. Considering the availability of these electron donors in seawater throughout Earth's history, Fe(II) and H_2 would likely have been the most widely utilized throughout most of the Archean and Paleoproterozoic. Sulfide (H_2S) could have been episodically abundant, particularly during punctuated intervals in the mid to late Proterozoic[44,51,52]. The availability of organic electron donors has received less attention. While they may have been relatively abundant in Earth's earliest history, the emergence and proliferation of heterotrophic bacteria and methanogens would likely have consumed organic compounds making them less available as primary electron donors for anoxygenic photosynthesis, although this idea should be further explored.

Both Fe(II) and H_2 are supplied through submarine volcanism and associated hydrothermal activity at rates that would support appreciable anoxygenic photosynthesis, particularly when marine sulfate concentrations were low[44,49,53]. For instance, hydrothermal Fe(II) fluxes could have been greater than 40 Tmol/yr prior to the GOE[54]. This flux is more than sufficient to account for the estimated Fe burial fluxes associated with the largest banded iron formations (BIFs) deposited in the Neoarchean to Paleoproterozoic[55]. To place this number into a biological context, we can assume that Fe(II) was oxidized by photoferrotrophs (photoautotrophs utilizing iron as their primary electron donor) in the following reaction:

$$4Fe^{2+} + CO_2 + 11H_2O \rightarrow CH_2O + 4Fe(OH)_3 + 8H^+$$

Given that this metabolism theoretically yields a molar ratio of 4Fe:1C, and assuming maximum efficiency in Fe(II) oxidation, then 40 Tmol/yr Fe(II) would generate 10 Tmol/yr of organic carbon via photoferrotrophy. This amount of net primary productivity (NPP) is lower than the NPP of a hypothetical marine biosphere dominated by H_2-based phototrophy, estimated at 20-90 TmolC/yr[56]. However, iron is rapidly recycled through respiration of organic matter derived from anoxygenic photosynthesis. Therefore, the 10 Tmol/yr of organic carbon produced via photoferrotrophy reflects a very conservative estimate of the extent of Fe(II)-based productivity. This tendency for recycling, however, also highlights that physical separation of oxides and organic matter are needed for preservation of either of these products of photoferrotrophy in the sedimentary record[54].

Sulfide can also be used in anoxygenic photosynthesis and is derived from similar pathways as Fe(II). Sulfide can come from hydrothermal systems, albeit at lower rates than Fe(II)[57]. Given these lower fluxes, sulfide likely played a more limited role as a primary electron donor for anoxygenic photosynthesis across most of Earth's history[44,49]. Concordantly, H_2S based phototrophy is estimated to have generated 4.7-6.7 Gmol C/yr[56], several orders of magnitude less than either H_2- or Fe(II)-based phototrophy. However, H_2S is also a product of dissimilatory sulfate reduction and so could have risen to prominence with the onset of strong oxidative weathering on the continents and the associated increase in sulfate fluxes to the oceans following the GOE[58–60].

Under widespread marine anoxia during the Proterozoic, sulfate reduction would have supported appreciable secondary H_2S production. At times of low marine Fe(II) concentrations, episodic and localized photic zone euxinia (anoxic and sulfidic conditions) could have supported extensive secondary H_2S dependent anoxygenic photosynthesis[61]. Nonetheless, given evidence for widespread ferruginous conditions throughout most of the Precambrian[62], the supply rate and availability of Fe(II) would have placed the primary constraints on rates of anoxygenic photosynthesis (Figure 2a).

Like all life, anoxygenic photosynthetic organisms require a number of bio-essential elements, including the macronutrients nitrogen, phosphorus, and sulfur as well as various micronutrients. The availability of these elements in the water column places a secondary constraint on rates of anoxygenic photosynthesis and the size and activity of the marine biosphere. Organismal nutrient quotas differ, but in the modern ocean roughly follow a defined stoichiometry that is well-represented by the Redfield ratio for macronutrients (106:16:1 C:N:P)[63]. Conservation of electrons by photosynthesis also means that there is a stoichiometric relationship between carbon fixed into biomass and the electron donor (e.g. Fe(II) or H_2) used and oxidized. There is also, by extension, a stoichiometric relationship between electron donor supply and nutrient uptake that dictates whether nutrients or electron donors limit anoxygenic photosynthesis. For example, when Fe(II) is used as the electron donor, the molar ratio of Fe(II) oxidized to carbon fixed (4:1) translates to a ratio of 424:1 Fe(II) oxidized per P needed. This means that supply rates of P less than 1/424th that of Fe(II) would lead to a biosphere limited by P, assuming negligible P recycling[64]. Similar arguments could be made for N, although N can be biologically fixed from an enormous reservoir of N_2 in the atmosphere (and corresponding aqueous N_2 in the water column). Nitrogen limitation (where N was the ultimate limiting nutrient, *cf.,*[65]) would have been less likely following the emergence of nitrogen fixation, which molecular phylogeny suggests took place in the early Archean[66]. Isotopic evidence has also be used to suggest a minimum age of 3.2 Ga[67]. Many extant anoxygenic phototrophs have the metabolic potential for N_2 fixation, including those that grow with Fe(II) and H_2 as electron donors[68]. Recent analyses further predict that stem-group photoferrotrophs likely had the capacity to fix N_2[69], though it results in slower growth rates than when exogenous N is abundant.

The evolution of oxygenic photosynthesis (see above), would have partly liberated total primary productivity from limitations imposed by electron donor availability, shifting limitation towards nutrient (P) availability[49,70]. The electron donor for oxygenic photosynthesis is water, which is almost infinitely available in all aquatic environments. The emergence of oxygenic photosynthesis would thus have allowed the biosphere to utilize any P that was still remaining in solution after anoxygenic photosynthesis had consumed electron donors (primarily Fe(II) and H2). Hence the biosphere as a whole would have likely shifted into a state of perpetual P limitation (Figure 2b). At the same time, the emergence of oxygenic photosynthesis would have initiated strong competition with anoxygenic photosynthesis for illuminated niche space[49,71]. Based on inference from the physiology of extant anoxygenic phototrophs, which are exceptionally good at growing under low-light conditions, relative to oxygenic phototrophs, anoxygenic phototrophs would have generally outcompeted their oxygenic counterparts as long as electron donor supplies were sufficient[49]. Anoxygenic phototrophs can reside deeper in the water column and have first access to nutrients upwelled from the deeper ocean. Oxygenic phototrophs, restricted to shallower environments above the anoxygenic phototrophs, would have been dependent on excess nutrients that escaped consumption by anoxygenic phototrophs due to electron donor limitation, or those supplied from above through atmospheric deposition and local riverine input. The stoichiometry of electron donor to nutrient supply would, therefore, have played a key role in regulating the balance between the activity of anoxygenic and oxygenic photosynthesis. In addition, the presence of potential 'toxins' to cyanobacteria need to be considered in this balance. If anoxygenic phototrophs did not quantitatively remove dissolved Fe(II), it could have inhibited cyanobacteria productivity, in part because of oxidative stress as a result of reactions between Fe(II) and oxygen that produce reactive oxygen species[12]. Accordingly, the proliferation of oxygenic photosynthesizers could have been delayed until either electron donor/toxin supplies collapsed, nutrient supply rates were enhanced, the redoxcline descended below the photic zone, or some combination of the above. The emergence of oxygenic photosynthesis would have further energized the biosphere through concurrent modes of photosynthesis, and would have created a photosynthetic biosphere essentially entirely limited by nutrient supply[70]. However, the presence of anoxygenic photosynthesis in a low-oxygen world with largely anoxic oceans provides a means to limit the scope of oxygenic photosynthesizers, and thus a way to stabilize the Earth system in a low oxygen state[49].

Over the past few years, there has been an increasing number of suggestions that total marine primary productivity by oxygenic photosynthesizers has increased over Earth's history[16,70,72–74]. Developing more robust constraints on primary production will require more work to answer two key questions: (1) how nutrient and substrate inventories and fluxes changed through Earth's history; and (2) how the ratio of primary productivity by anoxygenic and oxygenic phototrophs has evolved. These questions can best be answered through models that are quantitatively tethered to molecular biological histories and material fluxes recorded in the rock record. Nonetheless, it seems unavoidable given the emerging view Precambrian surface environments (i.e. widespread and even shallow marine anoxia[75]), that anoxygenic phototrophs were an important part of the biosphere—which would have limited the scope of oxygenic photosynthesizers.

Life on land

Much of the past and current research on Earth's early biosphere is directed at understanding the evolution of marine phototrophs—particularly cyanobacteria—and how they shaped the oxygen and carbon cycles. The community has, with key exceptions (e.g., [76–83]), largely ignored the importance of terrestrial ecosystems (by 'terrestrial' we mean all continent-based environments, subaerial or subaqueous, including uplands, arid lands, floodplains, lakes, and rivers). While much of the debate over cyanobacterial origins rests on evidence from the marine sedimentary record, there have also been multiple recent suggestions that cyanobacteria (or their oxygenic photosynthetic ancestors) evolved early and were common in terrestrial settings[77,78].

There are multiple lines of evidence for life on land prior to the mid-Paleozoic despite a strong preservation bias against microbial remains in continental environments[84]. Microbially induced sedimentary structures (MISS) in continental deposits are some of the earliest records of life on Earth, with evidence for robust mats in shallow, sandy, periodically exposed rivers by at least 3.2 Ga[77,85]. Moreover, element mobility patterns in ancient soils (paleosols) suggest weathering by organic acids—and consequently the presence of life on land—by at least 2.76 Ga[86,87]. The dearth of sedimentological evidence for microbial mats on land in the Precambrian is likely a consequence of their inability to stabilize sediment in the energetic depositional environments typical of continental settings.

Independent of the sedimentary record, molecular data have been suggested to provide evidence for a terrestrial origin of cyanobacteria (however, see also [88]). Phylogenomic analyses of modern cyanobacterial diversity may suggest a freshwater origin for the clade and indicate that filamentous cell types, a structural novelty enabling mat formation, originated soon after[89]. By contrast, these same analyses recover marine planktonic cyanobacteria as derived clades with multiple independent origins from an ancestral terrestrial or freshwater aquatic ecotype. Although still rare compared to clear evidence for microbial life in marine settings, these records—among many others—provide the tantalizing suggestion that, as a community, we may have underappreciated the role of terrestrial ecosystems in shaping Earth's biogeochemical cycles.

Modern mats are consortia of metabolically diverse prokaryotes in addition to cyanobacteria[90] and it is therefore possible that the communities responsible for microbial signatures in early terrestrial settings differed significantly from their modern counterparts. While sedimentological and geochemical indictors for life on land may well have been produced by chemotrophs or anoxygenic phototrophs[91], it is unclear whether these organisms could have formed globally extensive terrestrial mats. Anoxygenic phototrophs make up important albeit structurally minor components of some modern terrestrial cyanobacterial mats[83] and can form their own mats under rare instances of photic zone anoxia in subaqueous environments[92]. Terrestrial iron oxidizers, in particular, form land-based mats[93]. Further, in the Archean, in the absence of an ozone layer photosynthetic organisms would have experienced strong UV stress[94,95]. Nonetheless, considering redox balance, mat ecosystems in which cyanobacteria were the key primary producers represent the strongest potential contributors to life in continental settings throughout the Precambrian.

Although the earliest direct evidence for terrestrial mats comes from river margins[77], modern mats span a vast range of subaqueous and subaerial environments (Figure 3). Today, biological soil crusts (BSC) cover appreciable portions of arid and semi-arid lands where severe water limitation inhibits the growth of vascular plants[96], this includes some of the driest areas on the modern Earth such as the Atacama Desert in Chile[97] and the McMurdo Dry Valleys of Antarctica[98]. These mats survive by producing abundant extracellular polysaccharides (EPS) that bind loose materials together to form a cohesive crust, which both maintains hydration levels and protects against ultraviolet radiation[99]. In the absence of competitive exclusion from plants, the majority of Earth's habitable land surface could have been covered by microbial mats similar to modern BSC in terms of overall metabolic structure, if not composition. The success of BSC in extreme environments today gives reason to suspect that mats would have covered appreciable portions of the land surface prior to the emergence of vascular plants, and would have been able to survive even in the absence of ozone shielding prior to the GOE[99,100]. Critically, there is high phylogenetic diversity in these mats—indicating that potential to colonize BSC environments is broadly distributed and thus likely not a late stage biotic innovation[83,90]. Marine environments in the Precambrian have been commonly assumed to be nutrient-poor (e.g., [72]); in contrast, regolith on land would have provided an abundant source of bio-essential elements (foremost P) for terrestrial ecosystems assuming organisms had the capacity to access them in dissolved form via biologically-mediated mineral dissolution[86] and even store them intracellularly[101]. The biogeochemical implications for widespread mats on land in the Precambrian are substantial, in part because the oxygenic capacity of modern benthic cyanobacteria is tremendous; nowhere on the modern Earth is free O_2 found in greater excess than in photosynthetic mats dominated by cyanobacteria[83,102]. Consequently, terrestrial mats in the Precambrian may have comprised a much larger fraction of global gross and net primary productivity than traditionally envisioned.

Quantifying global NPP from terrestrial microbial mats on the early Earth (and the flux of O_2 from mat surfaces) is highly dependent on estimates of their aerial coverage and O_2 production rates per unit area. Environmental niche modeling puts modern BSC coverage at 12% of today's land surface, and up to 24% in the absence of anthropogenic disturbance[96]. By some estimates, these mats account for 7% of terrestrial NPP (325 Tmol C/yr) and potentially half of terrestrial nitrogen fixation (3.5 Tmol N/yr)[103,104]. Much of this area is arid land where competition with plants and grazing pressure from animals is minimal, but where low soil moisture also limits surface biomass and productivity (microbial mat O_2 production is typically < 0.2 nmol cm^{-2} s^{-1} in deserts versus an average of 0.4 nmol cm^{-2} s^{-1} in fully water saturated environments)[96,102,105,106]. In the absence of these ecological constraints in the Precambrian, mats would presumably also have filled all available ecospace in more humid regions, making their contribution to global primary productivity much greater.

The simplest approach to estimating the terrestrial biosphere's contribution to atmospheric O_2 fluxes during the Proterozoic is to multiply a flux range in modern mats by the total continental area they may have covered[83,102]. Today barren land, including unvegetated deserts and permanently ice-covered regions, comprises roughly 25% of the total land surface[107]. This leaves

75% as a potential upper limit for mat coverage. However, given that ice-free conditions appear to have persisted for the majority of Earth's history[4], the upper limit for habitable land area would likely have been higher. A lower limit of mat coverage can be placed by assuming that mats would have been restricted only to the equatorial rain belt, although the success of modern BSC in arid environments makes this unlikely. Based on current estimates of tropical rainforest cover, about 10% of total land area lies within this high-rainfall, high-productivity region[107]. A stochastic estimate using a distribution of O_2 production rates from modern mats and assuming a very conservative land surface coverage of 10-50% and a near-modern total exposed land area[108,109] gives an average terrestrial O_2 and equivalent organic carbon production rate (i.e., NPP) of approximately 18,000 Tmol/yr (Figure 4), which is surprisingly several times modern terrestrial NPP[110,111]. By comparison, the most recent estimates for marine NPP during the Proterozoic are 350-2,100 TmolC/yr[74]. There are multiple ways to reduce this estimate—for example considering seasonality in parts of the globe, or considering that mats may have been entirely lithotrophic or dominated by anoxygenic phototrophs, and therefore would have produced significantly less oxygen relative to their modern counterparts (although this does not preclude significant carbon fixation by anoxygenic phototrophs).

Given that field observations support a link between soil moisture and oxygen production in modern BSC[105,106], a potentially more rigorous estimation of O_2 production rates for terrestrial microbial mats can be derived from calculations of global surface soil moisture distributions.

Combining photosynthetic rates measured in modified natural settings[105] with outputs of ground temperature and water content in the top 10 cm of soil from historical climate models yields an average O_2 production rate of 0.0172 nmol cm^{-2} s^{-1} and global production of 681 Tmol/yr (Figure 5), which is likely an underestimate considering that this predictive model consistently underestimates point source fluxes from microbial mats that have been measured in the field[83,112,113]. Using monthly mean ground temperatures and water contents from June and December results in a seasonal range from 0.0154-0.0197 nmol cm^{-2} s^{-1} and 615-766 Tmol/yr, that monthly variability in ground temperature and soil moisture would strongly influence global O_2 production from a terrestrial biosphere dominated by microbial mats.

Secular changes in global surface temperature and precipitation across Earth history likely drove even greater variation in O_2 production. However, a lack of reliable precipitation proxies in deep time currently hampers any attempt to quantify this variability[114], forcing us to rely on less direct inferences. From one perspective, water vapor would not have penetrated as deeply into continental interiors in the absence of vascular plants that can store and release water via transpiration[115], meaning that global soil moisture availability would have been lower than modern. However, this very low-precipitation system in a pre-plant world is unlikely to have led to a stable global carbon cycle; without high soil CO_2 levels linked to plant biomass degradation, atmospheric CO_2 levels in a low-precipitation world would have increased (i.e., the CO_2 sinks would not have balanced the sources), leading to warming climate state and thus more precipitation (see Isson et al., 2020[13]). In a world without any terrestrial biomass, it has been estimated that rainfall on average must have been at least 3-4 meters per year to deliver enough dissolved CO_2 to sustain the rates of silicate weathering necessary to stabilize Earth's climate[13]. Because we conservatively assume modern precipitation levels, the actual O_2 production rates and NPP of Earth's earliest terrestrial biosphere were likely higher than the estimates we provide in Fig. 3. Our estamites of terrestiral NPP have large uncertainties. Nonetheless, using modern terrestrial mat-forming cyanobacteria as a guide, it seems unavoidable that these terrestrial ecosystems were a major component of the Precambrian biosphere. This leads us to conclude that terrestrial ecosystems may have accounted for the majority of primary productivity for much of Earth's history, and potentially by a substantial margin prior to the rise of vascular plants.

While a departure from the standard view, a higher-than-modern NPP may not be unreasonable considering that rapid turnover in microbial ecosystems allows high productivity relative to biomass[116]. Prokaryotic cells live on the order of days, while vascular plants regularly live tens of years and sometimes even thousands[117]. As a result, up to 70% of biomass in vascular plants does not contribute to primary productivity on an annual basis; this results in plants producing only half of global NPP despite making up over 80% of the planet's biomass[117]. An exclusively microbial terrestrial biosphere would almost certainly have been much smaller than modern in terms of standing biomass, but not necessarily in terms of gross or net primary productivity. We must also note that high NPP in terrestrial microbial mats does not imply an equal importance in regulating atmospheric pO_2. On geologic timescales, the persistence of free O_2 in the atmosphere can only be sustained by the long-term burial of organic carbon (C_{org}) in marine sediments. Given the high reactivity of labile organic matter produced by microbial mats and long oxygen exposure times during transport in surface and groundwaters, most C_{org} will reoxidize before reaching the oceans, consuming much of the O_2 produced during photosynthesis. The concept of enhanced oxidation potential in terrestrial, relative to marine, environments is well established[118]. In this regard, terrestrial primary productivity is likely to have a strong effect on the short term oxygen and carbon cycles, but a relatively minor effect on Earth's long-term oxygenation. However, these short-term fluxes can strongly impact geochemical processes that become preserved in the rock record, including the mobility of redox-sensitive trace metals used to reconstruct changes in atmospheric pO_2 through time[102] and the generation of triple-oxygen isotope anomalies used to estimate the long-term productivity of the biosphere[119]. Further, these mats may have been important sources of methane, helping provide an explanation for the presence of a stably warm Proterozoic climate without extremely elevated CO_2 levels[120].

While these O_2 production estimates apply to the Proterozoic, estimating terrestrial NPP for the Archean proves more difficult. Crustal growth models suggest lower continental exposure prior to the hypothesized onset of modern-style plate tectonics before 2.5 Ga[109], and very limited exposure prior to 3.0 Ga[108], constraining terrestrial O_2 fluxes considerably[83]. Additional constraints would have been placed on localized O_2 production by the lack of a protective ozone layer since unattenuated UV radiation would have severely limited the productivity of subaerially exposed mats[94,95]. Experimental work on modern mats shows that even moderately elevated UV irradiance can cut O_2 production by half[121], although cyanobacteria have numerous ways of reducing exposure including vertical migration, secretion of UV-absorbing extracellular polysaccharides,[99] growing under mineral grains,[122] or even precipitating their own mineral 'sunscreen'[123]. The relationship between UV exposure, biological attenuation, and oxygen production in mats prior to the GOE remains largely unknown and is a significant source of uncertainty in estimating the size of both the terrestrial and marine biospheres during this time[124], but given evidence for continental exposure going back to at least 3.2 – 3.0 Ga[108,125] together with fossil, molecular, and geochemical records and inferences from modern mat physiology[77,83,86,89], it seems possible that the locus of primary productivity for the majority of Earth's history has been on land, not the oceans.

The rise of algae and animals

For over 90% of Earth's history, ecosystems were dominated by single-celled organisms. The oldest potentially eukaryotic microfossils occur in the latest Paleoproterozoic Changzhougou Formation (ca. 1.8 Ga) and Chuanlinggou Formation (ca. 1.7 Ga) of North China[126,127]. However, the emerging view is that they were not an important part of the marine biosphere until roughly 800 million years ago, or later[128]. Between 1000 and 500 Ma multicellular organism rose to prominence via the radiation of modern animal phyla and more complex ecosystems (Figure

2c)[129,130]. There has been persistent debate about the drivers of this transition. The two end member views are that this event was tied to the removal of an environmental barrier or that it simply represents the timing of biotic novelties[131,132]. Trying to make sense of this transition has prompted one of the most fundamental questions we can ask about the evolution of life—is biotic complexity inevitable and self-promoting, or does the rise of complexity depend on planetary evolution toward favorable environmental conditions?

It has commonly been suggested that environmental factors including oxygen concentrations and the availability of nutrients in the marine realm (e.g., P) governed the rise of complex life. Specifically, ocean oxygenation may have played a central role in controlling the earliest appearance of eukaryotic clades, as well as their later radiation and rise to ecological prominence[133–135]. The 'oxygen control hypothesis' suggests that increased oxygen concentrations would have dictated the timing of the emergence of animals and their divergence in the latest Proterozoic (800 to 500 million years ago). Alternatively, it may have been biotic innovations independent of an environmental control (e.g., the appearance of algal clades) that drove the observed environmental changes (e.g., glaciations[136] and oxygenation[137]). In other words, the Neoproterozoic rise of eukaryotes to ecological dominance has been either attributed to an environmental trigger or implicated as the driver of the observed environmental changes.

The most obvious effect that animals and algae can have on the Earth system is transforming the biological pump and enhancing organic carbon export from the surface oceans[138]. For instance, in the Neoproterozoic, the shift from a cyanobacteria- to a eukaryote-dominated biological pump may have played a key role in driving ocean and atmospheric oxygenation, isotopic excursions, and climatic perturbations. In particular, it has been suggested that an algal-dominated carbon pump would promote faster organic carbon sinking rates due to an increase in average cell size and density[139]. In this framework, faster sinking rates and thus a less efficient biological pump would have spread oxygen demand over a greater depth of the water column, thus attenuating peak oxygen demand and shifting the oxygen minimum zone to deeper waters. It also would have increased the oxygen demand in shelf sediments.

Although the basics of this idea are simple—larger objects sink faster—a simple analysis for the effect of sinking rate on the carbon pump and oxygen dynamics in the oceans draws this idea into question (Box 2 and 3). Previous qualitative and quantitative models have simplified the role of marine aggregates—yet all sinking organic matter in marine systems will occur as aggregates rather than single cells, where even in the absence of fecal-producing organisms and bigger-cell sized algae there is appreciable aggregate formation comprised of only minerals and phytoplankton [140]. When the dynamics of marine aggregates are considered[141], the overall effect of switching primary producers and bringing metazoans into marine systems is fairly minor (Box 2). When particle disaggregation by animals—foremost by the smallest size classes of zooplankton—is considered[141,142], it is even more unlikely that there was a fundamental step change in the efficiency of organic carbon export when animals became an important component of marine ecosystems. Similar to eukaryotic algae, increased sinking rates of oceanic particles caused by, for example, the evolution of silica frustule biosynthesis in diatoms and fecal pellet production by grazing organisms, may not be strong enough to alter the efficiency of the carbon pump or to have a major impact on oxygen dynamics in the oceans (Box 2 and 3).

Environmental factors, on the other hand, could have exerted strong leverage on the Earth's biosphere. For instance, climate cooling events could have strongly impacted oxygen dynamics in the ocean-atmosphere system. Specifically, given temperature dependent metabolic rates, a cooler climate would have promoted high burial efficiency and high oxygen demand in the ocean by suppressing the rate of organic matter degradation in the surface ocean and increasing flux of organic matter into depths[143]. This, in turn, could have promoted anoxia at depth, while increasing the rate of oxygen efflux from the ocean. While other factors such as enhancement in oxygen solubility or change in ocean circulation patterns during cooling can influence oceanic oxygen dynamics, global cooling could translate into rather large fluxes of oxygen from the ocean to the atmosphere during the Neoproterozoic glaciations, providing one path to a strongly oxygenated atmosphere. Therefore, a simple quantitative exploration of marine carbon cycling (Box 2-3) questions the idea that the rise of animals or the rise of algae were first-order controls on the nature of Earth's marine biological carbon pump. On the contrary, environmental factors (e.g., temperature changes) appear to provide a more straightforward means to induce dramatic changes organic carbon remineralization efficiency over time.

The rise of plants

Plants account for roughly 60% of net primary productivity today[111], and it has long been assumed that their emergence and diversification fundamentally changed the scope of the biosphere[144]. However, increasing awareness of the ubiquity of cyanobacteria in terrestrial settings (see above) indicates that plants were not simply moving onto a barren landscape. Moreover, as discussed above, the ratio of terrestrial to marine net primary productivity is unlikely to have fundamentally changed with the rise of land plants. However, this does not mean that plants did not change the extent to which the biosphere can alter global biogeochemical cycles. Perhaps the most obvious change would have been the development of organic-rich soils with elevated CO_2 concentrations from the respiration of plant biomass[13]. Cyanobacteria appear to create millimeter- to centimeter-thick surficial mats and crusts while many forests and grasslands today create centimeter- to meter-thick topsoil[145]. High CO_2 concentrations in soils help to decouple atmospheric CO_2 levels from the rate of CO_2 consumption via silicate weathering[13]. As such, lower CO_2 levels are possible in a balanced carbon cycle with plants than without plants[13,144]. A low pH zone in soils also likely leads to enhanced P solubilization, given that P is not quantitively dissolved in most weathering environments and that apatite dissolution rates inversely scale with pH[146]. In this light, regardless of changes in composition of Earth's weatherable shell, plants would have transformed the amount of P made available to the biosphere . Higher rates of P solubilization should lead to higher globally integrated rates of primary productivity, all other factors held constant. However, the largest impact of land plants on the oxygen cycle may not be tied to P mobilization; it is simply that plants create P-poor recalcitrant organics (e.g., lignin) that contribute appreciably to global organic carbon burial[147,148].

An important recent idea is that the development of organic-rich soil layers have directly contributed to the rise of atmospheric oxygen[149]. On a million-year time scale the oxygen cycle is in steady state, which means that organic carbon burial must be balanced by oxidation of volcanic reductants, Fe(II) in rocks, and rock carbon. A lack of balanced fluxes would result in continual rise or fall of atmospheric oxygen. Development of soil organic matter (e.g., the formation of an O- horizon in the soil) would come with a greater soil oxygen demand, such that diffusive fluxes of oxygen from the atmosphere would need to be larger to achieve the same oxidative weathering rates as in the absence of an organic-rich soil layer[149]. To balance this with a comparable oxygen source from carbon burial in the ocean, oxygen would accumulate in the atmosphere to a level that supported this diffusive flux. Therefore, even if plants do not result in a substantial increase in net primary productivity, they are likely to have increased the ability of the biosphere to transform the atmosphere.

The globally integrated biosphere: Carbon isotopes

No tool has played as large of a role in advancing our understanding of the evolution of the scope of the biosphere as carbon isotopes[150–154]. The evolution of $\delta^{13}C_{carb}$ values is linked to the ratio of carbonate to organic carbon burial in the global ocean[154]. Following principles of mass balance, $\delta^{13}C_{carb}$ can be used to calculate the fraction of carbon buried as organic matter (f_{org})[154]. Because f_{org} is linked to primary productivity, it could theoretically track primary productivity through time.

Looking at the marine carbonate record, the global $\delta^{13}C_{carb}$ curve lacks any secular trend on a billion-year timescale and is characterized instead by perturbations around a baseline value of about 0‰[155,156]. Within the traditional interpretive framework, f_{org} would have been at 20-25% for the majority of Earth's history (Figure 1). Notable exceptions include the Paleoproterozoic Lomagundi-Jatuli Excursion, the largest and longest-sustained positive carbon isotope excursion ($\delta^{13}C_{carb}$ > 10‰ for up to 200 million years), which at face value suggests f_{org} greater than 50%[157,158], and the negative Shuram Excursion in the Neoproterozoic ($\delta^{13}C_{carb}$ < 10‰ for several million years), which would require negative f_{org} to satisfy mass balance[159,160] (Figure 1). However, each of these estimates assumes both a fixed isotopic composition for weathering inputs to the oceans ($\delta^{13}C_{w}$) and a fixed isotopic offset between buried carbonate and organic carbon (Δ_{B}), making f_{org} the sole driver of variation in $\delta^{13}C_{carb}$.

Although it has been long debated, there has been recently increasing appreciation that $\delta^{13}C_w$ has changed significantly throughout Earth's history[125–127]. Foremost, several recent modeling based studies have proposed that $\delta^{13}C_w$ was controlled by pO_2 for much of Earth's early history, as low atmospheric oxygen would have limited the oxidative weathering of sedimentary organic carbon[160,161]. Specifically, a reduced flux of isotopically light organic carbon to the oceans would have increased $\delta^{13}C_w$, requiring reduced f_{org} to maintain baseline $\delta^{13}C_{carb}$. Determinations of $\delta^{13}C_w$ based on previously developed organic carbon oxidation rate laws and current best estimates of pO_2 show that this was indeed the case for most of Earth's history. In order to reproduce the $\delta^{13}C_{carb}$ record, with common pO_2 estimates, f_{org} must have been roughly 10% or less during low-pO_2 intervals such as the Archean and mid-Proterozoic[160,161]. This is much lower than the widely accepted 20-25% and implies a much smaller global biosphere than previously recognized. Further, if $\delta^{13}C_w$ is allowed to vary with pO_2, a long-term increase in f_{org} keeping pace with atmospheric oxygenation could conceivably be "hidden" within a stable $\delta^{13}C_{carb}$ record[161]. Looking at this in another way, taking any estimate for Proterozoic pO_2 between 0.1 to 10% PAL (Figure 1), the amount of organic carbon burial—and by inference the extent of primary productivity—must have much been less than in the modern[162]. According to this view and accepting that there has been a protracted rsie in atmosphereic oxygen levels, instead of providing evidence for a constancy in organic carbon fluxes through Earth's history the carbon isotope record instead provides strong evidence that organic carbon burial and thus the scope of Earth's biosphere has increased through time.

Conclusions and future directions

We propose, based on in large part on recent work, that four major tenets of the traditional view of the long term evolution of the structure and scope of the biosphere (e.g., [163]) need to be revisited: that (1) primary productivity and organic carbon burial were roughly constant through most of Earth's history; (2) the marine realm was the focus of primary productivity prior to the rise of land plants; (3) primary productivity in the marine relam was dominated by oxygenic photosynthesizers for most of Earth's history; and (4) the rise of eukaryotes fundamentally reshaped the biological pump and global carbon cycling. We are proposing that marine primary productivity from oxygenic photosynthesizers increased dramatically though time[74,164,165], in part, because key nutrients (P) were taken up by anoxygenic photosynthesizers for most of Earth's history when predominantly reducing conditions prevailed[6,20,52,62,74]. However, the extent of primary productivity in terrestrial settings in the Precambrian—and the capacity of terrestrial ecosystems to affect global biogeochemical cycling—have likely been underestimated. Cyanobacteria thrive in a wide range of terrestrial environments today, and similar ecosystems would have been a major part of the biosphere before the rise of land plants. In fact, we propose that terrestrial ecosystems have been the locus of primary productivity for the majority of Earth's history. We further suggest that that the presence of larger cell sizes in primary producers (the rise of algae) or fecal pellet production (the rise of animals) may not have lead to a dramatically different marine carbon cycle. Studies of the modern biological pump have made it abundantly clear that the biological pump is complicated and that the recycling of particulate organic matter in Earth's oceans is dominated by the behavior of marine aggregates[140]. In this light, models focusing on individual cells or without robust and mechanistic representations of marine aggregate dynamics are unlikely to provide an accurate picture of the marine carbon cycle.

This perspective highlights more unknowns and outstanding questions about the long-term history of Earth's biosphere than it does present indisputable conclusions. Therefore, there is a clear need for more work on basic aspects of how Earth's biosphere has evolved and how the capacity of the biosphere to transform Earth's surface has changed through time. There is exciting, active debate about most aspects of how life has transformed our planet—the obvious path forward is working as a community towards resolution. However, we feel the most exciting advances are going to come from closer coupling of models and empirical records, more information from modern analogues for early Earth ecosystems, and consideration of the full history of the co-evolution of the biosphere and solid Earth processes—rather than focusing on specific intervals or perturbations.

Figures:

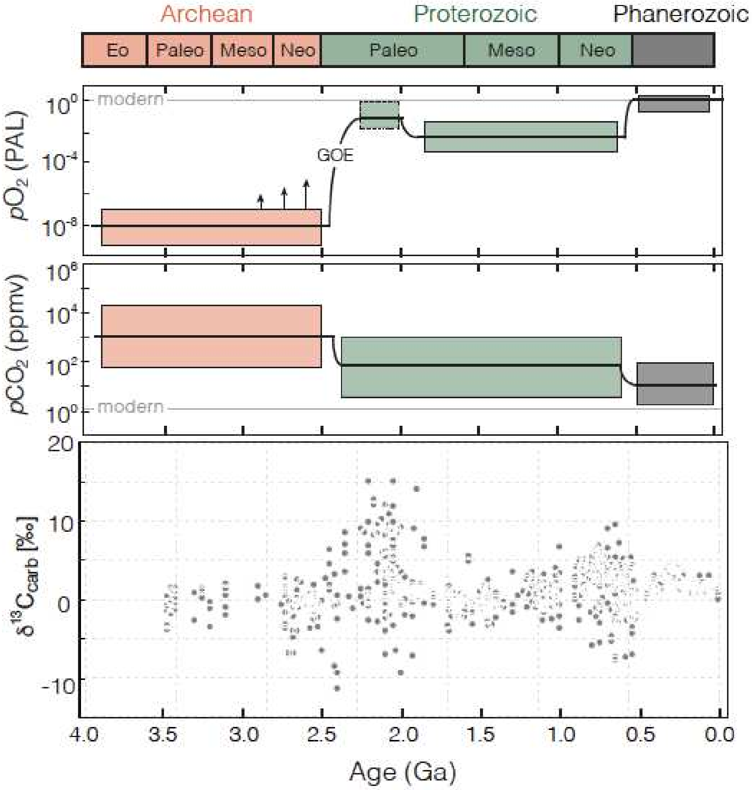
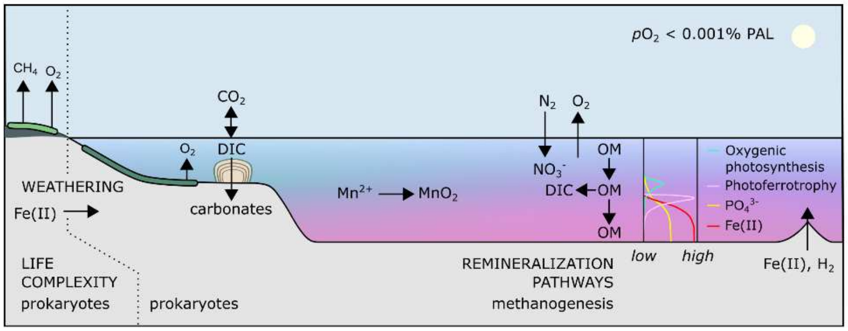
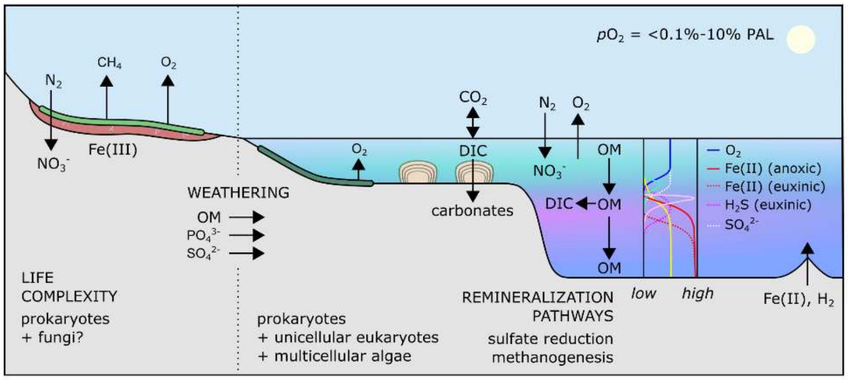


Figure 1. Change in atmospheric oxygen (a), CO_2 (b), and isotopic composition of marine carbonates (c) through time. The pO2 estimates are from Reinhard and Planavsky (2020)[166], *p*CO2 estimates are from Isson et al. (2020)[13], and the carbonate C isotope compilation is from Krissansen-Totton et al., (2015)[155].

a. Archean



b. Proterozoic to early Phanerozoic



c. middle to late Phanerozoic

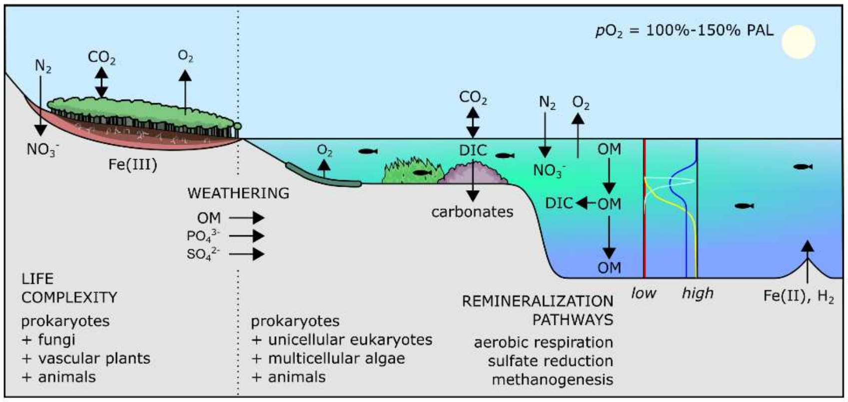


Figure 2. Schematic representation of the evolution the structure of the biosphere and its impact on global biogeochemical cycling.

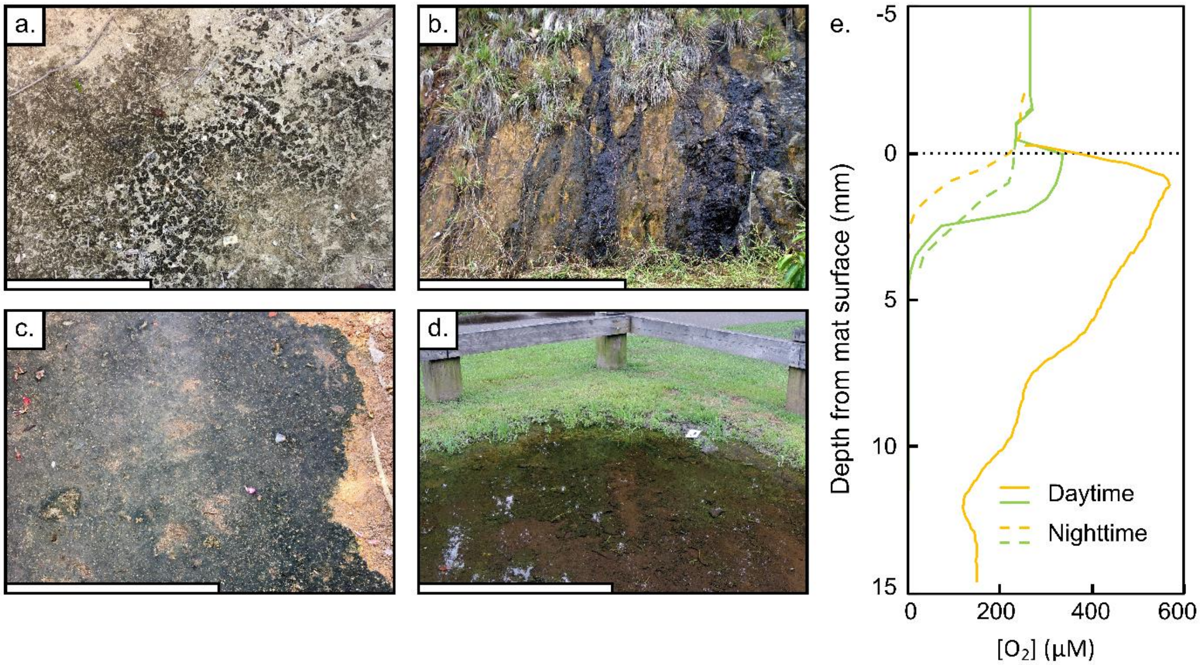


Figure 3. (a-d) Examples of modern terrestrial cyanobacterial mats: (a) Little Darby Island, The Bahamas, scale bar 30 cm; (b) Balambano Hydroelectric Dam, Indonesia, scale bar 2 m; (c) Lamma Island, Hong Kong, scale bar 50 cm; and (d) New Haven, Connecticut, United States, scale bar 1 m. These illustrate the range of environments and the diversity of basic structure found in mat ecosystems. (e) O_2 concentration profiles measured from the New Haven (green) and Balambano (yellow) mats. The New Haven mat was measured in situ with a fiberoptic O_2 sensor at 12:00 and 3:00 local time to determine gross photosynthesis and dark respiration, respectively. The Balambano mat was measured by Finke et al. (2019)[83] in a greenhouse with a Clark type microelectrode at 15:12 and 3:40 local time.

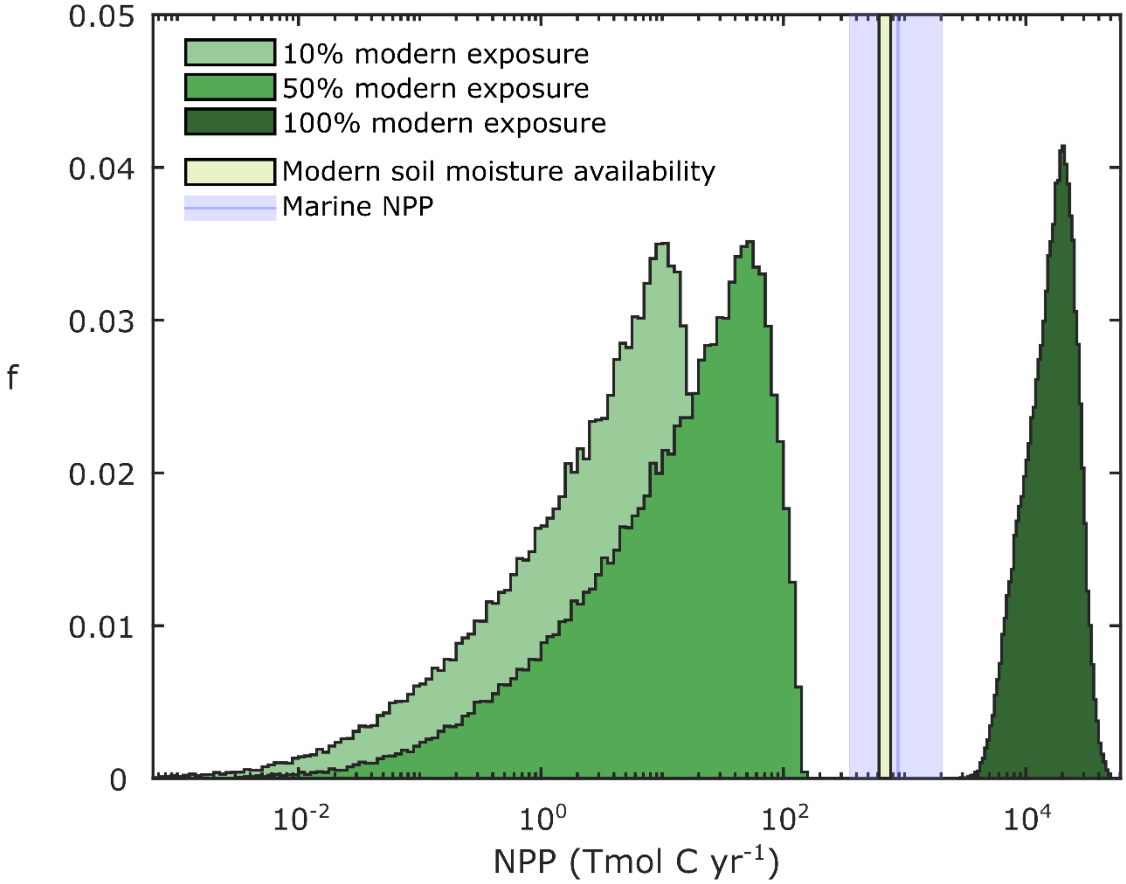


Figure 4. A stochastic estimation of global annual NPP from terrestrial microbial mats under different continental exposure scenarios. The probability distribution was calculated using O_2 production rates measured in modern terrestrial microbial mats[79] and a uniform mat coverage distribution from 10 to 50% total land area. Production rates were divided into a uniform distribution from 0.041-0.117 nmol cm^{-2} s^{-1} for mats in arid lands and a log-normal distribution with a mean of 0.244 nmol cm^{-2} s^{-1} and standard deviation of 0.233 nmol cm^{-2} s^{-1} for mats in non-arid lands. The fractional contribution of each land type to total coverage is estimated under the presumption that arid lands are uninhabited in our minimum-coverage scenario and almost completely inhabited in our maximum-coverage scenario (99%, which is the percent of modern arid land covered by any type of vegetation and is taken as the maximum potentially habitable area for mats in the absence of vascular plants; likewise, the percent of non-arid, non-glaciated land covered by vegetation today is 99.9%[82]). Arid lands are assumed to occupy 35% of the total land surface at any time[80]. Proterozoic continental exposure was likely similar to modern (1.49x10^{14} km^2) based on recent crustal growth models, while Archean exposure was likely much lower[83,84]. For comparison, recent estimates of marine NPP during the mid-Proterozoic from Ozaki et al. (2019)[66] are shown by the dashed

line (mean) and blue shaded region (95% confidence interval). The annual range of NPP estimates from our soil moisture analysis (Figure 5) is shown in the light green shaded region.

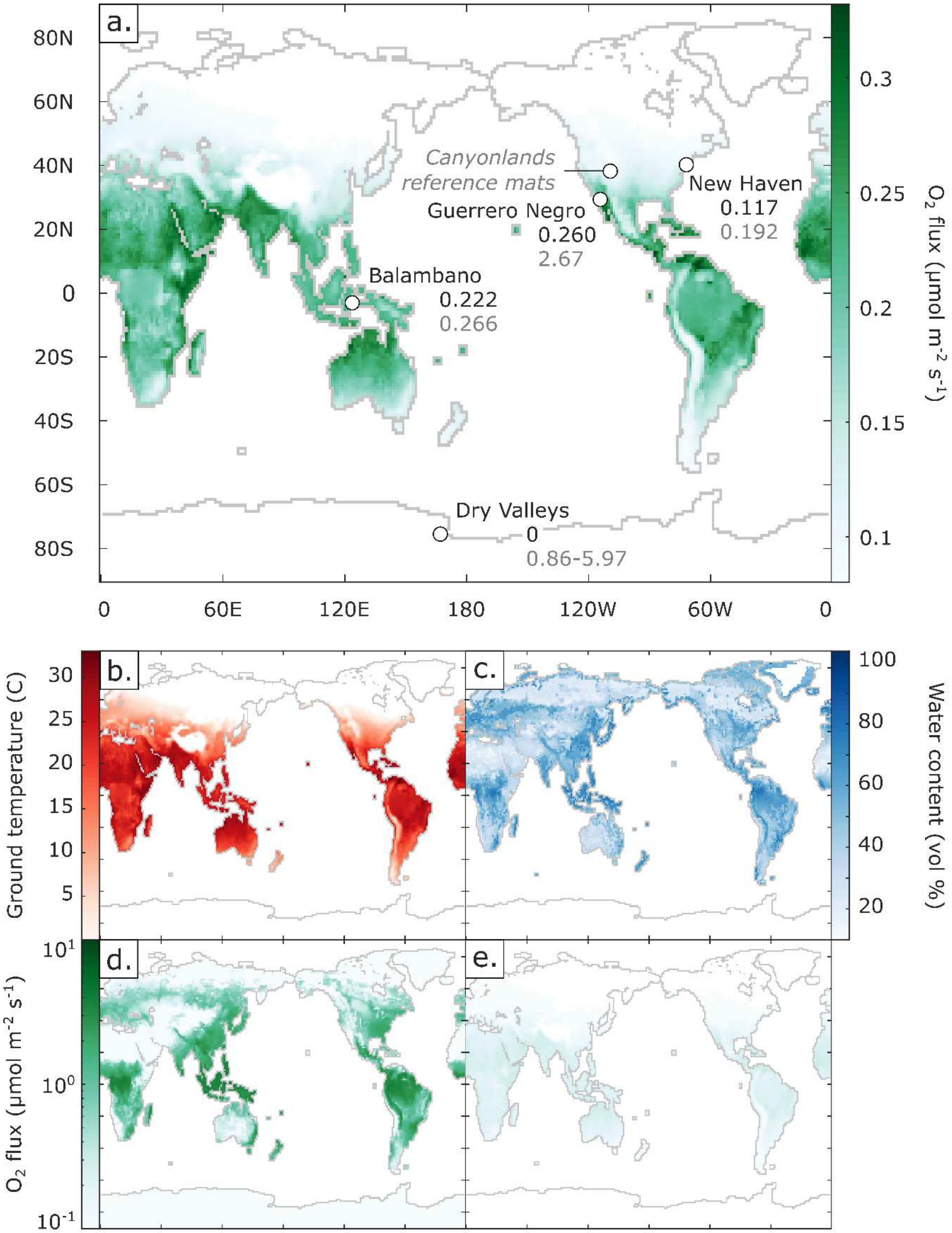

a.
80N
60N
40N
20N
0
20S
40S
60S
80S
0
60E
120E
180
120W
60W
0
Canyonlands
reference mats
New Haven
0.117
0.192
Guerrero Negro
0.260
2.67
Balambano
0.222
0.266
Dry Valleys
0
0.86-5.97
0.3
0.25
0.2
0.15
0.1
O_2 flux (μmol m^{-2} s^{-1})
b.
c.
Ground temperature (C)
30
25
20
15
10
5
100
80
60
40
20
Water content (vol %)
d.
e.
10^1
10^0
10^{-1}
O_2 flux (μmol m^{-2} s^{-1})

Figure 5. (a) Estimated O_2 fluxes from a terrestrial biosphere in which cyanobacterial mats are the sole primary producers. Our ecophysiological interpolation is based on a predicted relationship reported by Grote et al. (2010)[105] between temperature, soil moisture availability, and net photosynthesis in biological soil crusts (BSC) from Canyonlands National Park, Utah, United States, combined with climate model outputs from CESM-CAM5 averaged from 1850-2005 (obtained from earthsystemgrid.org). Estimated fluxes from selected microbial mats (black) largely underestimate actual fluxes (gray), especially in arid regions, indicating that our estimate of global NPP based on soil moisture availability is conservative. Inputs include whole-dataset averages of (b) ground temperature excluding frozen regions and (c) soil water content. O_2 fluxes from the modern terrestrial biosphere (d) are greater than those estimated for a terrestrial biosphere in which microbial mats are the only primary producers (e, same as a but scaled to d for an easier comparasion). Modern mat fluxes are reported from Guerro Negro, Mexico (Epping and Jorgensen, 1996)[113], Balambano, Indonesia (Finke et al., 2019)[83], the Dry Valleys of Antarctica (Vincent and Howard-Williams, 1986)[112], and New Haven, Connecticut, United States (this study). Modelled Balambano and Guerro Negro fluxes are derived from whole-dataset averages while New Haven and Dry Valleys fluxes come from August and December means, respectively, given significant seasonality in these locations.

Box 1: Terms to describe the evolution of biogeochemical cycling

Terms to describe the evolution of biogeochemical cycling

Term	**Definition**
Biotic scope	The relative importance of biological controls on Earth's surface geochemical processes
Ballasting	Processes that increase the density and sinking velocity of organic particles in the ocean, including mineral aggregation and biomineralization
Gross and net primary productivity	GPP: The rate at which CO_2 is consumed and O_2 produced via photosynthesis; NPP: GPP minus O_2 consumption and CO_2 production via internal (autotrophic) respiration, equivalent to the net flux of O_2 to the atmosphere from primary producers
Biological pump	The transport of organic carbon from the surface to deep ocean
Remineralization	The transformation of compounds from organic to inorganic (mineralized) forms, particularly organic carbon to carbon dioxide
Gibbs free energy (ΔG)	The amount of free energy in a thermodynamic system available for work (e.g. metabolism)
Weatherable shell	The uppermost layer of the lithosphere subject to weathering
Q10 temperature dependency factor	The effect of a 10 °C increase in temperature on the rate of a biochemical reaction
Redox balance	The conservation of electrons within a system of chemical reactions
Oxygen oases	Localized oxygenated environments within an otherwise anoxic global ocean

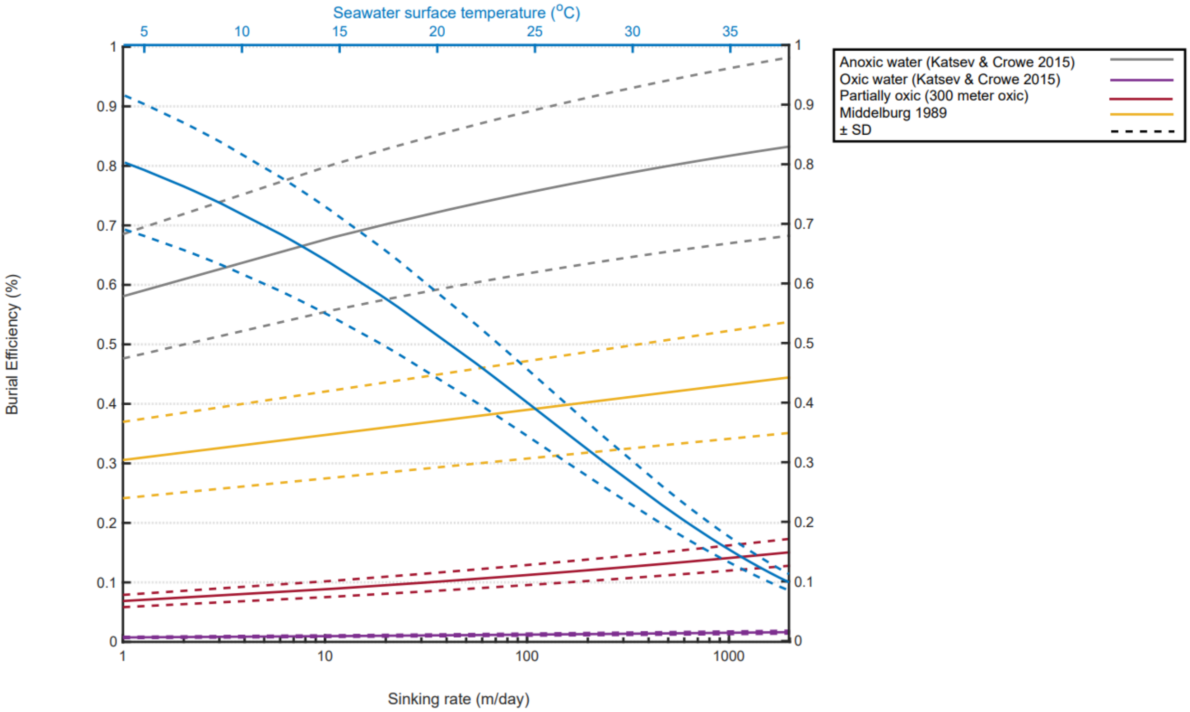
Box 2: Biological complexity and efficiency of carbon pump:

A shift from a cyanobacteria- to a eukaryote-dominated biological pump has been implicated in accelerated sinking fluxes of organic carbon as the result of increased average cell sizes, a greater propensity for such algae to form particulate aggregates and ballasting due to tests and scales[137]. While increased cell size might facilitate aggregation processes, which in turn would lead to a higher sinking velocity of oceanic aggregates[106], the impact that such a process might have on efficiency of the carbon pump and oxygen dynamics in the ocean is still poorly constrained.

We can explore the effect of biological complexity on the efficiency of the carbon pump by applying the range of sinking rate of marine aggregates into the rate of carbon degradation in the ocean. The rate of organic matter mineralization can be described as: $R_C = dC/dt = -kC$. where k and C are the reactivity and amount of organic matter, respectively. Empirical analysis[138] suggests that in marine environments, this relationship can be described as a power law $k = bt^{-a}$, where the exponent a is close to one and b is a constant. The coefficients a and b were recently found to be distinct under oxic and anoxic conditions, with a greater rate of carbon degradation under oxic vs anoxic[139]. To explore the effect of seawater temperature variation, we modify the rate law by including a temperature dependency factor, Q_{10}, where its value is between 2-3 for biological systems. Solving the rate equation for concentration, the efficiency of carbon pump (BE) as the ratio of organic matter concentration at the bottom and the surface of the ocean ($C_{bottom}/C_{surface}$) can be expressed as:

$$BE = \frac{C_{bottom}}{C_{surface}} = \exp\left(Q_{10}^{\frac{T-T_{ref}}{10}} \; \frac{-bt^{1-a}}{1-a}\right) \qquad (1)$$

Here, T_{ref} is the reference temperature for the temperature dependency factor which is assumed to be 25°C and the ocean depth is assumed to be 5 kms. The term t is time, which can be written as z/SR, where z is the ocean depth and SR is the sinking rate of particles. The change in burial efficiency as a function of the different sinking rates of known oceanic aggregates is shown. The change in the sinking rate using different rate expressions does not result in a significant (>5%) change in the burial efficiency of the carbon pump. In contrast, changes in temperature and power-law coefficients exert strong leverage on the BE (Box 2 Figure 1). This is obviously a simplification of the biological pump, but this exercise demonstrates the much more pronounced effects that temperature and marine redox conditions are likely to have on organic carbon burial efficiency than changes in sinking rates linked to biotic innovations like the rise the algae.



Box 2. Figure 1. Change in burial efficiency as a function of sinking rate and seawater temperature. The results for burial efficiency at different sinking rates (purple, red, orange, and grey lines) were obtained at no temperature dependency (Q_{10}=1). The range of sinking rates is obtained by considering a full range of observed sinking rates in the modern oceans. The range of Q_{10} for blue line that correspond to the effect of temperature on burial efficiency is between 1.5-2.5. The range of sinking rate used for blue line is between 100 – 1000 (m/day). The lines for the effect of varying sinking rates represent different power-law representations of organic carbon burial (how organic matter degradation rates changes with time). The Middleburg power law is commonly used, by does not separate anoxic and oxic remineralization. Error bars correspond to the range of coefficients for power-law carbon degradation, the range of net primary production (NPP = 100-500 gram/m^2/year), and the range of Q_{10} (1.5-2.5).

Box 3: Biological complexity and oxygen dynamics in the ocean

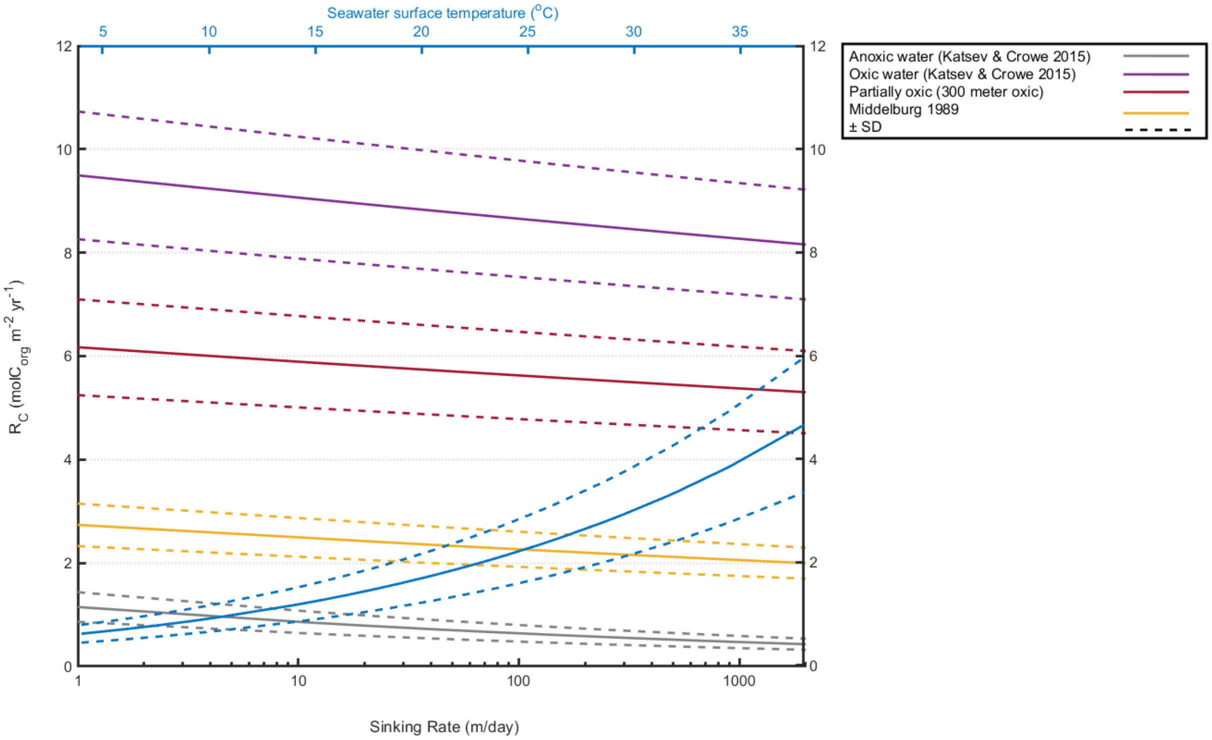
Oxygen dynamics in the ocean can be explored using a simple reaction transport model. At steady state the equation is:

$$0 = \frac{d}{dz}\left[K_z \frac{dO_2}{dz} - O_2(z)v(z)\right] \pm R \qquad (2)$$

The first part of the equation denotes the physical transport of molecular oxygen in the ocean (K_Z is the turbulent diffusion coefficient and z is the depth in the water column) and the second part is the sum of all the chemical reactions (R) that consume or produce oxygen. The rise of biological complexity can influence oxygen dynamics by modulating the rate of oxygen demand, which itself is a function of the carbon degradation rate. Using Michaelis-Menten kinetics, the oxygen respiration rate is:

$$R_{resp} = R_C \frac{[O_2]}{K_i + [O_2]} \qquad (3)$$

where R_c is the rate of organic matter degradation (described in box 1: $R = -kC; k = bt^{-a}$), K_i is the half-saturation, and O_2 is the concentration of oxygen. The change in the sinking rate of marine aggregates, caused by the evolution of larger cell-sized algae and fecal producing zooplanktons, may impact the rate of organic matter degradation by changing the amount of organic matter (C) and the time (t) in the rate equation (discussed in part I). Similar to the results in Box 2, changes in the sinking rate of particles did not lead to a major change in the rate of organic matter degradation. This indicates that biotic innovations would also play minor role in marine oxygen dynamics, relative to surface oxygen levels and temperature (Box 3 Figure 1).



Box 3. Figure 1. Change in the integrated rate of organic matter degradation as a function of sinking rate and seawater temperature. The values of Q_{10} for blue line and sinking rate for the effect of the sinking rate in purple, red, orange, and grey lines are similar to box Figure 1. The initial concentration of organic matter at the surface ($C_{surface}$) was calculated using the modern net primary production and sinking rate of oceanic aggregate. To account for lower productivity in the Precambrian ocean, the value of $C_{surface}$ was multiplied by 0.1. Error bars correspond to the range of coefficients for power-law carbon degradation, range of net primary production (NPP = 100-500 gram/m^2/year), and range of Q_{10} (1.5-2.5).

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