



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

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**Abstract** | Life on Earth has existed for over 3.5 billion years and has caused fundamental changes in Earth's biogeochemistry. However, the timing and impact of major events in the evolution of the biosphere are hotly contested, owing partially to the inherent difficulty in studying events that occurred in deep time. In this Review, we discuss the evolving structure of Earth's biosphere and major changes in its capacity to alter geochemical cycles. We describe evidence that oxygenic photosynthesis evolved relatively early, 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. Moreover, there are potential issues with the commonly held idea that the diversification of eukaryotes fundamentally altered ocean nutrient cycling and transformed the marine biological pump. Furthermore, we argue that terrestrial primary productivity was a substantial mode of biological carbon fixation following the widespread emergence of continental land masses, even before the rise of land plants, impacting carbon cycling on a global scale.

There is clear evidence that life evolved early in Earth's history and has persisted for well over 3.5 billion years<sup>1–3</sup>, but there are still large gaps in understanding of the basic history of biology on our planet. Historically, the most heated debates about Earth's atmospheric evolution have focused on when and why Earth's atmosphere became well oxygenated<sup>4–6</sup>. It is now generally accepted that Earth has undergone a protracted, several-billion-year oxygenation<sup>4</sup>, but there remains a lack of consensus about the roles that biotic innovations and the evolution of solid-Earth processes have played in driving this oxygenation<sup>7–9</sup>. It is accepted that atmospheric oxygen (O<sub>2</sub>) levels were low in the Archean, generally higher in the Proterozoic and higher still across much of the Phanerozoic<sup>4</sup> (FIG. 1). There is also consensus that this progressive rise in O<sub>2</sub> levels was essential for the rise of many lineages of eukaryotic life, including animals<sup>4,10,11</sup>. However, there is still debate about nearly all aspects of the history of this oxygenation, including its timing, pace and impact on the biosphere.

In one notable example, there is now agreement that O<sub>2</sub> first rose to appreciable levels between 2.4 and 2.3 billion years ago (Ga)<sup>12</sup>, but the trigger for this event — a shift in tectonic processes<sup>13,14</sup>, the onset of biological O<sub>2</sub> production by cyanobacteria<sup>15</sup> or removal of previous barriers to cyanobacterial proliferation<sup>16</sup> — remains

contested. In parallel, there is agreement that carbon dioxide (CO<sub>2</sub>) levels have gradually decreased through time<sup>17</sup>, maintaining a clement climate, with noteworthy but short-lived climate extremes<sup>18,19</sup>. Still, there remains no coherent view of the role that Earth's biosphere has played in driving the long-term secular decline in atmospheric CO<sub>2</sub> or major climate shifts<sup>20,21</sup>.

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)<sup>22</sup>. Even the timing of the evolution of 'highly influential novelties' — new metabolisms or basic cell types<sup>22</sup> — 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 time are limited and accompanied by large error estimates<sup>23,24</sup>. Nonetheless, the timeline and history of life on Earth is coming into better focus. Efforts over the last decade or so 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'.

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## Key points

- Although marine anoxia persisted for most of Earth's history, inorganic geochemical information suggests appreciable traces of O<sub>2</sub> in Earth's surface environments hundreds of millions of years before the Great Oxidation Event.
- Anoxygenic photosynthesis was likely a key metabolism in the early marine biosphere, and the presence of these organisms may have increased nutrient limitation amongst oxygenic phototrophs.
- Terrestrial microbial mats in the Precambrian could have been responsible for a substantial fraction of global primary productivity.
- The rise of animals or the rise of algae were not necessarily first-order controls on the nature of Earth's marine biological carbon pump, but environmental factors could have induced dramatic changes in organic-carbon-remobilization efficiency over time.

In this Review, we present a new view of the evolution of the structure and scope of life on our planet. We discuss the impact of key biotic innovations on global biogeochemical cycles on the planetary-scale evolution of Earth's biosphere. We argue for the relatively early evolution of oxygenic photosynthesis and a persistent dominance of a marine biosphere characterized by anoxygenic phototrophs and chemotrophs. Moreover, we challenge the standard view that the rise of eukaryotes to ecological prominence fundamentally altered marine nutrient cycling<sup>7,8,25</sup>. We posit that, although the emergence of plants had a major impact on the global carbon (C) cycle, terrestrial primary productivity was appreciable or even dominant, well before the rise of land plants. Collectively, these arguments represent 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. Nonetheless, by developing a cohesive narrative that connects the essential elements of this alternative view, its underlying evidence and existing knowledge gaps, we hope to inspire new lines of inquiry that will further advance conceptual and quantitative models of biospheric evolution.

### Early oxygen

The evolution of oxygenic photosynthesis, which was potentially as long as 3.8 Ga (REFS<sup>1,26</sup>), enabled a dramatic increase in the size and complexity of Earth's biosphere<sup>27</sup> (FIG. 1). 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<sub>2</sub>, which is required by animals and other complex life forms for respiration and the biosynthesis of key macromolecules<sup>4,27</sup>. The build-up of O<sub>2</sub> also allowed for the formation of an ozone layer, drastically reducing the harmful effects of ultraviolet (UV) radiation<sup>4</sup>. 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 there was a protracted and delayed increase in atmospheric oxygen levels<sup>28–30</sup>. 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 (REF.<sup>31</sup>) (the age of the oldest sedimentary rocks) to 2.4–2.3 Ga (REF.<sup>15</sup>). The latter date is coincident with the first permanent rise of atmospheric oxygen, the 'Great Oxidation Event', or GOE (FIG. 1), and, thus, represents the absolute youngest age for the onset of oxygenic photosynthesis<sup>32</sup>.

Though controversial, a wealth of inorganic geochemical information now suggests appreciable traces of O<sub>2</sub> in Earth's surface environments hundreds of millions, or perhaps more than a billion years, before the GOE<sup>29,33–37</sup>. Some of the earliest such evidence comes from molybdenum (Mo) isotopes<sup>33</sup>, and Mo and other metal elemental distributions in sedimentary rocks<sup>34,35</sup> deposited in the Neoproterozoic, more than 100 million years prior to the currently accepted date of ~2.4 Ga for the GOE<sup>38</sup>. Evidence for an even earlier rise of oxygenic photosynthesis comes from the distributions and isotope values of chromium (Cr), uranium (U) and Mo in 3.0-Ga palaeosols and banded iron formations from the Pongola Supergroup<sup>29,36,37</sup>. This interpretation is further supported by broadly contemporaneous sulfur (S) isotope systematics that point towards extensive oxidative S cycling<sup>39</sup>. A comprehensive summary of all evidence for pre-GOE oxygen is beyond the scope of this Review, but it is worth noting that there are a number of other examples between the Mesoarchean and the GOE, and a few, albeit more contentious, examples prior to 3.0 Ga (REFS<sup>40,41</sup>). Previous geochemical evidence of free oxygen has been met with considerable scepticism, however, and tracking early O<sub>2</sub> production by inorganic means has been hindered by concerns similar to those that plagued organic biomarker work, which was previously the most widely touted evidence of early O<sub>2</sub> production<sup>42,43</sup>. In particular, there are concerns surrounding whether geochemical records uniquely fingerprint biological oxygen production and whether geochemical records are truly recording primary palaeoenvironmental signals. For instance, signals of early O<sub>2</sub> in ancient rocks could, instead, be tied to secondary oxidation during surface weathering under today's O<sub>2</sub>-rich atmosphere<sup>44</sup>. In short, despite great effort, it has proven difficult to ensure that geochemical signatures diagnostically reveal the presence of oxygenic phototrophs<sup>45</sup> in past environments.

The most recent debate about when oxygenic photosynthesis evolved has focused on whether manganese (Mn) oxides in the pre-GOE rock record can be uniquely ascribed to Mn(II) oxidation with O<sub>2</sub> produced through oxygenic photosynthesis<sup>29,46</sup>. Most researchers agree that there was appreciable Mn(II) oxidation in the Archean<sup>47</sup>, but the requirement of O<sub>2</sub> for this oxidation has been questioned. Recent work<sup>48</sup> 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. However, it remains to be demonstrated that anaerobic Mn oxidation can account for signals observed in the Archean rock record. An instructive parallel is provided by anoxic photochemical Mn(II) oxidation, a well-known abiotic process that produces Mn oxides without O<sub>2</sub>. This process demonstrates that Mn oxidation does not have to be aerobic, but it is generally regarded that this process will not lead to

### Carbon fixation

The transformation of carbon from inorganic to organic form, particularly carbon dioxide to organic carbon during photosynthesis.

### Biotic scope

The relative importance of biological controls on Earth's surface geochemical processes.

### Oxygenic photosynthesis

Photosynthesis that produces free oxygen (O<sub>2</sub>).

### Anoxygenic phototrophs

Microorganisms that capture light energy to produce ATP without oxygen production; water is, thus, not used as an electron donor.

### Palaeosols

Ancient soils preserved in sedimentary successions.

### Banded iron formations

Iron-rich, chemically precipitated sedimentary rocks characterized by interbedded iron oxides and cherts, found almost exclusively in Proterozoic and earlier sedimentary successions.

### Secondary oxidation

Late-stage oxidation occurring after sediment burial and lithification, typically via surface weathering of exposed rock outcrops.

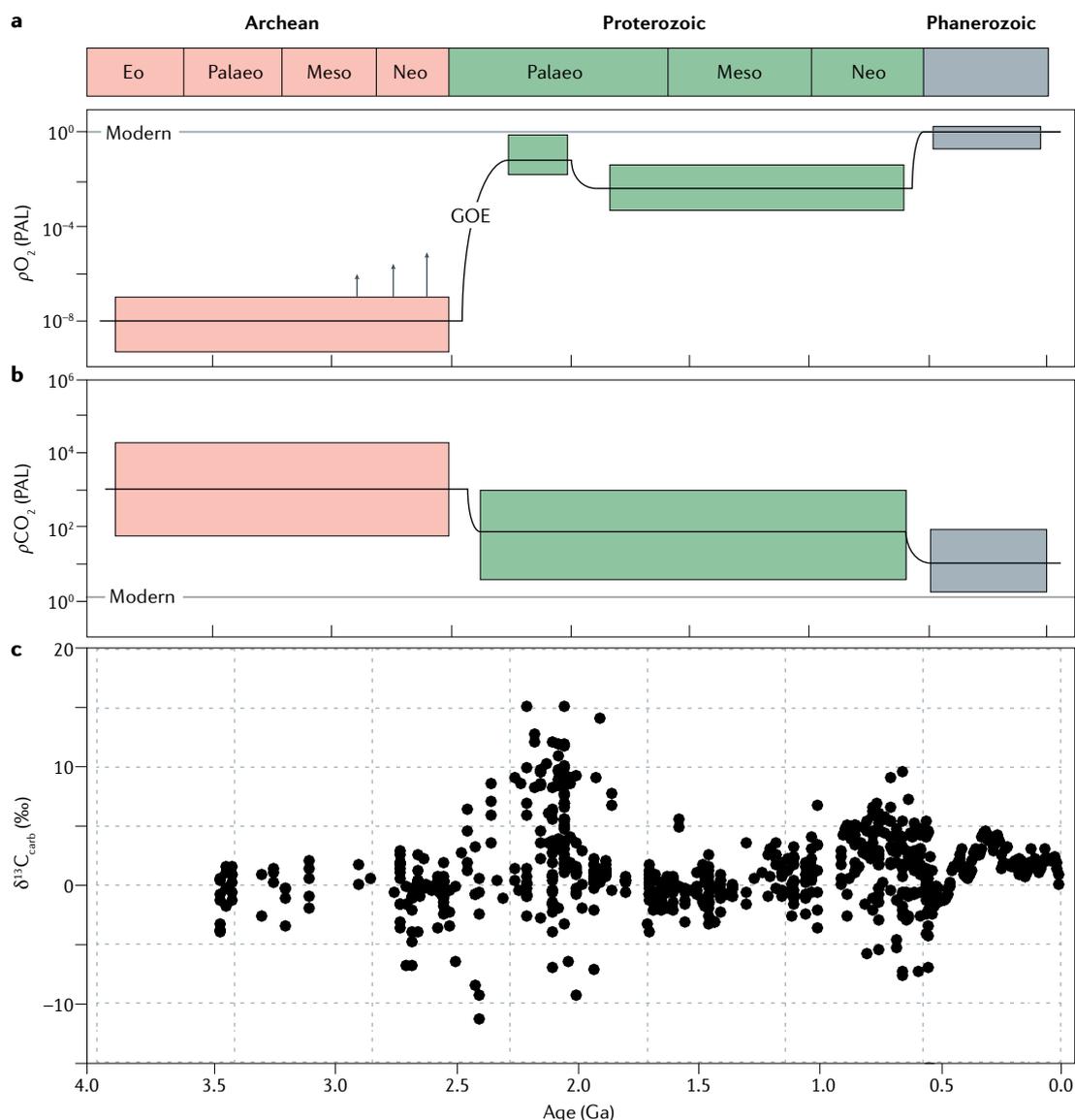


Fig. 1 | Estimates of change in atmospheric oxygen, CO<sub>2</sub> and isotopic composition of marine carbonates through time. **a** | Changes in  $pO_2$  relative to the present atmospheric level (PAL) from approximately 4 billion years ago (Ga) to the modern. **b** | Estimates of  $pCO_2$  in parts per million by volume (ppmv), based on REF.<sup>20</sup> | Carbonate C isotopic values,  $\delta^{13}C_{carb}$ , through time in parts per thousand (‰)<sup>163</sup>. GOE, Great Oxidation Event. Panels **a** and **b** adapted from REF.<sup>175</sup>, CC BY 3.0 (<https://creativecommons.org/licenses/by/3.0/>). Panel **c** modified with permission from REF.<sup>163</sup>, American Journal of Science.

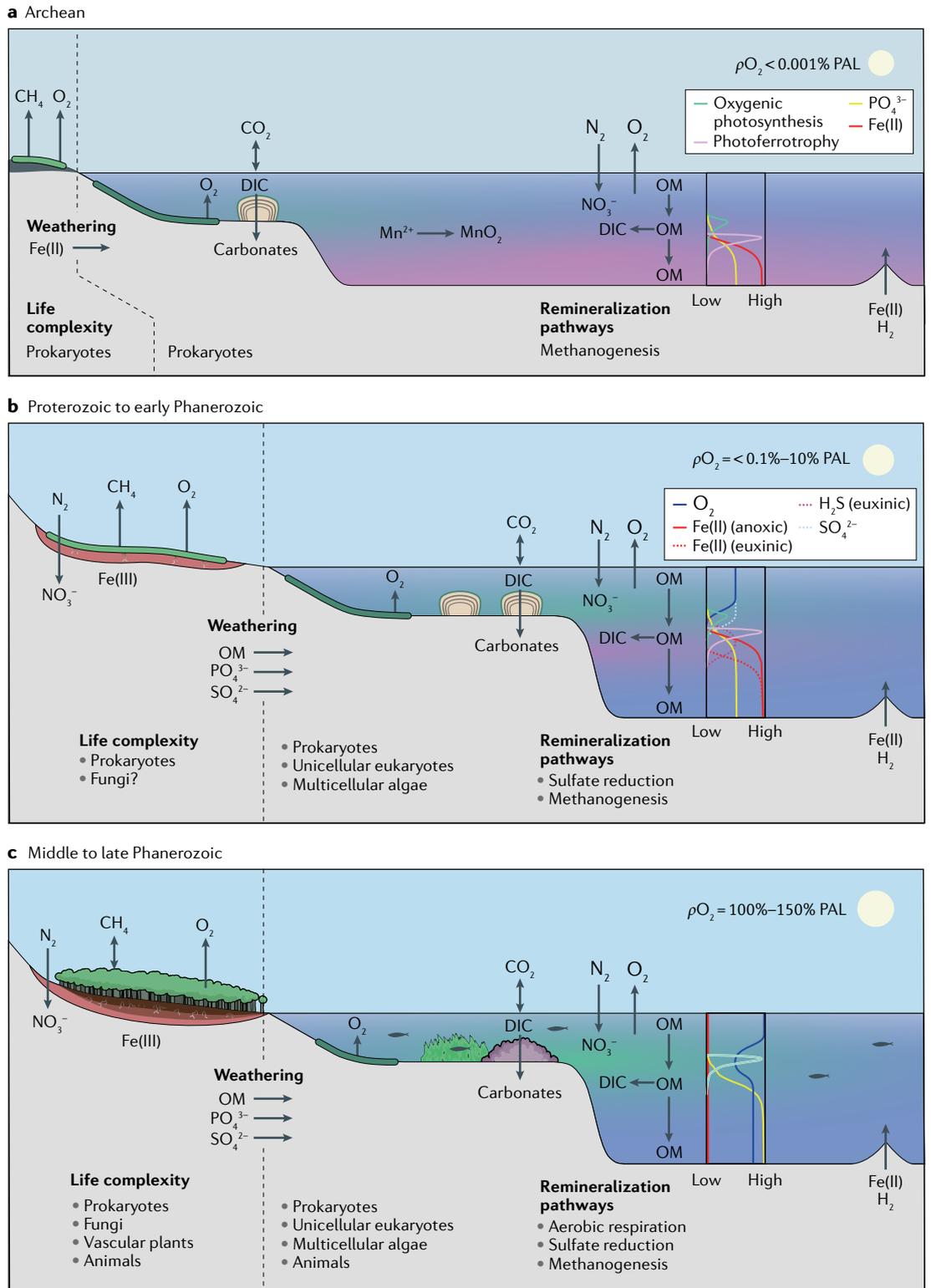
the preservation of oxidative geochemical signals from Archean oceans, as iron (Fe) cycling ultimately negates accumulation and transport of Mn oxides in early marine settings<sup>49</sup>.

Regardless, 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<sup>44</sup>. At the same time, researchers sceptical of the early rise of oxygenic photosynthesis must make efforts to ensure that their

own observations are placed into a framework that is fully consistent with the geologic record, including consideration of thermodynamic plausibility, downstream recycling of metabolites under Archean conditions and elemental mass fluxes in a sedimentological context. With that in mind, we argue that recent challenges to an early rise for biological oxygen production still fall short of providing the cogent argument necessary for overturning the current paradigm of an early (>3.0 Ga) rise of oxygenic photosynthesis<sup>29,36</sup>.

### Anoxygenic photosynthesis

The rise of oxygenic photosynthesis was a major event in Earth's history, but anoxygenic phototrophs likely played a key role in fuelling the biosphere and driving planetary



evolution throughout most of the first 3 billion years of Earth's history<sup>28,50-52</sup>. Phylogenetic analyses almost unanimously show that anoxygenic photosynthesis evolved prior to oxygenic photosynthesis<sup>32,53</sup> (however, see also REF.<sup>54</sup>), 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<sup>28,50-52</sup>. Models suggest that the emergence

of anoxygenic photosynthesis would have energized the biosphere, leading to global productivity greater than an exclusively chemosynthetic primary producers biosphere<sup>51,55</sup>. 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<sup>28,52,56</sup> (FIG. 2a), and anoxygenic photosynthesis likely played a

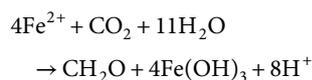
**Chemosynthetic primary producers**  
 Producing organic compounds using energy from inorganic chemical reactions, rather than sunlight.

◀ **Fig. 2 | Evolution of the structure of the biosphere and its impact on global biogeochemical cycling.** **a** | The Archean. Oxygenic photosynthesis is present in globally anoxic oceans but suppressed by competition with photoferrotrophs, with electron-donor limitation suppressing marine productivity. Oxygenic photosynthesis is also present on land but limited in scope by ultraviolet radiation stress and low continental exposure. **b** | The Proterozoic and early Phanerozoic. Oxidizing conditions prevail in terrestrial and surface ocean environments, while anoxia persists in the deep ocean, with nutrient limitation suppressing marine productivity. Meanwhile, substantial oxygen production on land potentially exceeds marine production. **c** | The middle to late Phanerozoic. Fully oxygenated surface conditions exclude anoxygenic photosynthesis, power higher global productivity and support complex multicellular life. Multicellular organisms are the dominant primary producers on land, whereas microbial life remains dominant in the oceans in terms of primary production and carbon burial. DIC, dissolved inorganic carbon; OM, organic matter; PAL, present atmospheric level.

key role in regulating global biogeochemical cycles until the ocean became fully oxygenated<sup>28,55</sup>.

Anoxygenic photosynthesis in the marine realm is driven by a suite of inorganic and organic electron donors that, together with bioessential nutrient elements like nitrogen and phosphorus, limit rates of photosynthesis<sup>52</sup>. Extant anoxygenic phototrophs are able to grow photosynthetically with Fe(II), molecular hydrogen (H<sub>2</sub>) and hydrogen sulfide (H<sub>2</sub>S), as well as some organic compounds, such as acetate and pyruvate<sup>51,52</sup>, as electron donors. Considering the availability of these electron donors in seawater throughout Earth's history<sup>51,56–58</sup>, Fe(II) and H<sub>2</sub> would likely have been the most widely utilized throughout most of the Archean and Palaeoproterozoic. In contrast, sulfide (H<sub>2</sub>S) is likely to have been only episodically abundant, and would have been particularly common in punctuated intervals in the Proterozoic<sup>51,59,60</sup>. Compared with these other compounds, the availability of organic electron donors has received less attention<sup>61</sup>. Although they could have been relatively abundant in Earth's earliest history<sup>56,62</sup>, the emergence and proliferation of heterotrophic bacteria and methanogens would likely have led to the remineralization of organic compounds, thus, making them less available as primary electron donors for anoxygenic photosynthesis — an idea that warrants further exploration.

Both Fe(II) and H<sub>2</sub> are supplied through submarine volcanism and associated hydrothermal activity at rates that would have supported appreciable anoxygenic photosynthesis, particularly when marine sulfate (SO<sub>4</sub><sup>2-</sup>) concentrations were low<sup>51,55,63</sup>. For instance, hydrothermal Fe(II) fluxes could have been greater than 40 Tmol per year prior to the GOE<sup>58</sup>. This flux is more than sufficient to account for the estimated Fe burial fluxes associated with the largest banded iron formations deposited in the Neoproterozoic to Palaeoproterozoic<sup>64</sup>. To place this number into a biological context, we can assume that Fe(II) was oxidized by photoferrotrophs in the following reaction:



Given that this metabolism theoretically yields a molar ratio of 4Fe:1C, and assuming maximum efficiency in Fe(II) oxidation, then 40 Tmol per year of Fe(II)

would generate 10 Tmol per year 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<sub>2</sub>-based phototrophy, estimated at 20–90 Tmol per year (REF.<sup>57</sup>). However, Fe is rapidly recycled through the respiration of organic matter derived from anoxygenic photosynthesis. Therefore, the 10 Tmol per year of organic carbon produced via photoferrotrophy reflects a conservative estimate for 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 photoferrotrophic products in the sedimentary record<sup>58</sup>.

Sulfide can also be used in anoxygenic photosynthesis and is derived from similar primary sources as Fe(II), such as hydrothermal vents, albeit at lower rates than Fe(II) under presumed Archean conditions<sup>65</sup>. Given these lower fluxes, H<sub>2</sub>S likely played a more limited role as a primary electron donor than Fe(II) for anoxygenic photosynthesis across most of Earth's history<sup>51,55</sup>. Concordantly, H<sub>2</sub>S-based phototrophy is estimated to have generated 4.7–6.7 Gmol C per year (REF.<sup>57</sup>), several orders of magnitude less than either H<sub>2</sub>-based or Fe(II)-based phototrophy. However, H<sub>2</sub>S 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 SO<sub>4</sub><sup>2-</sup> fluxes to the oceans following the GOE<sup>66,67</sup>. Under widespread marine anoxia during the Proterozoic, SO<sub>4</sub><sup>2-</sup> reduction would have supported appreciable secondary H<sub>2</sub>S production. At times of low marine Fe(II) concentrations, episodic and localized photic-zone euxinia could have supported extensive secondary H<sub>2</sub>S-dependent anoxygenic photosynthesis<sup>68,69</sup>. However, given evidence for widespread ferruginous conditions throughout most of the Precambrian<sup>69,70</sup>, we suggest that the supply rates and availability of Fe(II) and H<sub>2</sub> would have placed the primary constraint on rates of anoxygenic photosynthesis and the size of the biosphere (FIG. 2a).

Like all life, anoxygenic photosynthetic organisms require a number of bioessential elements, including nitrogen (N), phosphorus (P) and sulfur (S), as well as various micronutrients<sup>71</sup>. 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<sup>58</sup>. Organismal nutrient quotas differ but roughly follow a defined stoichiometry that is well represented by the Redfield ratio for macronutrients (106:16:1 C:N:P) in the modern ocean<sup>72</sup>. Conservation of electrons by photosynthesis also means that there is a stoichiometric relationship between carbon fixed into biomass and the electron donor (such as Fe(II) or H<sub>2</sub>) used and oxidized<sup>73</sup>. 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 ratio means that supply rates

#### Remineralization

The transformation of compounds from organic to inorganic form, particularly, organic carbon to carbon dioxide.

#### Photoferrotrophs

Anoxygenic phototrophic microbes that use ferrous iron as their primary electron donor and, in the process, produce ferric iron.

#### Net primary productivity

Rate at which carbon is fixed and O<sub>2</sub> produced via photosynthesis, minus the carbon remineralized and O<sub>2</sub> consumed via internal (autotrophic) respiration; equivalent to the net flux of O<sub>2</sub> to the atmosphere from primary producers.

#### Dissimilatory sulfate reduction

The anaerobic respiration of sulfate.

#### Euxinia

Anoxic and sulfidic water-column conditions.

#### Ferruginous

Anoxic and iron-rich water-column conditions.

of P less than 1/424th those of Fe(II) would lead to a biosphere limited by P, assuming negligible P recycling<sup>73</sup>. Similar arguments could be made for N, although N can be biologically fixed from an enormous reservoir of N<sub>2</sub> in the atmosphere (and corresponding aqueous N<sub>2</sub> in the water column). Nitrogen limitation (where N was the ultimate limiting nutrient<sup>74</sup>) would have been less likely following the emergence of nitrogen fixation, which molecular phylogeny<sup>75</sup> and isotopic evidence<sup>76</sup> suggest took place in the early Archean. Many extant anoxygenic phototrophs have the metabolic potential for N<sub>2</sub> fixation, including those that grow with Fe(II) and H<sub>2</sub> as electron donors<sup>77</sup>. Recent analyses further predict that stem-group photoferrotrophs likely had the capacity to fix N<sub>2</sub> (REF.<sup>78</sup>), though it results in slower growth rates than when exogenous fixed N is abundant.

The evolution of oxygenic photosynthesis would have partly liberated total primary productivity from limitations imposed by electron-donor availability, shifting limitation towards nutrient (P) availability<sup>55,79</sup>. 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 H<sub>2</sub>). As a result, the biosphere as a whole would likely have shifted into a state of perpetual P limitation (FIG. 2b). At the same time, the emergence of oxygenic photosynthesis would have initiated strong competition with anoxygenic photosynthesis for euphotic niche space<sup>55,80</sup>. Based on inferences 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<sup>55</sup>. Anoxygenic phototrophs can, thus, reside deeper in the water column and have first access to nutrients upwelled from the deeper ocean. Oxygenic phototrophs, restricted to shallower environments above 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.

The presence of potential ‘toxins’ to cyanobacteria also needs to be considered in this balance<sup>16</sup>. 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<sup>16</sup>. Accordingly, the proliferation of oxygenic photosynthesizers could have been delayed until either electron-donor and/or 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<sup>79</sup>. 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<sup>55</sup>.

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 (for instance, REFS<sup>23,61,79,81,82</sup>). Developing more robust constraints on primary production will require additional work on two key fronts: how nutrient and substrate inventories and fluxes have changed through Earth’s history, and 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 of Precambrian surface environments (widespread and even shallow marine anoxia<sup>83</sup>), that anoxygenic phototrophs were an important part of the biosphere and had potential to limit the scope of oxygenic photosynthesis.

### Life on land

Much of the past and current research on Earth’s early biosphere is directed at understanding the evolution of marine life — particularly cyanobacteria — and how it shapes the global oxygen and carbon cycles. The research community has, with key exceptions<sup>84–92</sup>, 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). Although 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<sup>85,86</sup>.

There are multiple lines of evidence for life on land prior to the mid-Palaeozoic, despite a strong preservation bias against microbial remains in continental environments<sup>93</sup>. Microbially induced sedimentary structures 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 (REFS<sup>85,94</sup>). Moreover, element-mobility patterns in palaeosols suggest weathering by organic acids — and, consequently, the presence of life on land — by at least 3.0 Ga (REFS<sup>92,95,96</sup>).

Independent of the sedimentary record, molecular data provide some evidence for a terrestrial origin of cyanobacteria<sup>96,97</sup>. Phylogenomic analyses of modern cyanobacterial diversity could suggest a freshwater origin for the clade and indicate that filamentous cell types, a structural novelty enabling mat formation, originated soon thereafter<sup>97</sup>. By contrast, these same analyses recover marine planktonic cyanobacteria as derived clades with multiple independent origins from an ancestral terrestrial

#### Stem-group

The group of extinct taxa within a clade that diverged prior to the most recent common ancestor of its living representatives.

#### Redoxcline

A steep, vertical gradient between oxidizing and reducing conditions in a water column.

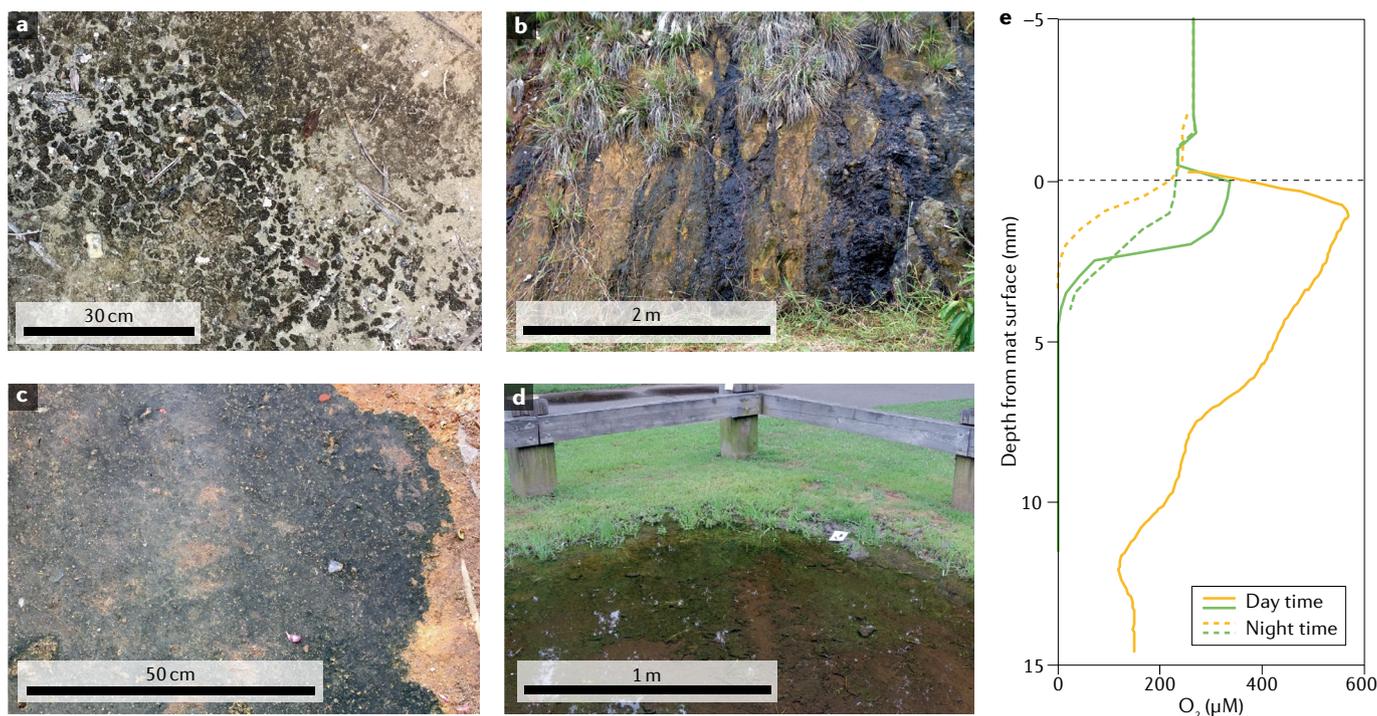


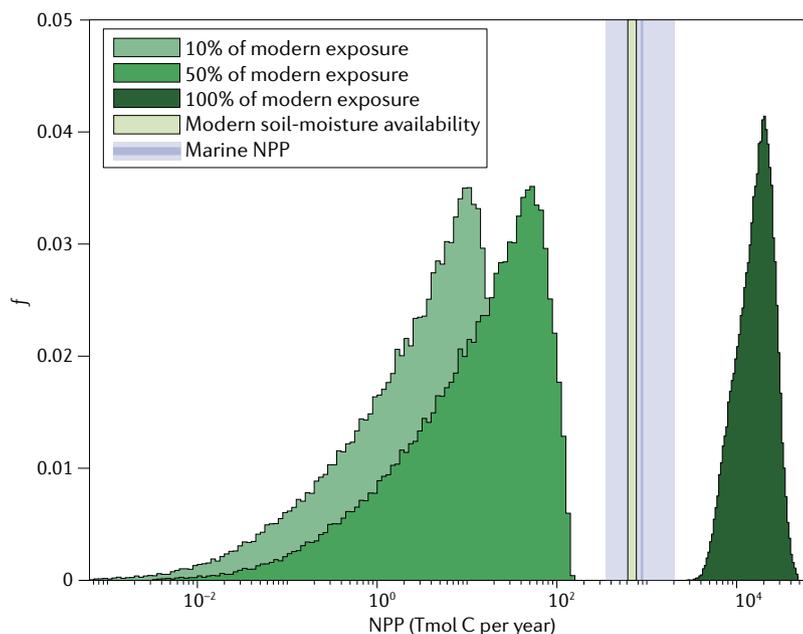
Fig. 3 | **Modern terrestrial cyanobacterial mats.** **a** | Little Darby Island, the Bahamas. **b** | Balambano Hydroelectric Dam, Indonesia. **c** | Lamma Island, Hong Kong. **d** | New Haven, Connecticut, USA. These modern mats illustrate the range of environments and the diversity of basic structure 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 fibre-optic  $O_2$  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)<sup>91</sup> in a greenhouse with a Clark-type microelectrode at 15:12 and 3:40 local time. Panel **e** adapted from REF.<sup>91</sup>, CC BY 4.0 (<https://creativecommons.org/licenses/by/4.0/>).

or freshwater aquatic ecotype. Although still rare compared with the clear evidence for microbial life in marine settings, these records — among many others — provide the tantalizing suggestion that the role of terrestrial ecosystems in shaping Earth's earliest biogeochemical cycles has been underappreciated.

Modern mats are consortia of metabolically diverse prokaryotes including cyanobacteria<sup>98</sup>, and it is therefore possible that the communities responsible for microbial signatures in early terrestrial settings differed significantly from their modern counterparts. Although sedimentological and geochemical indicators for life on land could well have been produced by chemotrophs or anoxygenic phototrophs<sup>99</sup>, it is still 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<sup>91</sup> and can form their own mats under rare instances of photic-zone anoxia in subaqueous environments<sup>100</sup>. Terrestrial iron oxidizers, in particular, form land-based mats<sup>101</sup>. Further, photosynthetic organisms would have experienced appreciable UV stress in the absence of an ozone layer in the Archean, making inferences about community composition from living microbial ecosystems somewhat challenging<sup>102–104</sup>.

Although the earliest direct evidence for terrestrial mats comes from river margins<sup>85</sup>, modern mats span a vast range of subaqueous and subaerial environments

(FIG. 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<sup>105</sup>, including some of the driest areas on Earth, such as the Atacama Desert in Chile<sup>106</sup> and the McMurdo Dry Valleys of Antarctica<sup>107</sup>. These mats survive by producing abundant extracellular polysaccharides that bind loose materials together to form a cohesive crust, which both maintains hydration levels and protects against UV radiation<sup>108</sup>. In the absence of competitive exclusion from plants, the majority of Earth's habitable land surface could potentially 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 could 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<sup>108,109</sup>. Critically, there is high phylogenetic diversity in these mats, indicating that the potential to colonize BSC environments is broadly distributed across multiple divergent microbial lineages and, thus, is likely not a late-stage biotic innovation<sup>91,98</sup>. Marine environments in the Precambrian have been commonly assumed to be nutrient-poor<sup>81</sup>, in contrast, regolith on land would have provided an abundant source of bioessential elements (foremost, P) for terrestrial ecosystems, assuming organisms had the capacity to access them in dissolved



**Fig. 4 | Estimated annual net primary production from terrestrial microbial mats.** Probability ( $f$ ) distributions for globally integrated net primary production (NPP) in Tmol C per year are shown for continental configurations that are 10% (light-green bars), 50% (medium-green bars) and 100% (dark-green bars) of the modern total land surface area ( $1.49 \times 10^{14}$  km<sup>2</sup>). The probability distributions were calculated using O<sub>2</sub> production rates measured in modern terrestrial microbial mats<sup>79</sup> and a uniform mat coverage distribution from 10 to 50% of the prescribed total land surface area. Production rates were divided into a uniform distribution from 0.041 to 0.117 nmol cm<sup>-2</sup> s<sup>-1</sup> for mats in arid lands and a log-normal distribution with a mean of 0.244 nmol cm<sup>-2</sup> s<sup>-1</sup> and standard deviation of 0.233 nmol cm<sup>-2</sup> s<sup>-1</sup> 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% (REF.<sup>82</sup>). Arid lands are assumed to occupy 35% of the total land surface at any time<sup>80</sup>. Proterozoic continental exposure was likely similar to modern based on recent crustal-growth models, whereas Archean exposure was likely much lower<sup>83,84</sup>. For comparison, recent estimates of marine net primary productivity (NPP) during the mid-Proterozoic from Ozaki et al. (2019)<sup>56</sup> are shown by the darker-blue line (mean) and blue-shaded region (95% confidence interval). The annual range of NPP estimates from our soil-moisture analysis is shown in the light-green-shaded region.

form via biologically mediated mineral dissolution<sup>95</sup> and even store them intracellularly<sup>110</sup>. The potential 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<sub>2</sub> found in greater excess than in photosynthetic mats dominated by cyanobacteria<sup>91,104</sup>. Consequently, terrestrial mats in the Precambrian might have comprised a much larger fraction of global gross and net primary productivity than traditionally envisioned.

Quantifying global NPP (and O<sub>2</sub> fluxes) from terrestrial microbial mats on the early Earth is highly dependent on estimates of their aerial coverage and O<sub>2</sub> production rates per unit area. Environmental niche modelling puts modern BSC coverage at 12% of today's land surface and up to 24% in the absence of anthropogenic disturbance<sup>105</sup>. By some estimates,

these mats account for 7% of terrestrial NPP (325 Tmol C per year) and potentially half of terrestrial nitrogen fixation (3.5 Tmol N per year)<sup>111,112</sup>. 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<sub>2</sub> production is typically <0.2 nmol cm<sup>-2</sup> s<sup>-1</sup> in deserts versus an average of 0.4 nmol cm<sup>-2</sup> s<sup>-1</sup> in fully water-saturated environments)<sup>104,105,113,114</sup>. 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 potential contribution to global primary productivity much greater.

The simplest approach towards estimating the terrestrial biosphere's contribution to atmospheric O<sub>2</sub> fluxes — applicable to periods of Proterozoic time — is to multiply a flux range in modern mats by the total continental area they might have covered<sup>91,104</sup>. Barren land today (including unvegetated deserts and permanently ice-covered regions) comprises roughly 25% of the total land surface<sup>115</sup>, leaving 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<sup>116</sup>, 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<sup>115</sup>. A stochastic estimate using a distribution of O<sub>2</sub> production rates from modern mats, a very conservative land-surface coverage of 10–50% and a near-modern total exposed land area<sup>117,118</sup> gives an average terrestrial O<sub>2</sub> and equivalent organic-carbon-production rate (that is, NPP) of approximately 18,000 Tmol C per year (FIG. 4), which is several times the modern terrestrial NPP value of approximately 5,000 Tmol C per year (REFS<sup>119,120</sup>). By comparison, the most recent estimates for marine NPP during the Proterozoic are 350–2,100 Tmol C per year (REF.<sup>82</sup>). There are multiple ways to reduce this estimate, for example, considering seasonality in parts of the globe or considering that mats might 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<sup>113,114</sup>, a more rigorous rough estimate of O<sub>2</sub> 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<sup>113</sup> (FIG. 5a) with outputs of ground temperature and water content in the top 10 cm of soil from the Community Earth System Model, Community Atmosphere Model version 5 (CESM-CAM5; <http://www.cesm.ucar.edu>) (FIG. 5b,c) yields an average O<sub>2</sub> production rate of 0.0172 nmol O<sub>2</sub> cm<sup>-2</sup> s<sup>-1</sup>

**Gross primary productivity**

The rate at which carbon is fixed and O<sub>2</sub> produced via photosynthesis, not accounting for internal respiration.

and global production of 681 Tmol C per year, which is about 14% of modern terrestrial NPP (FIG. 5a,d,e). This number is likely an underestimate, considering that our predictive model consistently underestimates point-source fluxes from modern mats<sup>91,121,122</sup>. It does, however, fit well with recent empirical evidence from triple oxygen isotopes in sulfates that mid-Proterozoic global gross primary productivity was 6–41% that of modern values<sup>23</sup>, suggesting that reduced productivity in the Proterozoic could have been driven, in part, by a reduced terrestrial biosphere.

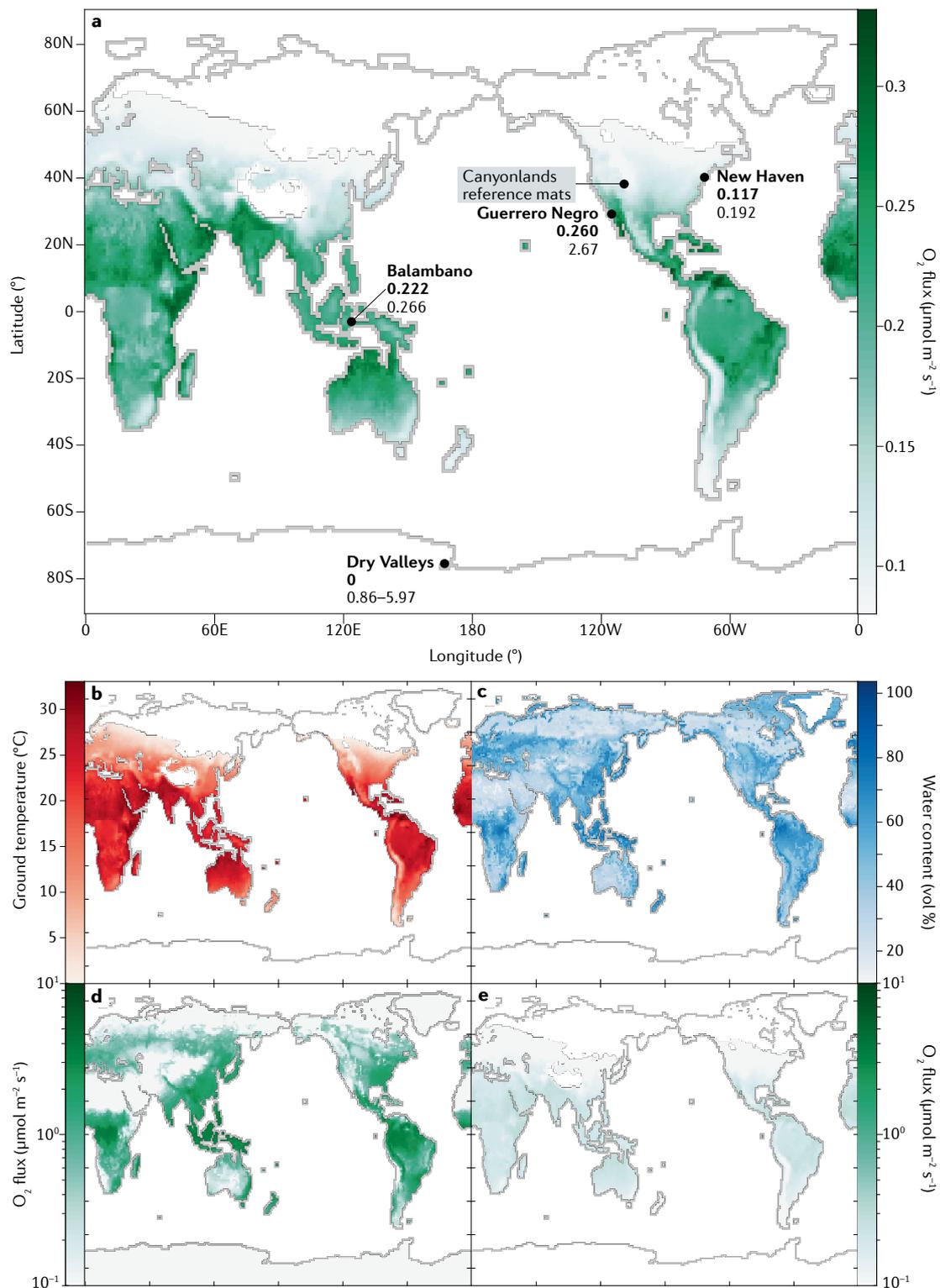
Unlike simple extrapolations based on continental coverage estimates, ecophysiological modelling of mat productivity using historical climate models allows us to explore temporal variability in global O<sub>2</sub> production. Using monthly mean ground temperatures and water contents from CESM-CAM5 for June and December results in a seasonal range of 0.0154–0.0197 nmol O<sub>2</sub> cm<sup>-2</sup> s<sup>-1</sup> and 615–766 Tmol O<sub>2</sub> per year, indicating that annual variation in ground temperature and soil moisture would strongly influence global O<sub>2</sub> production from a terrestrial biosphere dominated by microbial mats. Although our model only covers the historic range of climate variability, secular changes in global surface temperature and precipitation across Earth history likely drove even greater variation in O<sub>2</sub> production. However, a lack of reliable precipitation proxies in deep time currently hampers any attempt to reconstruct long-term changes in Earth's hydrologic cycle<sup>123</sup>, forcing reconstructions to rely on less direct inferences. From one perspective, water vapour would not have penetrated as deeply into continental interiors in the absence of vascular plants that can store and release water via transpiration<sup>124</sup>, meaning that global soil-moisture availability would have been lower than modern. However, very low continental precipitation in a pre-plant world is unlikely to have led to a stable global carbon cycle. Without high soil CO<sub>2</sub> levels linked to plant biomass degradation, rates of terrestrial silicate weathering — the primary sink for atmospheric CO<sub>2</sub> on geologic timescales<sup>20</sup> — would have been limited by the supply of CO<sub>2</sub> in rainwater. Consequently, atmospheric CO<sub>2</sub> sinks would not have balanced sources, leading to a rise in CO<sub>2</sub>, a warmer climate state, and more precipitation (see REF.<sup>20</sup>). In a world without any terrestrial biomass, it has been estimated that rainfall, on average, must have been at least ~3 m per year to deliver enough dissolved CO<sub>2</sub> to sustain the rates of silicate weathering necessary to stabilize Earth's climate<sup>20</sup>.

Because we conservatively assume modern precipitation levels, the actual O<sub>2</sub> production rates and NPP of Earth's earliest terrestrial biosphere were likely higher than the estimates we provide in FIGS 4,5. Our estimates of terrestrial NPP have large uncertainties, but if modern terrestrial mat-forming cyanobacteria are any guide, it seems unavoidable that these terrestrial ecosystems were a major component of the Precambrian biosphere. These estimates lead us to conclude that terrestrial ecosystems could have accounted for the majority of primary productivity for much of Earth's history, potentially by a substantial margin prior to the rise of vascular plants.

Although a departure from the standard view, substantial primary production on land prior to the rise of vascular plants might not be unreasonable, considering that rapid turnover in microbial ecosystems allows high productivity relative to biomass<sup>125</sup>. Prokaryotic cells live on the order of days, whereas vascular plants regularly live tens of years, and sometimes even thousands of years<sup>126</sup>. 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 roughly half of global NPP, despite making up over 80% of the planet's biomass<sup>126</sup>. 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 also emphasize that high NPP in terrestrial microbial mats does not imply an equal importance in regulating atmospheric pO<sub>2</sub>. On geologic timescales, the persistence of free O<sub>2</sub> in the atmosphere can only be sustained by the long-term burial of organic carbon (C<sub>org</sub>) in marine sediments<sup>8</sup>. Given the high reactivity of labile organic matter produced by microbial mats<sup>121</sup> and relatively long oxygen exposure times during transport in surface water and groundwater, we predict that most C<sub>org</sub> produced by terrestrial mats would reoxidize before reaching the oceans, consuming much of the O<sub>2</sub> produced during photosynthesis. Indeed, the concept of enhanced oxidation potential in terrestrial, relative to marine, environments is well established<sup>127</sup>. In this regard, terrestrial primary productivity by mat systems is likely to have had 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<sub>2</sub> through time<sup>104</sup> and the generation of triple oxygen isotope anomalies used to estimate the long-term productivity of the biosphere<sup>128</sup>. Further, these mats might have been important sources of methane, potentially providing an explanation for the presence of a stable, warm Proterozoic climate without extremely elevated CO<sub>2</sub> levels<sup>91,129</sup>.

Although these O<sub>2</sub> 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 (REF.<sup>118</sup>), and very limited exposure prior to 3.0 Ga (REF.<sup>117</sup>), constraining terrestrial O<sub>2</sub> fluxes considerably<sup>91</sup>. Additional constraints would have been placed on localized O<sub>2</sub> production by the lack of a protective ozone layer, since unattenuated UV radiation would have severely limited the productivity of subaerially exposed mats<sup>102,103</sup>. Experimental work on modern mats shows that even moderately elevated UV irradiance can reduce O<sub>2</sub> production by half<sup>30</sup>, although cyanobacteria have numerous ways of reducing exposure, including vertical migration, secretion of UV-absorbing extracellular polysaccharides<sup>108</sup>, growing under mineral grains<sup>131</sup> or even precipitating their own mineral 'sunscreen' (REF.<sup>132</sup>). The relationship between UV exposure, biological



attenuation and oxygen production in mats prior to the GOE remains largely unknown and is a large source of uncertainty in estimating the size of both the terrestrial and marine biospheres during this time<sup>133</sup>. Given evidence for continental exposure going back to at least 3.2–3.0 Ga (REFS<sup>117,134</sup>), together with fossil, molecular and geochemical records and inferences from modern mat physiology<sup>85,91,95,97</sup>, though, 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 Palaeoproterozoic Changzhougou Formation

◀ Fig. 5 | **Terrestrial oxygen-flux estimates in a microbial-mat-dominated world.**

Estimated O<sub>2</sub> fluxes from a terrestrial biosphere in which cyanobacterial mats are the sole primary producers (panel **a**). Our ecophysiological interpolation is based on a predicted relationship reported by Grote et al. (2010)<sup>113</sup> between temperature, soil-moisture availability and net photosynthesis in biological soil crusts from Canyonlands National Park, Utah, USA, combined with climate-model outputs from Community Earth System Model Community Atmosphere Model version 5 averaged from 1850 to 2005 (obtained from Earthsystemgrid.org). Estimated fluxes from selected microbial mats (bolded numbers underneath place names) largely underestimate actual fluxes (normal numbers under place names), especially in arid regions, indicating that our estimate of global net primary productivity based on soil-moisture availability is conservative. Inputs include whole-dataset averages of ground temperature excluding frozen regions (panel **b**) and soil water content (panel **c**). O<sub>2</sub> fluxes from the modern terrestrial biosphere (panel **d**) are greater than those estimated for a terrestrial biosphere in which microbial mats are the only primary producers (panel **e**). Note that panel **e** uses the same data as panel **a**, but its colour and size is scaled to match panel **d** for easier comparison. Modern mat fluxes are reported from Guerrero Negro, Mexico<sup>122</sup>, Balambano, Indonesia<sup>91</sup>, the Dry Valleys of Antarctica<sup>121</sup> and New Haven, Connecticut, USA. Modelled Balambano and Guerrero Negro fluxes are derived from whole-dataset averages, and New Haven and Dry Valleys fluxes come from August and December means, respectively, given substantial seasonality in these locations.

(ca. 1.8 Ga) and Chuanlinggou Formation (ca. 1.7 Ga) of North China<sup>135,136</sup>. However, the emerging view is that eukaryotes were not an important part of the marine biosphere until roughly 800 million years ago (Ma), or perhaps later<sup>137</sup>. Between 1,000 and 500 Ma, multicellular organisms rose to prominence via the radiation of modern animal phyla and more complex ecosystems<sup>138,139</sup> (FIG. 2c). There has been persistent debate about the drivers of this transition, and trying to make sense of it has prompted one of the most fundamental questions concerning the evolution of life — is biotic complexity inevitable and self-promoting or does the rise of complexity depend on planetary evolution towards favourable environmental conditions?

The two endmember views of the transition to modern animal phyla and complex ecosystems are that it was tied to the removal of an environmental barrier or that it simply represents the timing of biotic novelties<sup>7,140</sup>. The former view suggests that environmental factors, including oxygen concentrations and the availability of nutrients in the marine realm, governed the rise of complex life<sup>11,79,141</sup>. Specifically, ocean oxygenation could have played a central role in controlling the earliest appearance of eukaryotic clades, as well as their later radiation and rise to ecological prominence<sup>141–143</sup>. 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 Ma). In the latter view, biotic innovations independent of an environmental control (for example, the appearance of algal clades) potentially drove the observed environmental changes (such as glaciations<sup>144</sup> and oxygenation<sup>7,8,25,145</sup>). In other words, the Neoproterozoic rise of eukaryotes to ecological dominance has either been attributed to an environmental trigger or was the environmental trigger itself.

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<sup>7,8</sup>. For instance, in the Neoproterozoic, the shift from a cyanobacteria-dominated to a

eukaryote-dominated biological pump could 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 carbon pump would promote faster organic-carbon sinking rates due to an increase in average cell size and density<sup>7,146,147</sup>. In this framework, faster sinking rates, and thus a more 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<sup>9</sup>.

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 (BOXES 1,2). 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, and even in the absence of faecal-producing organisms and larger algae, there is appreciable aggregate formation comprised of only minerals and phytoplankton<sup>148</sup>. When the dynamics of marine aggregates are considered<sup>149</sup>, the overall effect of switching primary producers and bringing metazoans into marine systems is fairly minor (BOX 1). When particle disaggregation by animals — foremost by the smallest size classes of zooplankton — is considered<sup>149,150</sup>, 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 faecal-pellet production by grazing organisms might not be strong enough to alter the efficiency of the carbon pump or to have a major impact on oxygen dynamics in the oceans (BOXES 1,2).

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 could have promoted high burial efficiency by suppressing the rate of organic-matter degradation in the surface ocean and increasing the flux of organic matter into depths<sup>151</sup>. This, in turn, would have enhanced the rate of oxygen efflux from the ocean. Although other factors such as an enhancement in oxygen solubility or change in ocean-circulation patterns during cooling will also influence oceanic oxygen dynamics, global cooling could translate into rather large fluxes of oxygen from the ocean to the atmosphere (from enhanced organic-carbon burial) during the colder Neoproterozoic intervals, providing one path to a strongly oxygenated atmosphere. Therefore, a simple quantitative exploration of marine carbon cycling (BOXES 1,2) suggests that we should revisit 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

#### Biological pump

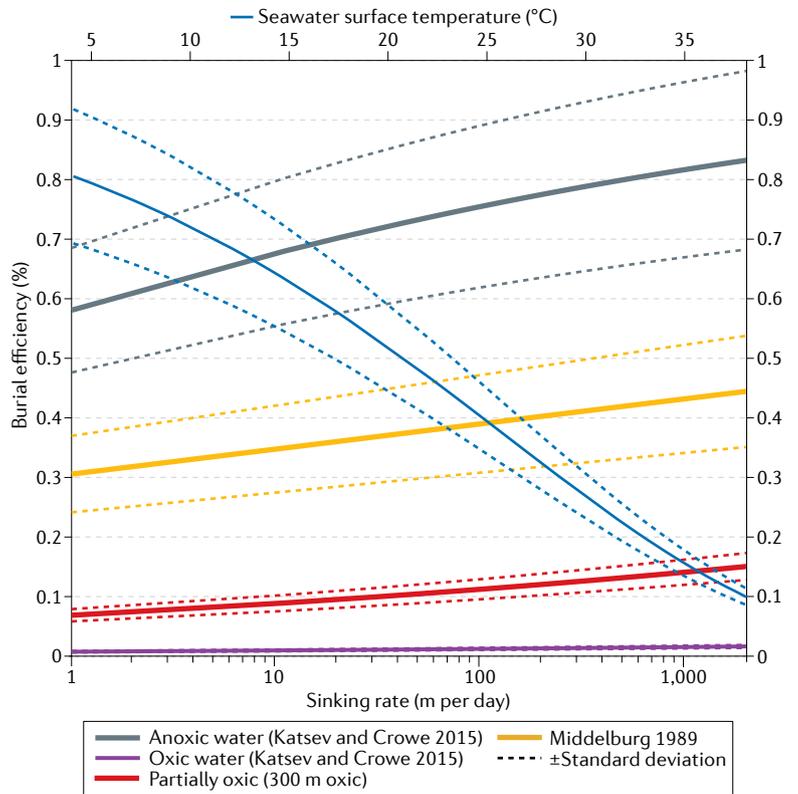
The transport of organic carbon from the surface to deep ocean.

Box 1 | Biological complexity and efficiency of the carbon pump

The effect of biological complexity on the efficiency of the carbon pump can be tested by applying a range of sinking rates of marine aggregates into the rate of carbon degradation in the ocean. The rate of organic-matter remineralization can be described as:  $R_c = dC/dt = -kC$ , where  $k$  and  $C$  are the reactivity and amount of organic matter, respectively. Empirical analysis<sup>176</sup> suggests that, in marine environments, this relationship can be described as a power law  $k = bt^{-a}$ , where the exponent  $a$  is close to 1 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 versus anoxic<sup>177</sup> conditions. 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 and 3 for biological systems<sup>178–180</sup>. Solving the rate equation for concentration, the burial efficiency of the carbon pump ( $BE$ ) as the ratio of organic-matter concentration at the bottom and at the surface of the ocean ( $C_{\text{bottom}}/C_{\text{surface}}$ ) can be expressed as:

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

Here,  $T_{\text{ref}}$  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 km. 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 in the box image. The purple, red, orange and grey lines were calculated across a range of modern-day sinking rates<sup>148,181,182</sup> and using a  $Q_{10}$  of 1, indicating no temperature dependency. The lines for the effect of varying sinking rates represent different power-law representations of organic-carbon burial. The Middelburg power law is commonly used (orange lines, but does not separate anoxic (grey) and oxic (purple) remineralization). Error bars correspond to the range of coefficients for power-law carbon degradation and the range of net primary production (100–500  $\text{g m}^{-2}$  per year). Although an increase in the sinking rate of marine aggregates does promote efficient transfer of fixed carbon into the ocean interior, its impact is not significant (>5%).



In contrast, changes in temperature and power-law coefficients exert stronger leverage on the  $BE$ , as illustrated by the blue line in the figure, which was determined using a range between 1.5 and 2.5 for  $Q_{10}$ , and a range of sinking rates between 100 and 1,000 (m per day). The blue dotted error bars show the  $Q_{10}$  range. Though the equations used here are obviously a simplification of the biological pump, 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 of algae.

factors (such as temperature changes) appear to provide a more straightforward means to induce dramatic changes in organic-carbon-remineralization efficiency over time.

**The rise of land plants**

Plants account for roughly 60% of NPP today<sup>120</sup>, and it has long been assumed that their emergence and diversification fundamentally changed the scope of the biosphere<sup>152</sup>. Although the ratio of terrestrial to marine NPP is unlikely to have fundamentally changed with the rise of land plants, the colonization of land by vascular plants would have dramatically impacted global biogeochemical cycles. Perhaps the most obvious change would have been the development of organic-rich soils with elevated  $\text{CO}_2$  concentrations from the respiration of plant biomass<sup>20</sup>. Whereas cyanobacteria appear to create millimetre-thick to centimetre-thick surficial mats and crusts, many forests and grasslands today create centimetre-thick to metre-thick topsoil<sup>153</sup>. Moreover, high  $\text{CO}_2$  concentrations in soils help to decouple

atmospheric  $\text{CO}_2$  levels from the rate of  $\text{CO}_2$  consumption via silicate weathering<sup>20</sup>. As such, lower  $\text{CO}_2$  levels are possible in a balanced carbon cycle with plants than without plants<sup>20,152</sup>.

A low-pH zone in soils also likely leads to enhanced P solubilization, given that P is not fully dissolved in most weathering environments and that apatite dissolution rates inversely scale with pH (REF.<sup>154</sup>). 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 might not be tied to P mobilization; it is simply that plants create P-poor recalcitrant organics (such as lignin) that contribute appreciably to global organic-carbon burial<sup>147,155</sup> and attendant  $\text{O}_2$  release.

A critical but historically overlooked idea is that the development of organic-rich soil layers has directly contributed to the rise of atmospheric oxygen<sup>156</sup>. The oxygen cycle is likely to be in steady state on a million-year timescale, which means that organic-carbon burial must be balanced by oxidation of volcanic reductants, Fe(II)

**Apatite**

A group of calcium-phosphate minerals, which, when formed in marine systems, have the general formula  $\text{Ca}_5(\text{PO}_4)_3(\text{F,Cl,OH})$ ; the most common mineral form of phosphorous.

Box 2 | 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:

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

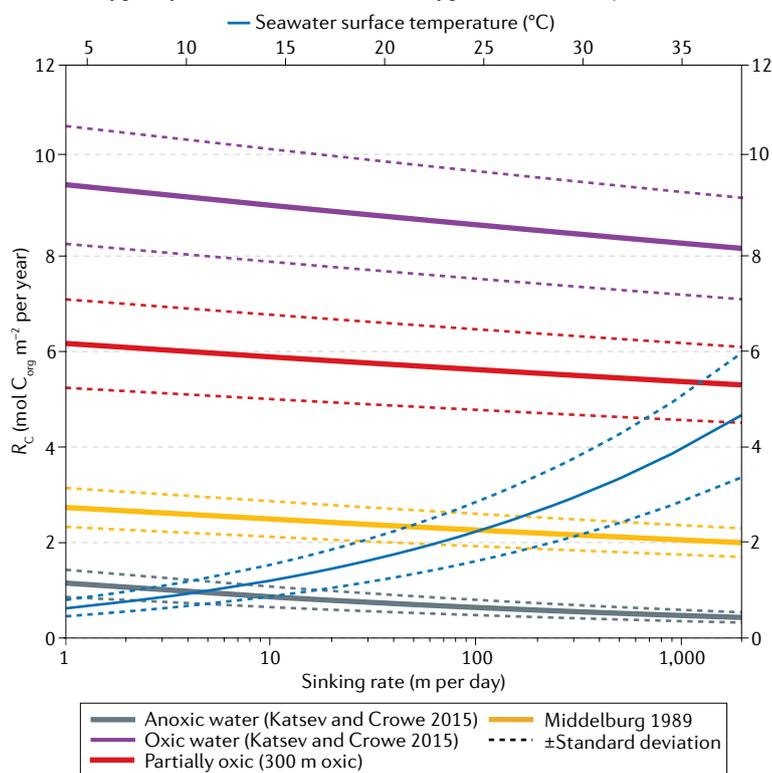
The first part of the equation denotes the physical transport of molecular oxygen in the ocean ( $K_z$  is the turbulent-diffusion coefficient and  $z$  is the depth in the water column) and the second part is the sum of all the chemical reactions ( $R$ ) that consume or produce oxygen. The rise of biological 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 aerobic respiration rate is:

$$R_{\text{resp}} = R_C \frac{[O_2]}{K_i + [O_2]}$$

where  $R_C$  is the rate of organic-matter degradation ( $R_C = -kC$ ;  $k = bt^{-n}$ ),  $K_i$  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 faecal-producing zooplankton, might impact the rate of organic-matter degradation by changing the amount of organic matter ( $C$ ) and the time ( $t$ ) in the rate equation.

The figure demonstrates the change in the integrated rate of organic-matter degradation as a function of sinking rate and seawater temperature. The values of  $Q_{10}$  for the blue line were in the range 1.5–2.5. The sinking rate for the effect of the sinking rate in the purple, red, orange and grey lines are similar to the figure for BOX 1. The initial concentration of organic matter at the surface ( $C_{\text{surface}}$ ) was calculated using a reasonable rate of modern net primary production (100–500  $\text{g m}^{-2}$  per year) and sinking rate of oceanic aggregates<sup>148,150</sup>. To account for the potential for lower productivity in the Precambrian ocean<sup>23</sup>, the value of  $C_{\text{surface}}$  was multiplied by 0.1. The error bars correspond to the range of coefficients for power-law carbon degradation, range of net primary production (purple, red, orange and grey lines) and range of  $Q_{10}$  (blue lines).

As shown in the figure, changes in the sinking rate of particles does not lead to a major change (<30%) in the rate of organic-matter degradation. Together, these mineralization values indicate that biotic innovations would also play a minor role in marine oxygen dynamics, relative to surface oxygen levels and temperature.



in rocks and organic carbon bound in rocks<sup>157</sup>. A lack of balanced fluxes would result in continual rise or fall of atmospheric  $O_2$ . Development of soil organic matter (through the formation of an O-horizon in the soil, for instance) would increase 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<sup>156</sup>. To be balanced with a comparable oxygen source from carbon burial in the ocean,  $O_2$  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 NPP, they are likely to have increased the ability of the biosphere to transform the atmosphere.

Carbon isotopes and the biosphere

No tool has played as large a role in reconstructing changes in the scope of the biosphere through time as carbon isotopes<sup>158–162</sup>. The evolution of  $\delta^{13}C_{\text{carb}}$  values is linked to the ratio of carbonate-to-organic carbon burial in the global ocean<sup>162</sup>. Following principles of mass balance,  $\delta^{13}C_{\text{carb}}$  can be used to calculate the fraction of carbon buried as organic matter ( $f_{\text{org}}$ )<sup>8,162</sup>. Because  $f_{\text{org}}$  is linked to primary productivity, it can theoretically be used to track primary productivity through time<sup>8</sup>.

In the marine carbonate record, the global  $\delta^{13}C_{\text{carb}}$  curve lacks any secular trend on a billion-year time-scale and is characterized instead by perturbations around a baseline value of about 0‰ (REFS<sup>163,164</sup>) (FIG. 1). Within the traditional interpretive framework<sup>8</sup>, this observation suggests that  $f_{\text{org}}$  has been at 20–25% for the majority of Earth’s history. Notable exceptions include the Palaeoproterozoic Lomagundi–Jatuli Excursion, the largest and longest-sustained positive carbon-isotope excursion ( $\delta^{13}C_{\text{carb}} > 10\text{‰}$  for up to 200 million years), which, at face value, suggests  $f_{\text{org}}$  greater than 50% (REFS<sup>165,166</sup>), and the negative Shuram Excursion in the Neoproterozoic ( $\delta^{13}C_{\text{carb}} < 10\text{‰}$  for several million years), which would require negative  $f_{\text{org}}$  to satisfy mass balance<sup>167,168</sup> (FIG. 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 ( $\Delta_B$ ), making  $f_{\text{org}}$  the sole driver of variation in  $\delta^{13}C_{\text{carb}}$  (REF.<sup>162</sup>).

Although it has been long debated, there has recently been increasing appreciation that  $\delta^{13}C_w$  has changed substantially throughout Earth’s history<sup>168,169</sup>. Foremost, several recent modelling studies have proposed that  $\delta^{13}C_w$  has been controlled by  $pO_2$  for much of Earth’s early history, as low atmospheric  $O_2$  concentrations would have limited the oxidative weathering of sedimentary organic carbon<sup>168,169</sup>. Specifically, a reduced flux of isotopically light organic carbon to the oceans would have increased  $\delta^{13}C_w$  requiring reduced  $f_{\text{org}}$  to maintain baseline  $\delta^{13}C_{\text{carb}}$ . 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<sup>168,169</sup>. In order to reproduce the  $\delta^{13}C_{\text{carb}}$  record with commonly utilized  $pO_2$  estimates (such as 1% present atmospheric level) and current

## Weatherable shell

The uppermost layer of the lithosphere subject to weathering.

organic-carbon-oxidation modelling schemes,  $f_{\text{org}}$  must have been roughly 10% during low- $p\text{O}_2$  intervals such as the Archean and mid-Proterozoic<sup>168,169</sup>. This  $f_{\text{org}}$  value is much lower than the widely accepted range 20–25% and implies a much smaller global biosphere than previously recognized<sup>170</sup>.

Further, if  $\delta^{13}\text{C}_w$  is allowed to vary with  $p\text{O}_2$ , a long-term increase in  $f_{\text{org}}$  keeping pace with atmospheric oxygenation could conceivably be ‘hidden’ within the stable  $\delta^{13}\text{C}_{\text{carb}}$  record<sup>169</sup>. Put another way, taking any estimate for Proterozoic  $p\text{O}_2$  between 0.1 and 10% present atmospheric level (FIG. 1), the amount of organic-carbon burial — and, by inference, the extent of primary productivity — would have been much less than in the modern for the same carbonate  $\delta^{13}\text{C}$  value<sup>171</sup>. However, if sedimentary organic matter is not efficiently subducted and removed from the upper continental crust, inhibited organic-carbon burial could lead to substantial growth of the crustal organic-carbon reservoir, as in REF.<sup>168</sup>. This steady growth of the crustal organic-carbon reservoir in the Earth’s weatherable shell under low-oxygen conditions might provide an explanation for the seemingly counter-intuitive observations recorded by some shale compilations of higher organic-carbon contents in Proterozoic shales relative to Phanerozoic shales<sup>79</sup>, in spite of commonly predicted lower rates of organic-carbon burial during the former interval<sup>81,82</sup>. However, whether shale compilations accurately track the composition of the upper continental crust remains a subject of contention. Therefore, testing whether geologic archives record signals consistent with extensive cycling of petrogenic organic carbon is an obvious target for future work.

### Conclusions and future directions

We propose, based 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<sup>172</sup> need to be revisited: first, that primary productivity in the marine realm was dominated by oxygenic photosynthesizers for most of Earth’s history; second, that the marine realm was the focus of primary productivity prior to the rise of land plants; third, that the rise of eukaryotes fundamentally reshaped the biological pump and global carbon cycling; and, fourth, that primary productivity and organic-carbon burial were roughly constant through most of Earth’s history. Instead, we suggest that marine

primary productivity from oxygenic photosynthesizers increased dramatically through time<sup>82,173,174</sup>, in part because key nutrients (P) were taken up by anoxygenic photosynthesizers for most of Earth’s history when predominantly reducing conditions prevailed in the ocean interior<sup>4,28,69,70,82</sup>. However, the extent of primary productivity in terrestrial settings during 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. Indeed, we argue that terrestrial ecosystems have been an important locus of primary productivity for the majority of Earth’s history, not just after the rise of land plants. We further suggest that the presence of larger cell sizes in primary producers (associated with the rise of algae) or faecal-pellet production (associated with the rise of animals) might not have dramatically altered the marine carbon cycle. Indeed, studies of the modern marine carbon fluxes 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 behaviour of marine aggregates<sup>148</sup>. 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 Review highlights more unknowns and outstanding questions about the long-term history of Earth’s biosphere than it does present indisputable conclusions. We see 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. Within these aims, we feel that the most exciting advances are going to come from closer coupling of mechanistic 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.

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#### Author contributions

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