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

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15 **We provide a new perspective on how the structure of Earth's biosphere and its capacity to**

16 **alter geochemical cycles have changed over its >3.5 billion-year history. We review evidence**

17 **that oxygenic photosynthesis evolved relatively early in Earth's history, but contend that**

18 **marine primary productivity was low, surface oxygen was scarce, and marine anoxia was**

19 **prevalent for the majority of Earth's history. Anoxygenic phototrophs were likely a key part**

20 **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

41   is likely that developing observational techniques[5] will permit us to remotely explore the

42   atmospheric composition of Earth-like planets. A solid knowledge of how our biosphere has

43   reshaped Earth's surface and atmosphere and what features constitute robust biosignatures will be

44   essential for interpreting these data[5]. Atmospheres integrate almost all planetary-scale processes,

45   both biotic and abiotic, and are possible to observe from afar. Much recent focus has, therefore,

46   been on the mechanisms that drive development of atmospheric biosignatures.

47

48   The most heated debates about Earth's atmospheric evolution, historically, have focused on when

49   and why Earth's atmosphere became well oxygenated[6,7]. It is now generally accepted that Earth

50   has undergone a protracted, several-billon-year oxygenation[6], but there is no sign of emerging

51   consensus about what role biotic innovations and the evolution of solid Earth processes played in

52   key steps in this oxygenation. It is clear that atmospheric oxygen levels were low in the Archean,

53   generally higher in the Proterozoic, and higher still across much of the Phanerozoic (Figure 1).

54   There is also general agreement that this progressive rise in oxygen levels was essential for the rise

55   of many lineages of eukaryotic life, including animals[6,8]. However, there is still debate about nearly

56   all aspects of the history of this oxygenation, including the timing, pace, and impact on the

57   biosphere. For example, there is now agreement that oxygen first rose to appreciable levels

58   between 2.4 and 2.3 Ga[9], but the trigger for this event, either a shift tectonic processes[10] or the

59   onset of biological oxygen production by cyanobacteria[11], or removal of previous brakes on

60   cyanobacterial proliferation[12], remains contested. There is agreement that carbon dioxide levels

61 have gradually decreased through time, maintaining a clement climate, with noteworthy but short-

62 lived climate extremes. However, there remains no coherent view of the role that the biosphere

63 played in driving climate shifts[13,14].

64

65 Debate stems, in part, from poor constraints on the timing of many key biotic novelties (the

66 formation of newly individuated characters and features) and innovations (when these novelties

67 began to alter and shape the structure or function of ecological networks)[15]. Even the timing of the

68 evolution of 'highly influential novelties'—new metabolisms or basic cell types[15]—remains a

69 strongly debated aspect of the history of life on Earth. Similarly, there is growing appreciation that

70 rates of biological carbon fixation have increased through Earth's history, but constraints on rates

71 of biospheric productivity through Earth's history are limited and accompanied by large error

72 estimates[16]. Nonetheless, the timeline and history of life on Earth is coming into better focus.

73 Recent efforts have revisited when particular groups of organisms appeared on Earth and have

74 sought to constrain when and how they first began to shape Earth's surface environments and

75 global biogeochemical cycles—a level of emergence we refer to here as "biotic scope".

76

77 Here, we present a new view of the evolution of the structure and scope of life on our planet. We

78 discuss the planetary-scale evolution of Earth's biosphere in terms of the impact of key biotic

79 innovations on global biogeochemical cycles. We argue for the relatively early evolution of

80 oxygenic photosynthesis and a persistent dominance of a marine biosphere characterized by

81   anoxygenic phototrophs and chemotrophs. We also challenge the standard view that the rise of

82   eukaryotes to ecological prominence fundamentally altered marine nutrient cycling. We argue that

83   although the emergence of plants had a major impact on the global carbon cycle, terrestrial primary

84   productivity was appreciable or even dominant, well before the emergence of land plants.

85   Collectively, this represents an alternative view of the co-evolution of Earth and life that is

86   grounded in current empirical records and mechanistic models. However, we highlight that there

87   are many aspects about this view that remain poorly constrained.

88

89   **Early oxygen**

90   The evolution of oxygenic photosynthesis, potentially as far back as 3.8 billion years ago (Ga)[1,17],

91   enabled a dramatic increase in the size and complexity of Earth's biosphere (Figure 2)[18]. This

92   evolutionary singularity was the first step in Earth's progressive oxygenation and subsequently

93   allowed organisms to colonize essentially all Earth surface environments. Photosynthesis is the

94   only process that releases appreciable oxygen to Earth's surface and leads to the accumulation of

95   free O_2, which is required by animals and other complex life forms for respiration and the

96   biosynthesis of key macromolecules[4]. The buildup of oxygen also allowed for the formation of an

97   ozone layer, drastically reducing the harmful effects of UV radiation. There has been continuous

98   debate as to whether the evolution of oxygenic photosynthesis immediately triggered a switch to a

99   more oxygenated atmosphere at the end of the Archean, or whether there was a protracted and

100   delayed increase in atmospheric oxygen levels[19–21]. Current estimates for the timing of the onset

101   of oxygenic photosynthesis span over a billion years of Earth's history, ranging from prior to 3.8

102   Ga[22] (the age of the oldest sedimentary rocks) to 2.4–2.3 Ga[11]. The latter date is coincident with

103   the first permanent rise of atmospheric oxygen, the "Great Oxidation Event" or GOE and thus

104   represents the absolute youngest age for the onset of oxygenic photosynthesis[9].

105

106   While controversial, a wealth of inorganic geochemical information now suggests appreciable

107   traces of oxygen in Earth's surface environments hundreds of millions, or perhaps more than a

108   billion years, before the GOE[21,23–27]. Some of the earliest such evidence comes from Mo isotopes[23]

109   and Mo and other metal elemental distributions in sedimentary rocks[24,25] deposited in the

110   Neoarchean, more than 100 Myr prior to the currently accepted date of ~2.4 Ga for the GOE[9].

111   Evidence for an even earlier rise of oxygenic photosynthesis comes from the distributions and

112   isotope values of Cr, U, and Mo in 3.0 Ga paleosols and IFs from the Pongola Supergroup[21,26,27].

113   This interpretation is further supported by broadly contemporaneous sulfur isotope systematics

114   that point toward extensive oxidative sulfur cycling[28]. While a comprehensive review of all

115   evidence for pre-GOE oxygen is beyond the scope of this review, it is worth noting that there are

116   a number of other examples between the Mesoarchean and the GOE, and a few, albeit more

117   controversial, examples before 3.0 Ga[29,30]. Previous geochemical evidence of free oxygen has been

118   controversial, however, and tracking early oxygen production by inorganic means has been

119   hindered by concerns similar to those that plagued biomarker work, which was previously the most

120   widely touted evidence of early oxygen[31,32]. There are concerns about whether geochemical

121 records uniquely fingerprint biological oxygen production and if geochemical records are truly

122 recording paleoenvironmental signals. For instance, signals of early oxygen could instead be tied

123 to secondary oxidation during surface weathering under today's oxygen-rich atmosphere[33]. In

124 short, despite great effort, it has proven difficult to ensure that geochemical signatures

125 diagnostically reveal the presence of oxygenic phototrophs[34,35] in past environments.

126

127 The most recent debate about when oxygenic photosynthesis evolved has focused on whether or

128 not manganese (Mn) oxides in the pre-GOE rock record can be uniquely ascribed to Mn(II)

129 oxidation with free oxygen produced through oxygenic photosynthesis[21,36]. There was, without

130 question, significant Mn(II) oxidation in the Archean[37], but it is less clear whether oxidation

131 required molecular oxygen. Recent work[19] suggested there could have been extensive anaerobic

132 Mn(III,IV) oxide production, challenging earlier views that oxidative geochemical signals reflect

133 the antiquity of oxygenic photosynthesis. Thermodynamic and basic mass balance considerations,

134 however, question the relevance of these new findings to Archean oceans, and the recent discovery

135 of anoxic microbial Mn(II) oxidation is potentially no more significant than the longstanding

136 observation of photochemical Mn(II) oxidation[38]. Photochemical Mn(II) oxidation has been

137 generally regarded as an essentially inconsequential process in the Archean oceans, as Fe cycling

138 ultimately dictates the fate of Mn oxides in early marine settings[38]. Further, it is not clear if recent

139 work on anoxygenic photosynthesis dependent Mn oxidation[19]—based on enrichment cultures

140 from a sulfidic lake—is relevant to the Archean oceans. Given the lack of any known high-

141   potential photosynthetic reaction center in the photosynthetic microorganisms in the enrichment

142   culture (e.g., green sulfur bacterium *Chlorobium* sp.), oxidation of manganese using elemental

143   sulfur is the only thermodynamically feasible Mn oxidation pathway. However, under reasonable

144   Archean conditions (e.g., pH = 7^{132}, [Mn] = 100µM[133], HS$^-$ and S^0 = 10µM[47]) the free energy of

145   this reaction is likely not high enough to support microbial metabolism (ΔG = -18 kJ/mol for

146   birnessite formation and 71 kJ/mol for pyrolusite formation[39–42]). These energy yields are both

147   below the commonly reported minimum requirement of about -15 to -20 kJ/mol for anaerobic

148   microbial metabolisms[135]. In the very likely case that [HS$^-$] > [S^0], energy yields from these

149   reactions are even lower.

150

151   Pinpointing when oxygenic photosynthesis evolved is one of the most important questions about

152   the history of Earth's biosphere. Although there is currently no consensus within the community

153   as to when this novelty arose, there is a clear path towards resolution—researchers pushing for the

154   early (pre-GOE) rise of oxygenic photosynthesis need to continue to carefully consider anoxic

155   oxidation pathways and the effects of secondary alteration on oxidation proxies[33]. At the same

156   time, researchers skeptical of the early rise of oxygenic photosynthesis need to make efforts to

157   ensure that their own observations are placed into a framework that is consistent with the geologic

158   record. In the context of the most recent debate[19], we argue that simple consideration of

159   thermodynamics and mass fluxes can be extremely powerful. With that in mind, we argue that

160   recent challenges to an early rise for biological oxygen production still fall well short of providing

161　the cogent argument necessary for overturning the current paradigm of an early (>3.0 Ga) rise of

162　oxygenic photosynthesis.

163

164　**Anoxygenic photosynthesis**

165　The rise of oxygenic photosynthesis was, without question, a major event in Earth's history, but

166　anoxygenic (i.e., non-oxygen producing) phototrophic microbes likely played a key role in fueling

167　the biosphere and driving planetary evolution throughout most of Earth's ~3 billion-year early

168　history[20,43–45]. Phylogenetic analyses almost unanimously show that anoxygenic photosynthesis

169　evolved prior to oxygenic photosynthesis (e.g., [46,47]; however see also[48]), and thus likely had

170　exclusive and unfettered access to the photosynthetic niche for hundreds of millions of years prior

171　to the emergence of oxygenic photosynthesis[20,43–45]. Models suggest that the emergence of

172　anoxygenic photosynthesis would have energized the biosphere, leading to global productivity far

173　greater than an exclusively chemosynthetic biosphere[44,49]. Nonetheless early in Earth's history this

174　anoxygenic photosynthetic biosphere would have been primarily responsible for interacting with

175　geophysical processes to regulate atmospheric composition and climate (Figure 2a)[20,45,50] and

176　anoxygenic photosynthetic likely played a key role in regulating global biogeochemical cycles

177　untiil the ocean became fully oxygenated[20,49].

178

179　Anoxygenic photosynthesis in the marine realm is driven by a suite of inorganic and organic

180　electron donors that, together with bio-essential nutrient elements like nitrogen and phosphorus,

181   limit rates of photosynthesis[45]. Extant anoxygenic phototrophs are able to grow photosynthetically

182   with Fe(II), H_2, and H_2S, as well as some organic compounds such as acetate and pyruvate[44,45] as

183   electron donors. Considering the availability of these electron donors in seawater throughout

184   Earth's history, Fe(II) and H_2 would likely have been the most widely utilized throughout most of

185   the Archean and Paleoproterozoic. Sulfide (H_2S) could have been episodically abundant,

186   particularly during punctuated intervals in the mid to late Proterozoic[44,51,52]. The availability of

187   organic electron donors has received less attention. While they may have been relatively abundant

188   in Earth's earliest history, the emergence and proliferation of heterotrophic bacteria and

189   methanogens would likely have consumed organic compounds making them less available as

190   primary electron donors for anoxygenic photosynthesis, although this idea should be further

191   explored.

192

193   Both Fe(II) and H_2 are supplied through submarine volcanism and associated hydrothermal activity

194   at rates that would support appreciable anoxygenic photosynthesis, particularly when marine

195   sulfate concentrations were low[44,49,53]. For instance, hydrothermal Fe(II) fluxes could have been

196   greater than 40 Tmol/yr prior to the GOE[54]. This flux is more than sufficient to account for the

197   estimated Fe burial fluxes associated with the largest banded iron formations (BIFs) deposited in

198   the Neoarchean to Paleoproterozoic[55]. To place this number into a biological context, we can

199   assume that Fe(II) was oxidized by photoferrotrophs (photoautotrophs utilizing iron as their

200   primary electron donor) in the following reaction:

201 $$4Fe^{2+} + CO_2 + 11H_2O \rightarrow CH_2O + 4Fe(OH)_3 + 8H^+$$

202   Given that this metabolism theoretically yields a molar ratio of 4Fe:1C, and assuming maximum

203   efficiency in Fe(II) oxidation, then 40 Tmol/yr Fe(II) would generate 10 Tmol/yr of organic carbon

204   via photoferrotrophy. This amount of net primary productivity (NPP) is lower than the NPP of a

205   hypothetical marine biosphere dominated by H_2-based phototrophy, estimated at 20-90

206   TmolC/yr[56]. However, iron is rapidly recycled through respiration of organic matter derived from

207   anoxygenic photosynthesis. Therefore, the 10 Tmol/yr of organic carbon produced via

208   photoferrotrophy reflects a very conservative estimate of the extent of Fe(II)-based productivity.

209   This tendency for recycling, however, also highlights that physical separation of oxides and

210   organic matter are needed for preservation of either of these products of photoferrotrophy in the

211   sedimentary record[54].

212

213   Sulfide can also be used in anoxygenic photosynthesis and is derived from similar pathways as

214   Fe(II). Sulfide can come from hydrothermal systems, albeit at lower rates than Fe(II)[57]. Given

215   these lower fluxes, sulfide likely played a more limited role as a primary electron donor for

216   anoxygenic photosynthesis across most of Earth's history[44,49]. Concordantly, H_2S based

217   phototrophy is estimated to have generated 4.7-6.7 Gmol C/yr[56], several orders of magnitude less

218   than either H_2- or Fe(II)-based phototrophy. However, H_2S is also a product of dissimilatory sulfate

219   reduction and so could have risen to prominence with the onset of strong oxidative weathering on

220   the continents and the associated increase in sulfate fluxes to the oceans following the GOE[58–60].

221 Under widespread marine anoxia during the Proterozoic, sulfate reduction would have supported

222 appreciable secondary H_2S production. At times of low marine Fe(II) concentrations, episodic and

223 localized photic zone euxinia (anoxic and sulfidic conditions) could have supported extensive

224 secondary H_2S dependent anoxygenic photosynthesis[61]. Nonetheless, given evidence for

225 widespread ferruginous conditions throughout most of the Precambrian[62], the supply rate and

226 availability of Fe(II) would have placed the primary constraints on rates of anoxygenic

227 photosynthesis (Figure 2a).

228

229 Like all life, anoxygenic photosynthetic organisms require a number of bio-essential elements,

230 including the macronutrients nitrogen, phosphorus, and sulfur as well as various micronutrients.

231 The availability of these elements in the water column places a secondary constraint on rates of

232 anoxygenic photosynthesis and the size and activity of the marine biosphere. Organismal nutrient

233 quotas differ, but in the modern ocean roughly follow a defined stoichiometry that is well-

234 represented by the Redfield ratio for macronutrients (106:16:1 C:N:P)[63]. Conservation of electrons

235 by photosynthesis also means that there is a stoichiometric relationship between carbon fixed into

236 biomass and the electron donor (e.g. Fe(II) or H_2) used and oxidized. There is also, by extension,

237 a stoichiometric relationship between electron donor supply and nutrient uptake that dictates

238 whether nutrients or electron donors limit anoxygenic photosynthesis. For example, when Fe(II)

239 is used as the electron donor, the molar ratio of Fe(II) oxidized to carbon fixed (4:1) translates to

240 a ratio of 424:1 Fe(II) oxidized per P needed. This means that supply rates of P less than 1/424th

241   that of Fe(II) would lead to a biosphere limited by P, assuming negligible P recycling[64]. Similar

242   arguments could be made for N, although N can be biologically fixed from an enormous reservoir

243   of N_2 in the atmosphere (and corresponding aqueous N_2 in the water column). Nitrogen limitation

244   (where N was the ultimate limiting nutrient, *cf.,*[65]) would have been less likely following the

245   emergence of nitrogen fixation, which molecular phylogeny suggests took place in the early

246   Archean[66]. Isotopic evidence has also be used to suggest a minimum age of 3.2 Ga[67]. Many extant

247   anoxygenic phototrophs have the metabolic potential for N_2 fixation, including those that grow

248   with Fe(II) and H_2 as electron donors[68]. Recent analyses further predict that stem-group

249   photoferrotrophs likely had the capacity to fix N_2[69], though it results in slower growth rates than

250   when exogenous N is abundant.

251

252   The evolution of oxygenic photosynthesis (see above), would have partly liberated total primary

253   productivity from limitations imposed by electron donor availability, shifting limitation towards

254   nutrient (P) availability[49,70]. The electron donor for oxygenic photosynthesis is water, which is

255   almost infinitely available in all aquatic environments. The emergence of oxygenic photosynthesis

256   would thus have allowed the biosphere to utilize any P that was still remaining in solution after

257   anoxygenic photosynthesis had consumed electron donors (primarily Fe(II) and H2). Hence the

258   biosphere as a whole would have likely shifted into a state of perpetual P limitation (Figure 2b).

259   At the same time, the emergence of oxygenic photosynthesis would have initiated strong

260   competition with anoxygenic photosynthesis for illuminated niche space[49,71]. Based on inference

261 from the physiology of extant anoxygenic phototrophs, which are exceptionally good at growing

262 under low-light conditions, relative to oxygenic phototrophs, anoxygenic phototrophs would have

263 generally outcompeted their oxygenic counterparts as long as electron donor supplies were

264 sufficient[49]. Anoxygenic phototrophs can reside deeper in the water column and have first access

265 to nutrients upwelled from the deeper ocean. Oxygenic phototrophs, restricted to shallower

266 environments above the anoxygenic phototrophs, would have been dependent on excess nutrients

267 that escaped consumption by anoxygenic phototrophs due to electron donor limitation, or those

268 supplied from above through atmospheric deposition and local riverine input. The stoichiometry

269 of electron donor to nutrient supply would, therefore, have played a key role in regulating the

270 balance between the activity of anoxygenic and oxygenic photosynthesis. In addition, the presence

271 of potential 'toxins' to cyanobacteria need to be considered in this balance. If anoxygenic

272 phototrophs did not quantitatively remove dissolved Fe(II), it could have inhibited cyanobacteria

273 productivity, in part because of oxidative stress as a result of reactions between Fe(II) and oxygen

274 that produce reactive oxygen species[12]. Accordingly, the proliferation of oxygenic

275 photosynthesizers could have been delayed until either electron donor/toxin supplies collapsed,

276 nutrient supply rates were enhanced, the redoxcline descended below the photic zone, or some

277 combination of the above. The emergence of oxygenic photosynthesis would have further

278 energized the biosphere through concurrent modes of photosynthesis, and would have created a

279 photosynthetic biosphere essentially entirely limited by nutrient supply[70]. However, the presence

280 of anoxygenic photosynthesis in a low-oxygen world with largely anoxic oceans provides a means

14

281   to limit the scope of oxygenic photosynthesizers, and thus a way to stabilize the Earth system in a

282   low oxygen state[49].

283

284   Over the past few years, there has been an increasing number of suggestions that total marine

285   primary productivity by oxygenic photosynthesizers has increased over Earth's history[16,70,72–74].

286   Developing more robust constraints on primary production will require more work to answer two

287   key questions: (1) how nutrient and substrate inventories and fluxes changed through Earth's

288   history; and (2) how the ratio of primary productivity by anoxygenic and oxygenic phototrophs

289   has evolved. These questions can best be answered through models that are quantitatively tethered

290   to molecular biological histories and material fluxes recorded in the rock record. Nonetheless, it

291   seems unavoidable given the emerging view Precambrian surface environments (i.e. widespread

292   and even shallow marine anoxia[75]), that anoxygenic phototrophs were an important part of the

293   biosphere—which would have limited the scope of oxygenic photosynthesizers.

294

295   **Life on land**

296   Much of the past and current research on Earth's early biosphere is directed at understanding the

297   evolution of marine phototrophs—particularly cyanobacteria—and how they shaped the oxygen

298   and carbon cycles. The community has, with key exceptions (e.g., [76–83]), largely ignored the

299   importance of terrestrial ecosystems (by 'terrestrial' we mean all continent-based environments,

300   subaerial or subaqueous, including uplands, arid lands, floodplains, lakes, and rivers). While much

301   of the debate over cyanobacterial origins rests on evidence from the marine sedimentary record,

302   there have also been multiple recent suggestions that cyanobacteria (or their oxygenic

303   photosynthetic ancestors) evolved early and were common in terrestrial settings[77,78].

304

305   There are multiple lines of evidence for life on land prior to the mid-Paleozoic despite a strong

306   preservation bias against microbial remains in continental environments[84]. Microbially induced

307   sedimentary structures (MISS) in continental deposits are some of the earliest records of life on

308   Earth, with evidence for robust mats in shallow, sandy, periodically exposed rivers by at least 3.2

309   Ga[77,85]. Moreover, element mobility patterns in ancient soils (paleosols) suggest weathering by

310   organic acids—and consequently the presence of life on land—by at least 2.76 Ga[86,87]. The dearth

311   of sedimentological evidence for microbial mats on land in the Precambrian is likely a consequence

312   of their inability to stabilize sediment in the energetic depositional environments typical of

313   continental settings.

314

315   Independent of the sedimentary record, molecular data have been suggested to provide evidence

316   for a terrestrial origin of cyanobacteria (however, see also [88]). Phylogenomic analyses of modern

317   cyanobacterial diversity may suggest a freshwater origin for the clade and indicate that filamentous

318   cell types, a structural novelty enabling mat formation, originated soon after[89]. By contrast, these

319   same analyses recover marine planktonic cyanobacteria as derived clades with multiple

320   independent origins from an ancestral terrestrial or freshwater aquatic ecotype. Although still rare

321   compared to clear evidence for microbial life in marine settings, these records—among many

322   others—provide the tantalizing suggestion that, as a community, we may have underappreciated

323   the role of terrestrial ecosystems in shaping Earth's biogeochemical cycles.

324

325   Modern mats are consortia of metabolically diverse prokaryotes in addition to cyanobacteria[90] and

326   it is therefore possible that the communities responsible for microbial signatures in early terrestrial

327   settings differed significantly from their modern counterparts. While sedimentological and

328   geochemical indictors for life on land may well have been produced by chemotrophs or anoxygenic

329   phototrophs[91], it is unclear whether these organisms could have formed globally extensive

330   terrestrial mats. Anoxygenic phototrophs make up important albeit structurally minor components

331   of some modern terrestrial cyanobacterial mats[83] and can form their own mats under rare instances

332   of photic zone anoxia in subaqueous environments[92]. Terrestrial iron oxidizers, in particular, form

333   land-based mats[93]. Further, in the Archean, in the absence of an ozone layer photosynthetic

334   organisms would have experienced strong UV stress[94,95]. Nonetheless, considering redox balance,

335   mat ecosystems in which cyanobacteria were the key primary producers represent the strongest

336   potential contributors to life in continental settings throughout the Precambrian.

337

338   Although the earliest direct evidence for terrestrial mats comes from river margins[77], modern mats

339   span a vast range of subaqueous and subaerial environments (Figure 3). Today, biological soil

340   crusts (BSC) cover appreciable portions of arid and semi-arid lands where severe water limitation

341   inhibits the growth of vascular plants[96], this includes some of the driest areas on the modern Earth

342   such as the Atacama Desert in Chile[97] and the McMurdo Dry Valleys of Antarctica[98]. These mats

343   survive by producing abundant extracellular polysaccharides (EPS) that bind loose materials

344   together to form a cohesive crust, which both maintains hydration levels and protects against

345   ultraviolet radiation[99]. In the absence of competitive exclusion from plants, the majority of Earth's

346   habitable land surface could have been covered by microbial mats similar to modern BSC in terms

347   of overall metabolic structure, if not composition. The success of BSC in extreme environments

348   today gives reason to suspect that mats would have covered appreciable portions of the land surface

349   prior to the emergence of vascular plants, and would have been able to survive even in the absence

350   of ozone shielding prior to the GOE[99,100]. Critically, there is high phylogenetic diversity in these

351   mats—indicating that potential to colonize BSC environments is broadly distributed and thus

352   likely not a late stage biotic innovation[83,90]. Marine environments in the Precambrian have been

353   commonly assumed to be nutrient-poor (e.g., [72]); in contrast, regolith on land would have provided

354   an abundant source of bio-essential elements (foremost P) for terrestrial ecosystems assuming

355   organisms had the capacity to access them in dissolved form via biologically-mediated mineral

356   dissolution[86] and even store them intracellularly[101]. The biogeochemical implications for

357   widespread mats on land in the Precambrian are substantial, in part because the oxygenic capacity

358   of modern benthic cyanobacteria is tremendous; nowhere on the modern Earth is free O_2 found in

359   greater excess than in photosynthetic mats dominated by cyanobacteria[83,102]. Consequently,

360   terrestrial mats in the Precambrian may have comprised a much larger fraction of global gross and

361   net primary productivity than traditionally envisioned.

362

363   Quantifying global NPP from terrestrial microbial mats on the early Earth (and the flux of O_2 from

364   mat surfaces) is highly dependent on estimates of their aerial coverage and O_2 production rates per

365   unit area. Environmental niche modeling puts modern BSC coverage at 12% of today's land

366   surface, and up to 24% in the absence of anthropogenic disturbance[96]. By some estimates, these

367   mats account for 7% of terrestrial NPP (325 Tmol C/yr) and potentially half of terrestrial nitrogen

368   fixation (3.5 Tmol N/yr)[103,104]. Much of this area is arid land where competition with plants and

369   grazing pressure from animals is minimal, but where low soil moisture also limits surface biomass

370   and productivity (microbial mat O_2 production is typically < 0.2 nmol $cm^{-2} s^{-1}$ in deserts versus an

371   average of 0.4 nmol $cm^{-2} s^{-1}$ in fully water saturated environments)[96,102,105,106]. In the absence of

372   these ecological constraints in the Precambrian, mats would presumably also have filled all

373   available ecospace in more humid regions, making their contribution to global primary

374   productivity much greater.

375

376   The simplest approach to estimating the terrestrial biosphere's contribution to atmospheric O_2

377   fluxes during the Proterozoic is to multiply a flux range in modern mats by the total continental

378   area they may have covered[83,102]. Today barren land, including unvegetated deserts and

379   permanently ice-covered regions, comprises roughly 25% of the total land surface[107]. This leaves

380   75% as a potential upper limit for mat coverage. However, given that ice-free conditions appear to

381   have persisted for the majority of Earth's history[4], the upper limit for habitable land area would

382   likely have been higher. A lower limit of mat coverage can be placed by assuming that mats would

383   have been restricted only to the equatorial rain belt, although the success of modern BSC in arid

384   environments makes this unlikely. Based on current estimates of tropical rainforest cover, about

385   10% of total land area lies within this high-rainfall, high-productivity region[107]. A stochastic

386   estimate using a distribution of O_2 production rates from modern mats and assuming a very

387   conservative land surface coverage of 10-50% and a near-modern total exposed land area[108,109]

388   gives an average terrestrial O_2 and equivalent organic carbon production rate (i.e., NPP) of

389   approximately 18,000 Tmol/yr (Figure 4), which is surprisingly several times modern terrestrial

390   NPP[110,111]. By comparison, the most recent estimates for marine NPP during the Proterozoic are

391   350-2,100 TmolC/yr[74]. There are multiple ways to reduce this estimate—for example considering

392   seasonality in parts of the globe, or considering that mats may have been entirely lithotrophic or

393   dominated by anoxygenic phototrophs, and therefore would have produced significantly less

394   oxygen relative to their modern counterparts (although this does not preclude significant carbon

395   fixation by anoxygenic phototrophs).

396

397   Given that field observations support a link between soil moisture and oxygen production in

398   modern BSC[105,106], a potentially more rigorous estimation of O_2 production rates for terrestrial

399   microbial mats can be derived from calculations of global surface soil moisture distributions.

400 Combining photosynthetic rates measured in modified natural settings[105] with outputs of ground

401 temperature and water content in the top 10 cm of soil from historical climate models yields an

402 average O_2 production rate of 0.0172 nmol cm^{-2} s^{-1} and global production of 681 Tmol/yr (Figure

403 5), which is likely an underestimate considering that this predictive model consistently

404 underestimates point source fluxes from microbial mats that have been measured in the

405 field[83,112,113]. Using monthly mean ground temperatures and water contents from June and

406 December results in a seasonal range from 0.0154-0.0197 nmol cm^{-2} s^{-1} and 615-766 Tmol/yr, that

407 monthly variability in ground temperature and soil moisture would strongly influence global O_2

408 production from a terrestrial biosphere dominated by microbial mats.

409

410 Secular changes in global surface temperature and precipitation across Earth history likely drove

411 even greater variation in O_2 production. However, a lack of reliable precipitation proxies in deep

412 time currently hampers any attempt to quantify this variability[114], forcing us to rely on less direct

413 inferences. From one perspective, water vapor would not have penetrated as deeply into

414 continental interiors in the absence of vascular plants that can store and release water via

415 transpiration[115], meaning that global soil moisture availability would have been lower than modern.

416 However, this very low-precipitation system in a pre-plant world is unlikely to have led to a stable

417 global carbon cycle; without high soil CO_2 levels linked to plant biomass degradation, atmospheric

418 CO_2 levels in a low-precipitation world would have increased (i.e., the CO_2 sinks would not have

419 balanced the sources), leading to warming climate state and thus more precipitation (see Isson et

420   al., 2020[13]). In a world without any terrestrial biomass, it has been estimated that rainfall on

421   average must have been at least 3-4 meters per year to deliver enough dissolved CO_2 to sustain the

422   rates of silicate weathering necessary to stabilize Earth's climate[13]. Because we conservatively

423   assume modern precipitation levels, the actual O_2 production rates and NPP of Earth's earliest

424   terrestrial biosphere were likely higher than the estimates we provide in Fig. 3. Our estamites of

425   terrestiral NPP have large uncertainties. Nonetheless, using modern terrestrial mat-forming

426   cyanobacteria as a guide, it seems unavoidable that these terrestrial ecosystems were a major

427   component of the Precambrian biosphere. This leads us to conclude that terrestrial ecosystems may

428   have accounted for the majority of primary productivity for much of Earth's history, and

429   potentially by a substantial margin prior to the rise of vascular plants.

430

431   While a departure from the standard view, a higher-than-modern NPP may not be unreasonable

432   considering that rapid turnover in microbial ecosystems allows high productivity relative to

433   biomass[116]. Prokaryotic cells live on the order of days, while vascular plants regularly live tens of

434   years and sometimes even thousands[117]. As a result, up to 70% of biomass in vascular plants does

435   not contribute to primary productivity on an annual basis; this results in plants producing only half

436   of global NPP despite making up over 80% of the planet's biomass[117]. An exclusively microbial

437   terrestrial biosphere would almost certainly have been much smaller than modern in terms of

438   standing biomass, but not necessarily in terms of gross or net primary productivity. We must also

439   note that high NPP in terrestrial microbial mats does not imply an equal importance in regulating

440   atmospheric pO$_2$. On geologic timescales, the persistence of free O$_2$ in the atmosphere can only be

441   sustained by the long-term burial of organic carbon (C$_{org}$) in marine sediments. Given the high

442   reactivity of labile organic matter produced by microbial mats and long oxygen exposure times

443   during transport in surface and groundwaters, most C$_{org}$ will reoxidize before reaching the oceans,

444   consuming much of the O$_2$ produced during photosynthesis. The concept of enhanced oxidation

445   potential in terrestrial, relative to marine, environments is well established[118]. In this regard,

446   terrestrial primary productivity is likely to have a strong effect on the short term oxygen and carbon

447   cycles, but a relatively minor effect on Earth's long-term oxygenation. However, these short-term

448   fluxes can strongly impact geochemical processes that become preserved in the rock record,

449   including the mobility of redox-sensitive trace metals used to reconstruct changes in atmospheric

450   pO$_2$ through time[102] and the generation of triple-oxygen isotope anomalies used to estimate the

451   long-term productivity of the biosphere[119]. Further, these mats may have been important sources

452   of methane, helping provide an explanation for the presence of a stably warm Proterozoic climate

453   without extremely elevated CO$_2$ levels[120].

454

455   While these O$_2$ production estimates apply to the Proterozoic, estimating terrestrial NPP for the

456   Archean proves more difficult. Crustal growth models suggest lower continental exposure prior

457   to the hypothesized onset of modern-style plate tectonics before 2.5 Ga[109], and very limited

458   exposure prior to 3.0 Ga[108], constraining terrestrial O$_2$ fluxes considerably[83]. Additional

459   constraints would have been placed on localized O$_2$ production by the lack of a protective ozone

460   layer since unattenuated UV radiation would have severely limited the productivity of

461   subaerially exposed mats[94,95]. Experimental work on modern mats shows that even moderately

462   elevated UV irradiance can cut O_2 production by half[121], although cyanobacteria have numerous

463   ways of reducing exposure including vertical migration, secretion of UV-absorbing extracellular

464   polysaccharides,[99] growing under mineral grains,[122] or even precipitating their own mineral

465   'sunscreen'[123]. The relationship between UV exposure, biological attenuation, and oxygen

466   production in mats prior to the GOE remains largely unknown and is a significant source of

467   uncertainty in estimating the size of both the terrestrial and marine biospheres during this time[124],

468   but given evidence for continental exposure going back to at least 3.2 – 3.0 Ga[108,125] together

469   with fossil, molecular, and geochemical records and inferences from modern mat

470   physiology[77,83,86,89], it seems possible that the locus of primary productivity for the majority of

471   Earth's history has been on land, not the oceans.

472

473   **The rise of algae and animals**

474   For over 90% of Earth's history, ecosystems were dominated by single-celled organisms. The

475   oldest potentially eukaryotic microfossils occur in the latest Paleoproterozoic Changzhougou

476   Formation (ca. 1.8 Ga) and Chuanlinggou Formation (ca. 1.7 Ga) of North China[126,127]. However,

477   the emerging view is that they were not an important part of the marine biosphere until roughly

478   800 million years ago, or later[128]. Between 1000 and 500 Ma multicellular organism rose to

479   prominence via the radiation of modern animal phyla and more complex ecosystems (Figure

480   2c)[129,130]. There has been persistent debate about the drivers of this transition. The two end member

481   views are that this event was tied to the removal of an environmental barrier or that it simply

482   represents the timing of biotic novelties[131,132]. Trying to make sense of this transition has prompted

483   one of the most fundamental questions we can ask about the evolution of life—is biotic complexity

484   inevitable and self-promoting, or does the rise of complexity depend on planetary evolution toward

485   favorable environmental conditions?

486

487   It has commonly been suggested that environmental factors including oxygen concentrations and

488   the availability of nutrients in the marine realm (e.g., P) governed the rise of complex life.

489   Specifically, ocean oxygenation may have played a central role in controlling the earliest

490   appearance of eukaryotic clades, as well as their later radiation and rise to ecological

491   prominence[133–135]. The 'oxygen control hypothesis' suggests that increased oxygen concentrations

492   would have dictated the timing of the emergence of animals and their divergence in the latest

493   Proterozoic (800 to 500 million years ago). Alternatively, it may have been biotic innovations

494   independent of an environmental control (e.g., the appearance of algal clades) that drove the

495   observed environmental changes (e.g., glaciations[136] and oxygenation[137]). In other words, the

496   Neoproterozoic rise of eukaryotes to ecological dominance has been either attributed to an

497   environmental trigger or implicated as the driver of the observed environmental changes.

498

499   The most obvious effect that animals and algae can have on the Earth system is transforming the

500   biological pump and enhancing organic carbon export from the surface oceans[138]. For instance, in

501   the Neoproterozoic, the shift from a cyanobacteria- to a eukaryote-dominated biological pump may

502   have played a key role in driving ocean and atmospheric oxygenation, isotopic excursions, and

503   climatic perturbations. In particular, it has been suggested that an algal-dominated carbon pump

504   would promote faster organic carbon sinking rates due to an increase in average cell size and

505   density[139]. In this framework, faster sinking rates and thus a less efficient biological pump would

506   have spread oxygen demand over a greater depth of the water column, thus attenuating peak

507   oxygen demand and shifting the oxygen minimum zone to deeper waters. It also would have

508   increased the oxygen demand in shelf sediments.

509

510   Although the basics of this idea are simple—larger objects sink faster—a simple analysis for the

511   effect of sinking rate on the carbon pump and oxygen dynamics in the oceans draws this idea into

512   question (Box 2 and 3). Previous qualitative and quantitative models have simplified the role of

513   marine aggregates—yet all sinking organic matter in marine systems will occur as aggregates

514   rather than single cells, where even in the absence of fecal-producing organisms and bigger-cell

515   sized algae there is appreciable aggregate formation comprised of only minerals and phytoplankton

516   [140]. When the dynamics of marine aggregates are considered[141], the overall effect of switching

517   primary producers and bringing metazoans into marine systems is fairly minor (Box 2). When

518   particle disaggregation by animals—foremost by the smallest size classes of zooplankton—is

519   considered[141,142], it is even more unlikely that there was a fundamental step change in the efficiency

520   of organic carbon export when animals became an important component of marine ecosystems.

521   Similar to eukaryotic algae, increased sinking rates of oceanic particles caused by, for example,

522   the evolution of silica frustule biosynthesis in diatoms and fecal pellet production by grazing

523   organisms, may not be strong enough to alter the efficiency of the carbon pump or to have a major

524   impact on oxygen dynamics in the oceans (Box 2 and 3).

525

526   Environmental factors, on the other hand, could have exerted strong leverage on the Earth's

527   biosphere. For instance, climate cooling events could have strongly impacted oxygen dynamics in

528   the ocean-atmosphere system. Specifically, given temperature dependent metabolic rates, a cooler

529   climate would have promoted high burial efficiency and high oxygen demand in the ocean by

530   suppressing the rate of organic matter degradation in the surface ocean and increasing flux of

531   organic matter into depths[143]. This, in turn, could have promoted anoxia at depth, while increasing

532   the rate of oxygen efflux from the ocean. While other factors such as enhancement in oxygen

533   solubility or change in ocean circulation patterns during cooling can influence oceanic oxygen

534   dynamics, global cooling could translate into rather large fluxes of oxygen from the ocean to the

535   atmosphere during the Neoproterozoic glaciations, providing one path to a strongly oxygenated

536   atmosphere. Therefore, a simple quantitative exploration of marine carbon cycling (Box 2-3)

537   questions the idea that the rise of animals or the rise of algae were first-order controls on the nature

538   of Earth's marine biological carbon pump. On the contrary, environmental factors (e.g.,

539　temperature changes) appear to provide a more straightforward means to induce dramatic changes

540　organic carbon remineralization efficiency over time.

541

542

543　**The rise of plants**

544　Plants account for roughly 60% of net primary productivity today[111], and it has long been assumed

545　that their emergence and diversification fundamentally changed the scope of the biosphere[144].

546　However, increasing awareness of the ubiquity of cyanobacteria in terrestrial settings (see above)

547　indicates that plants were not simply moving onto a barren landscape. Moreover, as discussed

548　above, the ratio of terrestrial to marine net primary productivity is unlikely to have fundamentally

549　changed with the rise of land plants. However, this does not mean that plants did not change the

550　extent to which the biosphere can alter global biogeochemical cycles. Perhaps the most obvious

551　change would have been the development of organic-rich soils with elevated CO_2 concentrations

552　from the respiration of plant biomass[13]. Cyanobacteria appear to create millimeter- to centimeter-

553　thick surficial mats and crusts while many forests and grasslands today create centimeter- to meter-

554　thick topsoil[145]. High CO_2 concentrations in soils help to decouple atmospheric CO_2 levels from

555　the rate of CO_2 consumption via silicate weathering[13]. As such, lower CO_2 levels are possible in a

556　balanced carbon cycle with plants than without plants[13,144]. A low pH zone in soils also likely leads

557　to enhanced P solubilization, given that P is not quantitively dissolved in most weathering

558　environments and that apatite dissolution rates inversely scale with pH[146]. In this light, regardless

28

559   of changes in composition of Earth's weatherable shell, plants would have transformed the amount

560   of P made available to the biosphere . Higher rates of P solubilization should lead to higher globally

561   integrated rates of primary productivity, all other factors held constant. However, the largest

562   impact of land plants on the oxygen cycle may not be tied to P mobilization; it is simply that plants

563   create P-poor recalcitrant organics (e.g., lignin) that contribute appreciably to global organic

564   carbon burial[147,148].

565

566   An important recent idea is that the development of organic-rich soil layers have directly

567   contributed to the rise of atmospheric oxygen[149]. On a million-year time scale the oxygen cycle is

568   in steady state, which means that organic carbon burial must be balanced by oxidation of volcanic

569   reductants, Fe(II) in rocks, and rock carbon. A lack of balanced fluxes would result in continual

570   rise or fall of atmospheric oxygen. Development of soil organic matter (e.g., the formation of an

571   O- horizon in the soil) would come with a greater soil oxygen demand, such that diffusive fluxes

572   of oxygen from the atmosphere would need to be larger to achieve the same oxidative weathering

573   rates as in the absence of an organic-rich soil layer[149]. To balance this with a comparable oxygen

574   source from carbon burial in the ocean, oxygen would accumulate in the atmosphere to a level that

575   supported this diffusive flux. Therefore, even if plants do not result in a substantial increase in net

576   primary productivity, they are likely to have increased the ability of the biosphere to transform the

577   atmosphere.

578

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 $\delta^{13}C_{carb}$.

598   Although it has been long debated, there has been recently increasing appreciation that $\delta^{13}C_w$ has

599   changed significantly throughout Earth's history[125–127]. Foremost, several recent modeling based

600   studies have proposed that $\delta^{13}C_w$ was controlled by pO_2 for much of Earth's early history, as low

601   atmospheric oxygen would have limited the oxidative weathering of sedimentary organic

602   carbon[160,161]. Specifically, a reduced flux of isotopically light organic carbon to the oceans would

603   have increased $\delta^{13}C_w$, requiring reduced f_{org} to maintain baseline $\delta^{13}C_{carb}$. Determinations of $\delta^{13}C_w$

604   based on previously developed organic carbon oxidation rate laws and current best estimates of

605   pO_2 show that this was indeed the case for most of Earth's history. In order to reproduce the $\delta^{13}C_{carb}$

606   record, with common pO_2 estimates, f_{org} must have been roughly 10% or less during low-pO_2

607   intervals such as the Archean and mid-Proterozoic[160,161]. This is much lower than the widely

608   accepted 20-25% and implies a much smaller global biosphere than previously recognized.

609   Further, if $\delta^{13}C_w$ is allowed to vary with pO_2, a long-term increase in f_{org} keeping pace with

610   atmospheric oxygenation could conceivably be "hidden" within a stable $\delta^{13}C_{carb}$ record[161]. Looking

611   at this in another way, taking any estimate for Proterozoic pO_2 between 0.1 to 10% PAL (Figure

612   1), the amount of organic carbon burial—and by inference the extent of primary productivity—

613   must have much been less than in the modern[162]. According to this view and accepting that there

614   has been a protracted rsie in atmosphereic oxygen levels, instead of providing evidence for a

615   constancy in organic carbon fluxes through Earth's history the carbon isotope record instead

616   provides strong evidence that organic carbon burial and thus the scope of Earth's biosphere has

617   increased through time.

618   **Conclusions and future directions**

619   We propose, based on in large part on recent work, that four major tenets of the traditional view of

620   the long term evolution of the structure and scope of the biosphere (e.g., [163]) need to be revisited:

621   that (1) primary productivity and organic carbon burial were roughly constant through most of

622   Earth's history; (2) the marine realm was the focus of primary productivity prior to the rise of land

623   plants; (3) primary productivity in the marine relam was dominated by oxygenic photosynthesizers

624   for most of Earth's history; and (4) the rise of eukaryotes fundamentally reshaped the biological

625   pump and global carbon cycling. We are proposing that marine primary productivity from

626   oxygenic photosynthesizers increased dramatically though time[74,164,165], in part, because key

627   nutrients (P) were taken up by anoxygenic photosynthesizers for most of Earth's history when

628   predominantly reducing conditions prevailed[6,20,52,62,74]. However, the extent of primary

629   productivity in terrestrial settings in the Precambrian—and the capacity of terrestrial ecosystems

630   to affect global biogeochemical cycling—have likely been underestimated. Cyanobacteria thrive

631   in a wide range of terrestrial environments today, and similar ecosystems would have been a major

632   part of the biosphere before the rise of land plants. In fact, we propose that terrestrial ecosystems

633   have been the locus of primary productivity for the majority of Earth's history. We further suggest

634   that that the presence of larger cell sizes in primary producers (the rise of algae) or fecal pellet

635   production (the rise of animals) may not have lead to a dramatically different marine carbon cycle.

636   Studies of the modern biological pump have made it abundantly clear that the biological pump is

637   complicated and that the recycling of particulate organic matter in Earth's oceans is dominated by

638   the behavior of marine aggregates[140]. In this light, models focusing on individual cells or without

639   robust and mechanistic representations of marine aggregate dynamics are unlikely to provide an

640   accurate picture of the marine carbon cycle.

641

642   This perspective highlights more unknowns and outstanding questions about the long-term history

643   of Earth's biosphere than it does present indisputable conclusions. Therefore, there is a clear need

644   for more work on basic aspects of how Earth's biosphere has evolved and how the capacity of the

645   biosphere to transform Earth's surface has changed through time. There is exciting, active debate

646   about most aspects of how life has transformed our planet—the obvious path forward is working

647   as a community towards resolution. However, we feel the most exciting advances are going to

648   come from closer coupling of models and empirical records, more information from modern

649   analogues for early Earth ecosystems, and consideration of the full history of the co-evolution of

650   the biosphere and solid Earth processes—rather than focusing on specific intervals or

651   perturbations.

Figures:
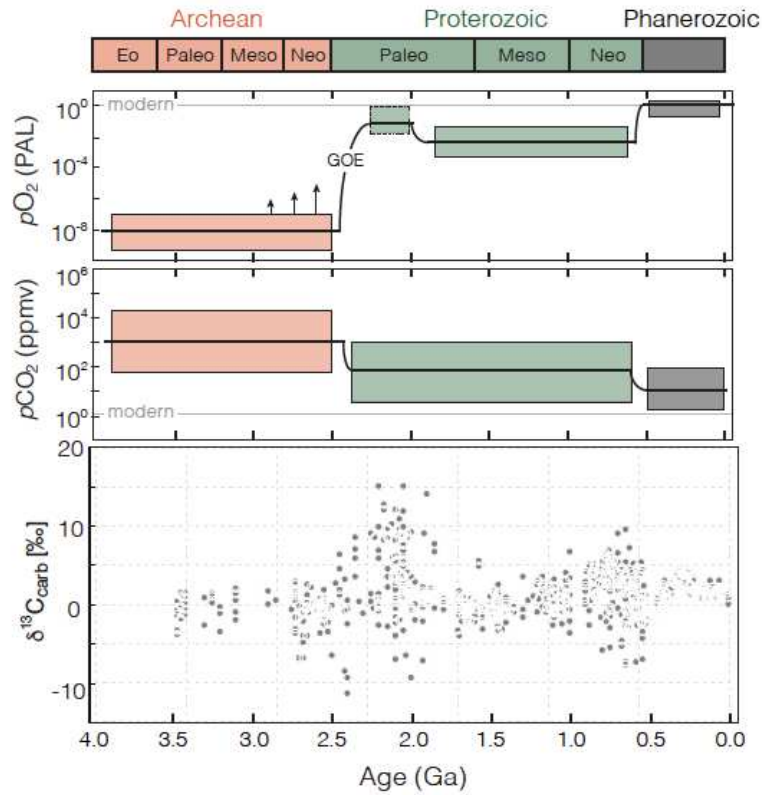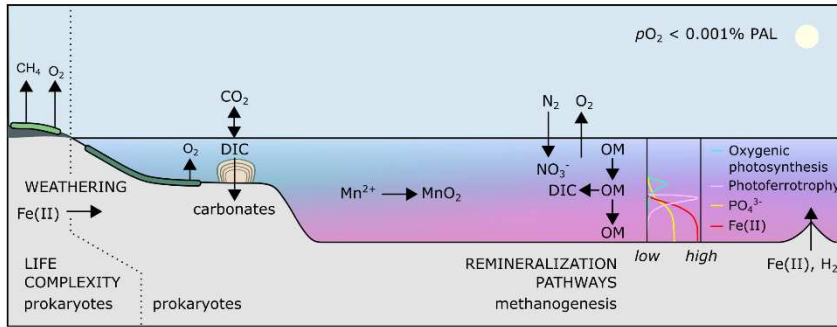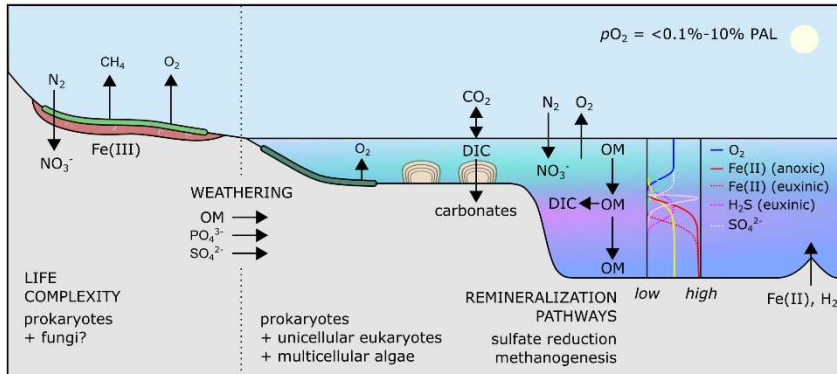

Figure 1. Change in atmospheric oxygen (a), CO_2 (b), and isotopic composition of marine carbonates (c) through time. The pO2 estimates are from Reinhard and Planavsky (2020)[166], pCO2 estimates are from Isson et al. (2020)[13], and the carbonate C isotope compilation is from Krissansen-Totton et al., (2015)[155].
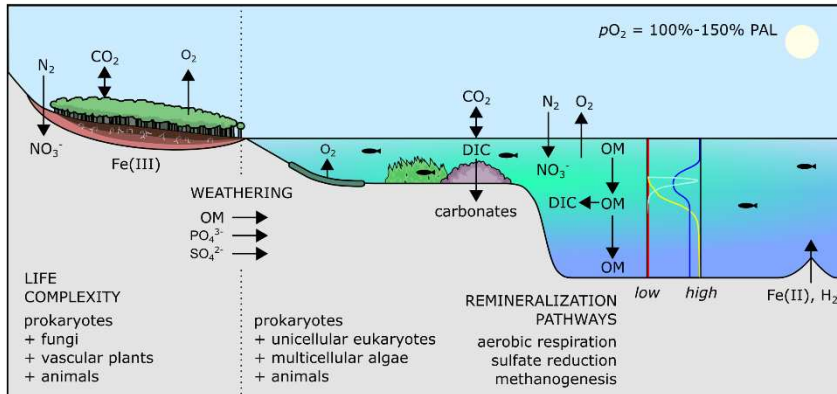
a. Archean

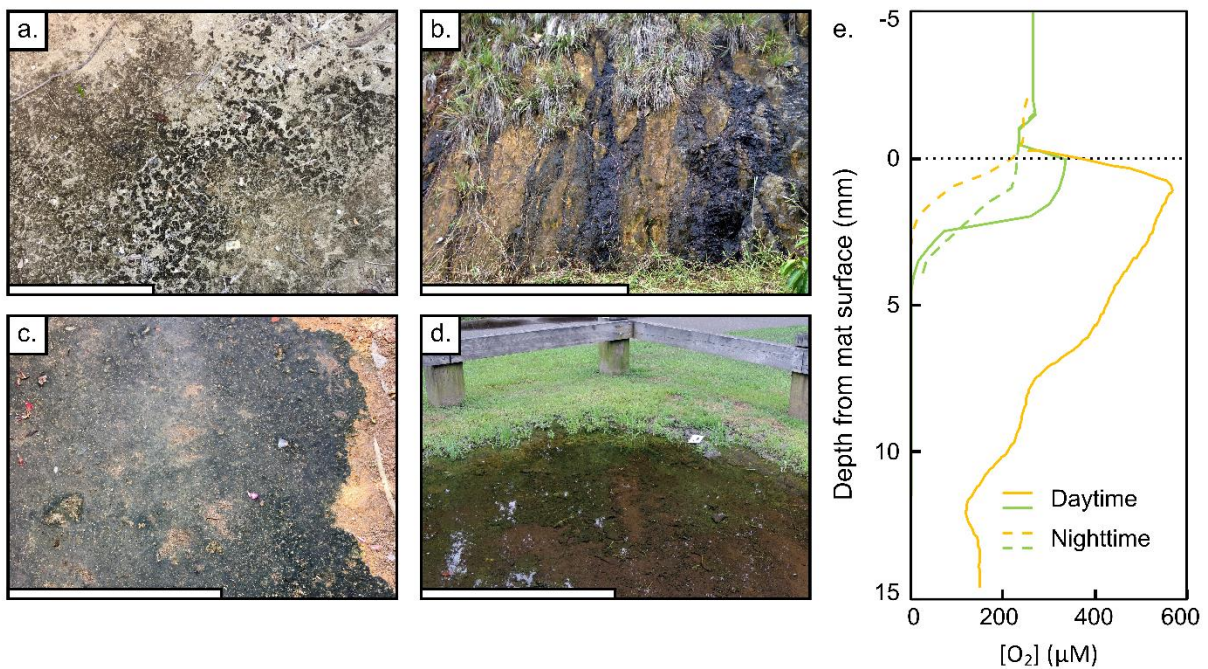## b. Proterozoic to early Phanerozoic


c. middle to late Phanerozoic

576

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

707

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.

716
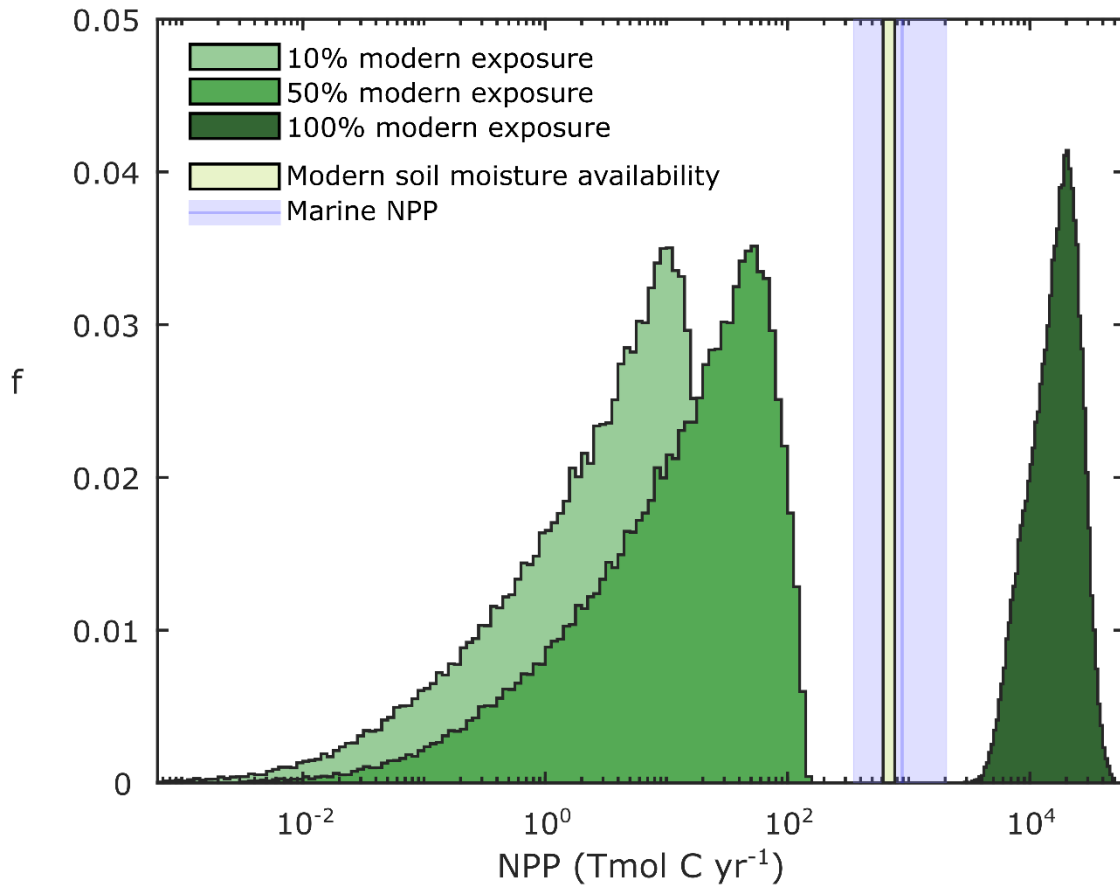
Figure 4. A stochastic estimation of global annual NPP from terrestrial microbial mats under different continental exposure scenarios. The probability distribution was calculated using O_2 production rates measured in modern terrestrial microbial mats[79] and a uniform mat coverage distribution from 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

732   line (mean) and blue shaded region (95% confidence interval). The annual range of NPP estimates from

733   our soil moisture analysis (Figure 5) is shown in the light green shaded region.
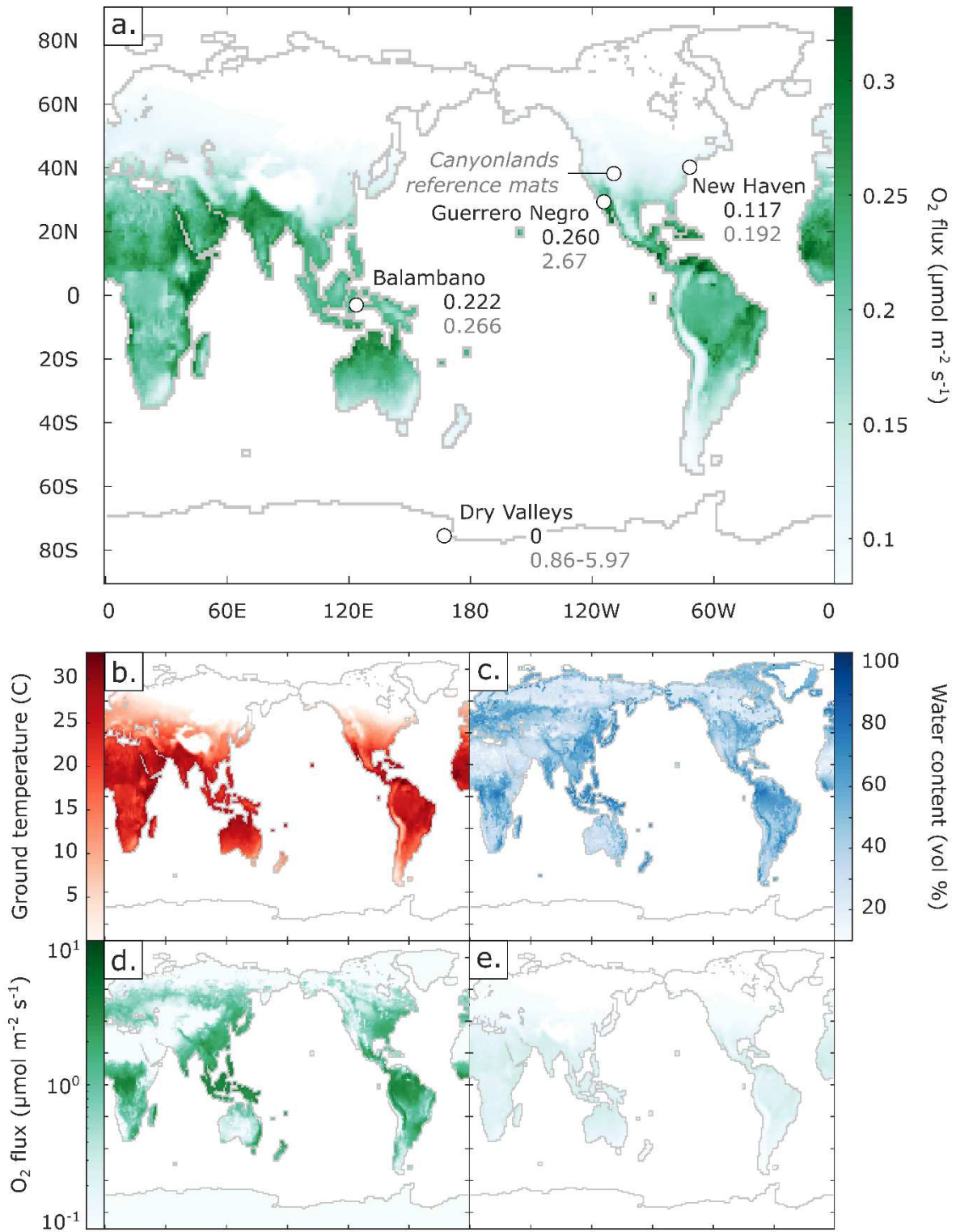
Figure 5. (a) Estimated O_2 fluxes from a terrestrial biosphere in which cyanobacterial mats are the sole primary producers. Our ecophysiological interpolation is based on a predicted relationship reported by Grote et al. (2010)[105] between temperature, soil moisture availability, and net photosynthesis 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.

752 **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

753

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:

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

775   Here, T_{ref} is the reference temperature for the temperature dependency factor which is assumed to

776   be 25ºC and the ocean depth is assumed to be 5 kms. The term t is time, which can be written as

777   z/SR, where z is the ocean depth and SR is the sinking rate of particles. The change in burial

778   efficiency as a function of the different sinking rates of known oceanic aggregates is shown. The

779   change in the sinking rate using different rate expressions does not result in a significant (>5%)

780   change in the burial efficiency of the carbon pump. In contrast, changes in temperature and power-

781   law coefficients exert strong leverage on the BE (Box 2 Figure 1). This is obviously a

782   simplification of the biological pump, but this exercise demonstrates the much more pronounced

783   effects that temperature and marine redox conditions are likely to have on organic carbon burial

784   efficiency than changes in sinking rates linked to biotic innovations like the rise the algae.

785
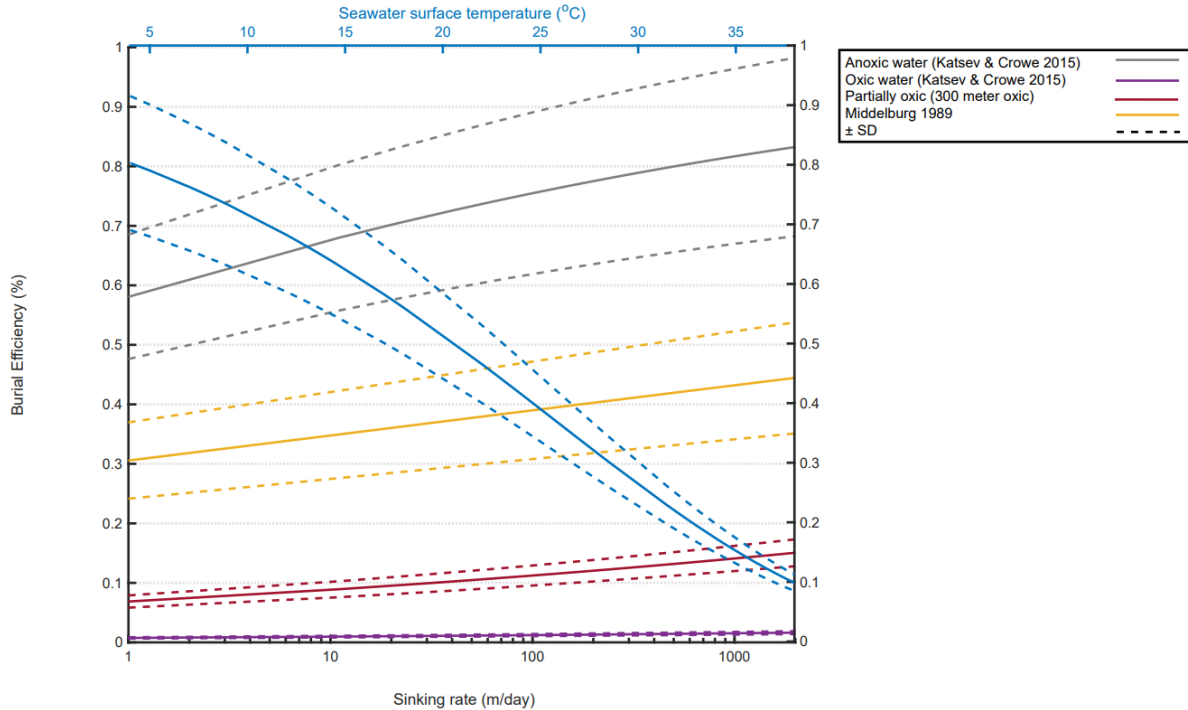
Box 2. Figure 1. Change in burial efficiency as a function of sinking rate and seawater temperature. The results for burial efficiency at different sinking rates (purple, red, orange, and grey lines) were obtained at no temperature dependency (Q_{10}=1). The range of sinking rates is obtained by considering 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).

796

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:

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

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:

$$R_{resp} = R_C \frac{[O_2]}{K_i + [O_2]} \tag{3}$$

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

814   degradation. This indicates that biotic innovations would also play minor role in marine oxygen

815   dynamics, relative to surface oxygen levels and temperature (Box 3 Figure 1).

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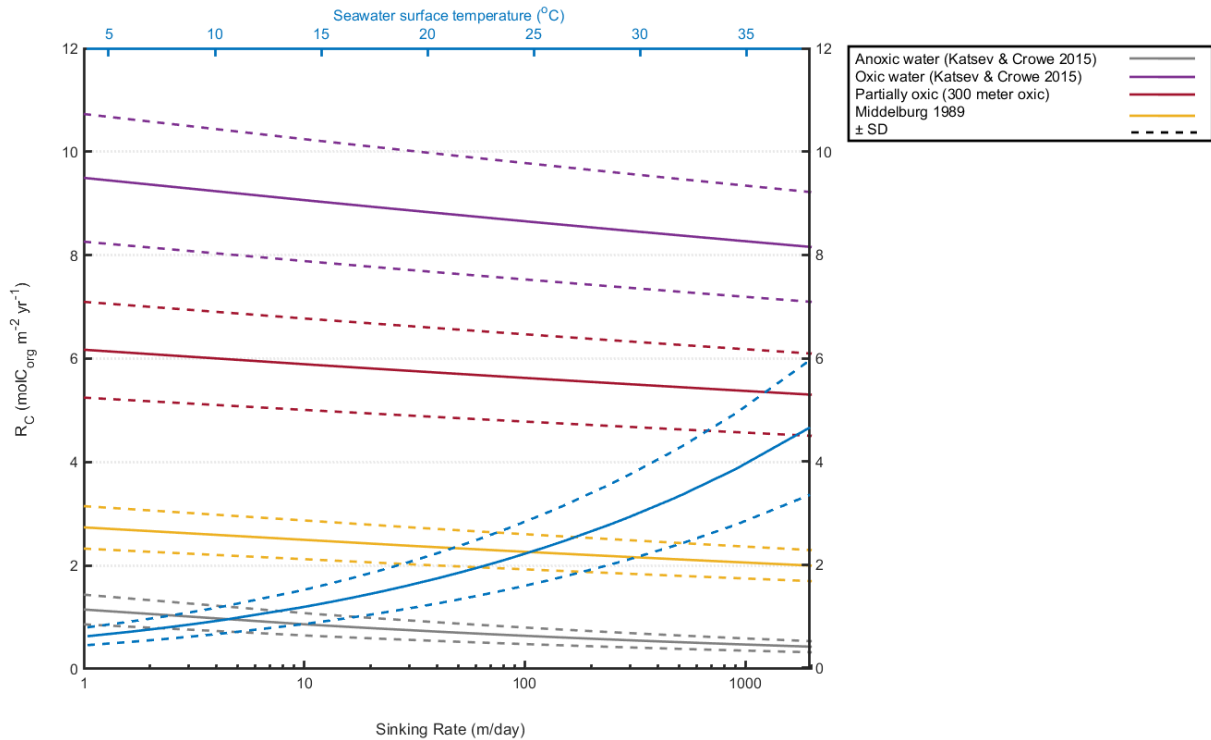
817

818   **Box 3. Figure 1.** Change in the integrated rate of organic matter degradation as a function of sinking

819   rate and seawater temperature. The values of Q_{10} for blue line and sinking rate for the effect of the sinking

820   rate in purple, red, orange, and grey lines are similar to box Figure 1. The initial concentration of organic

821   matter at the surface ($C_{surface}$) was calculated using the modern net primary production and sinking rate of

822   oceanic aggregate. To account for lower productivity in the Precambrian ocean, the value of $C_{surface}$ was

823   multiplied by 0.1. Error bars correspond to the range of coefficients for power-law carbon degradation,

824   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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