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# The Deep History of Earth's Biomass

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**Abstract:** The subsurface “deep biosphere” represents one-tenth to one-third of Earth’s total global present-day biomass. The rest is dominated by land plants, a relatively recent development in geological history. Before ~400 Ma, a relatively low surface biomass with high productivity and fast turnover supplied carbon to a deep biosphere with high biomass but low productivity and slow turnover. Here, we argue that the deep biosphere outweighed the surface biosphere by about one order of magnitude for at least half of the history of life on Earth. This result offers a new perspective on the history of life on Earth with important implications for the search for life on other worlds.

Since the realization that life is widespread within the Earth’s crust (e.g. Whitman *et al.* 1998, Heberling *et al.* 2010, Edwards *et al.* 2012), the deep biosphere has been recognized as an ancient, disparate and diverse ecosystem of global biogeochemical significance that provides analogues for habitats on Mars (Fisk & Giovannoni 1999, Weiss *et al.* 2000, Michalski *et al.* 2013) as well as extrasolar planets (McMahon *et al.* 2013). However, estimates of the magnitude of the subsurface biomass on Earth have ranged widely. A highly cited estimate by Whitman *et al.* (1998) proposes a sub-seafloor prokaryotic biomass an order of magnitude greater than the surface prokaryotic biomass, and a sub-continental biomass intermediate between the two. Taking account of land plants, the total subsurface biomass (carbon) would be nearly half of the total global biomass (Whitman *et al.*, 1998); other estimates vary between less than 1% and a third of the total biomass (Fry *et al.*, 2008; Schrenk *et al.*, 2010, Kallmeyer *et al.* 2012; McMahon and Parnell, 2014; Bar-On *et al.*, 2018).

Regardless of which value for subsurface biomass is adopted, it is overwhelmingly dwarfed by ~500 Pg C of land plants (Whitman *et al.*, 1998; Polis, 1999; Saugier *et al.* 2001; Carvalhais *et al.* 2014; 1 Pg = 10<sup>15</sup> g carbon); animals contain less than 2 Pg C (Smil, 2002; Jennings *et al.*, 2008). The high plant biomass reflects colonisation of the free space above the soil, the large mass possible for a rooted sessile organism, access to abundant solar energy, and the preponderance of carbon-rich structural polymers and dead tissues in these organisms. Land plants are a young component of the biosphere, appearing in the Ordovician (~470 Ma) but probably dominating global biomass only since the Devonian-Carboniferous (~380-300 Ma) (Kenrick *et al.*, 2012).

46 In contrast, the deep biosphere is ancient. Its fossil record is regrettably under-explored, but dates  
47 back at least to the early Palaeoproterozoic (Bengtson et al., 2017) and possibly to the Archean  
48 (Rasmussen, 2000). The modern deep biosphere is dominated by prokaryotic phyla with  
49 evolutionary origins in the Archean, (e.g., *Proteobacteria*, *Firmicutes*, *Chloroflexi*,  
50 *Crenarchaeota*, *Euryarchaeota* and *Thaumarchaeota*; Magnabosco et al., 2014, 2016; Parkes et  
51 al., 2014; Kieft, 2016; for divergence time estimates see, e.g., Battistuzzi et al., 2004;  
52 Magnabosco et al., 2018; Wolfe and Fournier, 2018) and by similarly ancient autotrophic and  
53 heterotrophic metabolic strategies, including methanogenesis and sulphur cycling (e.g., Ueno et  
54 al., 2006; Shen et al., 2009; Bontognali et al., 2012; Knoll et al., 2016).

55  
56 These considerations suggest that the deep biosphere could have hosted most of Earth's biomass  
57 prior to the Devonian. To investigate this hypothesis, this contribution reviews the distribution of  
58 biomass on the modern Earth, and compares it with the interval between ~2.0 Ga and the spread  
59 of land plants about 0.4 Ga. This geologically well-documented timeframe post-dates the great  
60 oxygenation event at ~2.4 Ga, and represents about half the history of life on Earth.

61  
62

### 63 **The distribution of biomass**

64

65 We revisit the exhaustive classification of Earth's biomass given by Whitman *et al.* (1998) to  
66 describe Earth's biomass distribution today and in the interval from 2.0–0.4 Ga, prior to the  
67 proliferation of land plants (**Figure 1**).

68

#### 69 Land plant biomass

70 Whitman *et al.* (1998), following Olson *et al.* (1983), estimated total modern plant biomass to be  
71 ~560 Pg C, including 470 Pg in forests/woodlands and 90 Pg in other ecosystems. More recent  
72 estimates of forest/woodland biomass range from 429 to 536 Pg (Carvalhais *et al.* 2014; Saugier  
73 *et al.* 2001). This value can be scaled up to correct for recent deforestation (Crowther *et al.*  
74 2015), yielding a total pre-human plant biomass of ~980 Pg C. Somewhat higher values may  
75 have obtained in Earth's history (e.g., during the Carboniferous), but the negative feedback effect  
76 of increased forest fires under higher atmospheric oxygen concentrations would not allow global  
77 plant biomass to rise much further (Lenton and Watson, 2000).

78

#### 79 Soil and shallow terrestrial biomass

80 *Today:* Soils contain an immense reservoir of organic carbon, but this is mostly non-living  
81 detritus (Trumbore, 1997). Whitman *et al.*'s (1998) estimated microbial biomass of 26 Pg in  
82 modern terrestrial soils has recently been revised down to ~15 Pg, including all prokaryotes and  
83 fungi at the Earth's land surface and within the metre below it (Serna-Chavez *et al.*, 2013).

84

85 *Pre-vegetation:* From the Archean until the rise of land plants, the land surface hosted  
86 widespread microbial communities reliant on oxygenic photosynthesis for carbon fixation  
87 (Konhauser and Lalonde, 2015; Lenton and Daines, 2017). Evidence for these early terrestrial  
88 mats and soil crusts includes widely reported geochemical signatures of oxidative weathering,  
89 carbon fixation, organic acids and ligand production in palaeosols (e.g., Watanabe et al., 2000;  
90 Beukes et al., 2002; Neaman et al., 2005; Crowe et al., 2013; Lenton and Daines, 2017); fossils  
91 of terrestrial stromatolites and microbial mats (e.g., Buick, 1992; Eriksson et al., 2000; Prave,

92 2002); and the rising abundance of sulphur in marine sediments from ~2.5 Ga, attributed to  
93 microbial pyrite oxidation on land (Stüeken et al., 2012). It has been suggested that cryptogamic  
94 ground cover expanded significantly in the Neoproterozoic, but this is contested (Knauth and  
95 Kennedy, 2009; Lenton and Daines 2017).

96  
97 Plants significantly increase the carbon content, nutrient availability and microbial activity of  
98 soil, as well as its volume. However, Serna-Chavez *et al.* (2013) show that soils in tropical  
99 forests (the most microbe-rich major soil biome) typically contain only ~4.5x as much microbial  
100 biomass per volume as those in arid deserts, the most plant- and microbe-poor land-surface  
101 biome. If this sparse desert biome covered the entire ice-free land surface, microbial soil biomass  
102 would still be as high as ~5 Pg C. Even in deserts, however, soil microbial biomass is tightly  
103 concentrated around plants, and would be much lower without their fertilizing effects (e.g.,  
104 Gallardo and Schlesinger, 1992; Wardle, 1992; Herman et al., 1995). We therefore suggest a pre-  
105 vegetation soil biomass range of ~0.5–5 Pg C.

106  
107 *Aquatic biomass*

108 *Today:* Aquatic biomass is dominated by microscopic marine plankton and relatively low in  
109 aggregate. Whitman *et al.* (1998) estimated that prokaryotes in aquatic environments represent  
110 2.2 Pg C. Buitenhuis *et al.* (2013) estimated a range of 2.5 to 7.0 Pg C for most marine plankton;  
111 including the autotrophic dinoflagellates and some nanophytoplankton missing from this  
112 estimate would raise the total to ~3 to 8.5 Pg C (E. Buitenhuis, personal communication).

113  
114 *Pre-vegetation:* Aquatic biomass reflects a complicated interplay of climatic, bathymetric, biotic  
115 and biogeochemical factors. These factors include the nature of the dominant primary producers  
116 (once cyanobacteria, now eukaryotes), the supply of nutrients to the photic zone by runoff and  
117 upwelling, and the area and volume of shallow seas. It is unclear to what extent the proliferation  
118 of land plants increased the delivery of terrigenous nutrients to the oceans; vegetation  
119 inaugurated new and more pervasive processes of mineral weathering on land, but also  
120 permanently reduced atmospheric CO<sub>2</sub> (suppressing weathering) and increased the retention of  
121 fines in terrestrial settings (Algeo et al., 1995; McMahon & Davies, 2018). Nevertheless, the  
122 fossil record hints at a gradual increase in marine productivity through the Phanerozoic (e.g.,  
123 Bambach, 1993; Martin *et al.*, 1996; Falkowski et al., 2004). Primary productivity would have  
124 been favoured by higher CO<sub>2</sub> before the Devonian, but suppressed during periods of ocean  
125 stratification and redox-controlled phosphorus limitation during the Proterozoic (e.g., Reinhard  
126 et al., 2017). Autotrophic aquatic biomass may have been smaller before eukaryotic  
127 phytoplankton rose to dominance (Falkowski et al., 2004), and heterotrophic aquatic biomass  
128 (today twice as large as autotrophic biomass) would have been much smaller prior to the  
129 stepwise oxygenation of the oceans and the rise of metazoans through the Phanerozoic (e.g.,  
130 Bambach, 1993; Martin *et al.*, 1996). In the absence of better constraints, we suggest that the  
131 sum of modern prokaryotic aquatic biomass represents a reasonable first order estimate of total  
132 aquatic biomass in the interval from 2.0 to 0.4 Ga; i.e., about ~1.5–3.5 Pg C (Buitenhuis et al.,  
133 2013).

134  
135 *Subseafloor biomass*

136 *Today:* This reservoir encompasses biomass in sediments and rocks beneath the seafloor.  
137 Kallmeyer *et al.* (2012) show on the basis of a large data set that marine sediments support a

138 biomass in the range of 1.5 to 22 Pg C (expected value ~ 4.1 Pg C), much less than the 303 Pg C  
139 proposed by Whitman *et al.* (1998). This dramatic downsizing was upheld by the meta-analysis  
140 of Bar-on *et al.*, (2018), which yielded an expected value of ~7 Pg C. This biomass is sustained  
141 chiefly by heterotrophy, as shown by the fact that cell counts in marine sediments are much  
142 higher at continental margins than under the open ocean where very little carbon is buried  
143 (Kallmeyer *et al.*, 2012). In contrast, the underlying basaltic/gabbroic basement of the oceanic  
144 crust appears to be a significant habitat for chemoautotrophs fuelled by water-rock reactions  
145 (Orcutt *et al.*, 2011). Heberling *et al.* (2010) estimated that this largely unexplored region could  
146 support a biomass of 200 Pg, chiefly in pillow basalt. However, the few cell counts thus far  
147 reported from oceanic basement are much lower than this model would predict, including those  
148 measured close to mid-ocean ridges where hydrothermal circulation should create favourable  
149 conditions for life (e.g., Mason *et al.*, 2010; Salas *et al.*, 2015 ). The available cell counts have  
150 recently been extrapolated to a biomass of oceanic basement in the range 0.5–5.0 Pg C (Bar-On  
151 *et al.*, 2018). Total subseafloor biomass today is therefore likely to be close to 10 Pg C.

152  
153 *Pre-vegetation:* Despite secular continental growth, the volume of the subseafloor habitat has  
154 been relatively stable through the last 2 Ga (Heberling *et al.* (2010). The productivity of the  
155 sediment-hosted biome is controlled by the burial of organic carbon, most of which derives from  
156 marine plankton rather than terrestrial plants. Export productivity may have increased through  
157 geological time (e.g., Bambach, 1993; Martin *et al.*, 1996), but productivity is not the sole  
158 determinant of carbon burial, and organic-rich shales are common even in the Archean and early  
159 Proterozoic (Condie *et al.* 2001; Lyons *et al.*, 2014 ). Indeed, persistent oceanic anoxia until the  
160 middle Palaeozoic facilitated copious carbon burial and could at times have supported higher  
161 subseafloor biomass than today, especially when shallow seas were more widespread.

162  
163 Where carbon is plentiful, suitable electron acceptors such as sulphate and nitrate are limiting  
164 instead. Subseafloor biomass must have grown both in the basement and the sediment cover as  
165 oxidants became increasingly available beneath the oceans—a secular change that began in the  
166 Archean and accelerated with the rise of land plants (e.g., Wallace *et al.*, 2017; Stolper & Keller,  
167 2018). The magnitude and rate of the growth in biomass accompanying this gradual shift in  
168 redox conditions is difficult to estimate. Energy limitation thresholds are very low in the  
169 metabolically ultra-slow deep biosphere (Hoehler & Jørgensen, 2013), methanogens would  
170 probably have thrived beneath the low-sulphate Proterozoic oceans (e.g., Habicht *et al.*, 2002;  
171 Crowe *et al.*, 2011), and there is plausible fossil evidence of a deep marine biosphere as early as  
172 2.4 Ga (Bengtson *et al.*, 2017). Reconstructing deep subseafloor biomass through deep time is a  
173 formidable challenge, but a conservative representative value for ~2.0–0.4 Ga would be in the  
174 range 5–10 Pg C.

175  
176 *Continental deep biomass*

177 *Today:* In contrast to the downsizing of subseafloor biomass, new cell count data from the past  
178 two decades have broadly maintained Whitman *et al.*'s (1998) estimate of deep continental  
179 biomass in the range of 22–215 Pg C. McMahon and Parnell (2014) derived a range of 14 to 135  
180 Pg from these new data, but taking account of more recent groundwater distribution models  
181 (Gleeson *et al.*, 2016) would raise this range to within 10% of Whitman *et al.*'s original estimate.  
182 The order-of-magnitude uncertainty remaining stems from the difficulty of scaling up from  
183 unattached cell numbers measured in water to total cell numbers that include a majority adhering

184 to mineral surfaces. However, independent estimates based on pore occupancy models and cell  
185 counts from bulk rock/sediment yield ranges of similar magnitude (Whitman *et al.*, 1998; Onstott  
186 *et al.*, 1998).

187  
188 *Pre-vegetation*: Whereas photosynthetic organic carbon supply appears to exert an  
189 overwhelming influence on cell counts in marine sediments, no such single overriding factor has  
190 been identified in the continental crust, which sustains a higher microbial population density  
191 (Kallmeyer *et al.*, 2012; McMahon and Parnell, 2014). The factors limiting continental deep  
192 biomass are highly localised, and include photosynthetic carbon supply, electron donors, electron  
193 acceptors, and physical conditions, notably temperature (e.g., Moser *et al.*, 2005; Onstott *et al.*  
194 2014); the relative importance of these factors in shaping the total biomass remains unclear.

195  
196 Carbon limitation was probably more widespread prior to the rise of land plants; cryptogamic  
197 ground cover contributes only around ~4% of terrestrial net primary production today (Elbert *et al.*  
198 *et al.*, 2012). However, these communities are highly photosynthetically active; a cm-thick  
199 microbial mat can be as productive as a water column tens to hundreds of metres deep (Lalonde  
200 and Konhauser, 2015). Moreover, prior to the spread of land plants, these communities would  
201 have occupied a much larger proportion of Earth's surface and fixed carbon at a higher rate  
202 under the higher atmospheric CO<sub>2</sub> concentrations then prevailing (e.g., Rothschild and  
203 Mancinelli, 1990). Microbial mats may also have exported carbon more efficiently to  
204 groundwater prior to the development of thick, extensively grazed, organic-rich soil layers,  
205 which recycle and respire carbon. Abiotic hydrocarbons, CO<sub>2</sub> and CH<sub>4</sub> would have provided an  
206 additional, independent carbon source for the deep biosphere, just as they do today (e.g.,  
207 Chapelle *et al.*, 2002; Sherwood Lollar, 2007). Molecular hydrogen is also widely available as an  
208 alternative electron donor in continental crust (Chapelle *et al.*, 2002; Lin *et al.*, 2005; Sherwood  
209 Lollar *et al.*, 2007) and has been generated by radiolysis, serpentinization, and other processes  
210 throughout Earth history. Electron acceptors derived from photosynthetic oxygen pervaded the  
211 continental subsurface much earlier than the marine subsurface; the sulphate flux from oxidative  
212 pyrite weathering was comparable to modern values by 2.0 Ga (Stüeken *et al.*, 2012).

213  
214 Variation in physical conditions such as crustal thickness, geothermal gradients, and porosity–  
215 depth relationships may also have mediated continental biomass through deep time. The balance  
216 between sedimentary rocks and crystalline basement in the composition of the continents is  
217 especially pertinent, since sedimentary rocks are more porous; today they host ~15× more  
218 groundwater—and correspondingly more biomass—than crystalline rocks (Gleeson *et al.*, 2016).  
219 Through the Phanerozoic the proportion of basement covered by sedimentary rock fluctuated by  
220 a factor of ~2 (Ronov 1980). Erosion which led to the global unconformity at the Precambrian-  
221 Cambrian boundary left a paucity of sediment at that time, and has removed much of the  
222 Proterozoic record (Peters & Husson 2017). Nevertheless the record of shallow marine  
223 sedimentation was constant through the Proterozoic (Peters & Husson 2017) and there is no  
224 reason to think that continental composition or total volume in the Proterozoic was  
225 systematically different from the Phanerozoic. Taken together, these considerations strongly  
226 suggest that the terrestrial subsurface biomass has been, conservatively, at least 10% its current  
227 size for ~ 2 billion years, i.e., at least 2–20 Pg C.

228

## 229 **Discussion**

<b>Table 1.</b>	<b>Continental subsurface</b>	<b>Subseafloor</b>	<b>Aquatic</b>	<b>Soil</b>	<b>Plants</b>
Biomass, Pg C					
<b>With plants (pre-human)</b>	20–200 <sup>a,b,c</sup>	10 <sup>c,d</sup>	3–8.5 <sup>e</sup>	15 <sup>f</sup>	980 <sup>g,h,i</sup>
<b>Before plants (&lt;2.0 Ga)</b>	2–20*	5–10	1.5–3.5	0.5–5	0

230 \*Conservative lower limit (10% of modern)

231 (a) Whitman et al., 1998

232 (b) McMahon & Parnell, 2014

233 (c) Bar-On et al., 2018

234 (d) Kallmeyer et al., 2012

235 (e) Buitenhuis et al., 2013

236 (f) Serna-Chavez et al., 2013

237 (g) Saugier et al., 2001

238 (h) Carvalhais et al., 2014

239 (i) Crowther et al., 2015

240

241 **Table 1.** Illustrative values and approximate ranges of biomass carbon in different reservoirs.

242 Modern (pre-human) values are used for the post-vegetation interval. The pre-vegetation values  
243 were estimated by the present study, as explained in the text.

244 The estimates discussed in the previous section are summarized in **Table 1**. Despite poor  
245 constraints on the estimated values of individual biomass reservoirs, it is difficult to avoid the  
246 conclusion that subsurface environments hosted the majority of Earth’s biomass from 2.0 to 0.4  
247 Ga. Even if the continental deep biosphere was as little as 10% of its present size (as in **Table 1**  
248 and **Figure 1**), the ranges and representative values we derive indicate a deep biosphere carbon  
249 reservoir ~1–15× as large as the remaining “surface biosphere” during this interval. Only after  
250 the rise of land plants did the biosphere become top-heavy, dominated by eukaryotes, and close  
251 to its present size.

252

253 Although much of the deep biosphere derives carbon from photosynthesis at the surface, this  
254 relationship does not require high surface biomass, only high surface productivity. Marine  
255 phytoplankton may account for about half of all primary productivity but contribute less than 1%  
256 of global biomass (Falkowski *et al.*, 2004). Similarly, microbial mats and lithic crusts maintain a  
257 low standing biomass but rapidly turn over carbon (Lalonde and Konhauser, 2015). Thus, like  
258 modern oceans, the ancient continents were probably characterised by high-productivity, low-  
259 biomass surface populations and low-productivity, high-biomass deep populations with long  
260 carbon residence times.

261

262 The extensive evidence for a subsurface biosphere on Earth has raised the possibility that other  
263 planets may also support life in a subsurface biosphere (Sherwood Lollar *et al.*, 2007, Edwards *et al.*,  
264 2012). Given that plants proliferated so recently and are expected to die out with declining  
265 CO<sub>2</sub> less than 1 Ga from now (O’Malley James *et al.*, 2013), the evidence summarised here  
266 suggests that a smaller biosphere dominated by subsurface life could be considered more typical  
267 for even the most “Earth-like” inhabited terrestrial planets than the status quo on Earth itself. In  
268 fact, the hydrogen-generating mechanisms that occur in the Earth’s crust should all occur on any  
269 rocky planet. The constraints of surface water, surface irradiation spectrum and surface  
270 temperature used to characterize planetary habitability do not apply to a subsurface biosphere.

271 Therefore, the number of habitable planets around other stars may be substantially greater than is  
272 commonly supposed on the basis of surface habitability (McMahon *et al.*, 2013). Despite the  
273 limits of restricted space, there are diverse eukaryotes in the terrestrial deep biosphere, including  
274 fungi, nematodes and protists (Ekendahl *et al.*, 2003; Borgonie *et al.*, 2011). Clearly, energy and  
275 nutrient availability in the subsurface are sufficient to support complex multicellular life. If life  
276 can originate in the subsurface, as implied by some models of abiogenesis (Sleep and Bird, 2007;  
277 Martin *et al.*, 2008), a large proportion of life-bearing planets may be inhabited only in the  
278 subsurface. Whether such biospheres can ever be detected remains to be seen.

279

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281

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286

## 287 **References**

288

- 289 1. Algeo, T.J., Berner, R.A., Maynard, J.B. and Scheckler, S.E., 1995. Late Devonian  
290 oceanic anoxic events and biotic crises: “rooted” in the evolution of vascular land  
291 plants. *GSA Today*, v. 5, p. 45-66.
- 292 2. Amend, J.P. & Teske, A., 2005. Expanding frontiers in deep subsurface microbiology:  
293 *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 219, p. 131-155.
- 294 3. Bambach, R.K., 1993. Seafood through time: changes in biomass, energetics, and  
295 productivity in the marine ecosystem. *Paleobiology*, v. 19, p. 372-397.
- 296 4. Bar-On, Y.M., Phillips, R., & Milo, R., 2018. The biomass distribution on Earth.  
297 *Proceedings of the National Academy of Sciences*, online view:  
298 <https://doi.org/10.1073/pnas.1711842115>.
- 299 5. Battistuzzi, F.U., Feijao, A. & Hedges, S.B., 2004. A genomic timescale of prokaryote  
300 evolution: insights into the origin of methanogenesis, phototrophy, and the colonization  
301 of land. *BMC Evolutionary Biology*, v. 4, p. 44.
- 302 6. Bengtson, S., Rasmussen, B., Ivarsson, M., Muhling, J., Broman, C., Marone, F.,  
303 Stampanoni, M. and Bekker, A., 2017. Fungus-like mycelial fossils in 2.4-billion-year-  
304 old vesicular basalt. *Nature Ecology & Evolution*, v. 1, 0141.
- 305 7. Beukes, N.J., Dorland, H., Gutzmer, J., Nedachi, M., & Ohmoto, H., 2002. Tropical  
306 laterites, life on land, and the history of atmospheric oxygen in the Paleoproterozoic.  
307 *Geology*, v. 30, p. 491–494.
- 308 8. Bontognali, T. R. R., Sessions, A. L., Allwood, A. C., Fischer, W. W., Grotzinger, J. P.,  
309 Summons, R. E., & Eiler, J. M., 2012. Sulfur isotopes of organic matter preserved in  
310  
311  
312  
313  
314



- 315 3.45-billion-year-old stromatolites reveal microbial metabolism. Proceedings of the  
316 National Academy of Sciences, v. 109, p. 15146–15151.
- 317
- 318 9. Borgonie, G., García-Moyano, A., Litthauer, D., Bert, W., Bester, A., van Heerden, E.,  
319 Möller, C., Erasmus, M. & Onstott, T.C., 2011. Nematoda from the terrestrial deep  
320 subsurface of South Africa. *Nature*, v. 474, p. 79-82.
- 321
- 322 10. Buick, R., 1992. The antiquity of oxygenic photosynthesis: Evidence from stromatolites  
323 in sulphate-deficient Archean lakes. *Science*, v. 255, p. 74–77.
- 324
- 325 11. Buitenhuis, E.T., Vogt, M., Moriarty, R., Bednaršek, N., Doney, S.C., Leblanc, K., Le  
326 Quère, C., Luo, Y.W., O'Brien, C., O'Brien, T., Peloquin, J., Schiebel, R. & Swan, C.  
327 2013. MAREDAT: towards a world atlas of MARine Ecosystem DATA. *Earth System*  
328 *Science Data*, v. 5, p. 227-239.
- 329 12. Carvalhais, N. *et al.* 2014. Global covariation of carbon turnover times with climate in  
330 terrestrial ecosystems. *Nature*, v. 514, p. 213-217.
- 331 13. Cawood, P.A., Hawkesworth, C.J. & Dhuime, B. 2013. The continental record and the  
332 generation of continental crust. *Geological Society of America Bulletin*, 125, 14-32.
- 333 14. Chapelle, F.H., O'Neill, K., Bradley, P.M., Methé, B.A., Ciuffo, S.A., Knobel, L.L. &  
334 Lovley, D.R., 2002. A hydrogen-based subsurface microbial community dominated by  
335 methanogens. *Nature*, v. 415, p. 312-315.
- 336 15. Condie K.C., Des Marais, D.J. & Abbott, D. 2001. Precambrian superplumes and  
337 supercontinents: a record in black shales, carbon isotopes, and paleoclimates?  
338 *Precambrian Research*, 106, 239-260.
- 339 16. Crowe, S.A., Dossing, L.N., Beukes, N.J., Bau, M., Kruger, S.J., Frei, R., & Canfield,  
340 D.E., 2013. Atmospheric oxygenation three billion years ago. *Nature*, v. 501, p. 535-538.
- 341 17. Crowther, T.W. *et al.* 2015. Mapping tree density at a global scale. *Nature*, v. 525, p.  
342 201-205.
- 343 18. D'Hondt, S. *et al.* 2015. Presence of oxygen and aerobic communities from sea floor to  
344 basement in deep-sea sediments. *Nature Geoscience*, v. 8, p. 299-303.
- 345 19. Druffel, E.R.M., Williams, P.M., Bauer, J.E. & Ertel, J.R., 1992. Cycling of dissolved  
346 and particulate organic-matter in the open ocean. *Journal of Geophysical Research*, v. 97,  
347 p. 15639-15659.
- 348 20. Dubessy, J., Pagel, M., Beny, J.-M., Christensen, H., Hickel, B., Kosztolanyi, C. & Poty,  
349 B., 1988. Radiolysis evidenced by H<sub>2</sub>-O<sub>2</sub> and H<sub>2</sub>-bearing fluid inclusions in three  
350 uranium deposits. *Geochimica et Cosmochimica Acta*, v. 52, p. 1155-1167.
- 351 21. Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O. & Pöschl,  
352 U. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen.  
353 *Nature Geoscience*, 5, 459-462.

- 354 22. Edwards, K.J., Becker, K. & Colwell, F., 2012. The deep, dark energy biosphere:  
355 Intraterrestrial life on Earth. *Annual Reviews of Earth and Planetary Sciences*, v. 40, p.  
356 551-568.
- 357 23. Ekendahl, S., O'Neill, A.H., Thomsson, E. & Pedersen, K., 2003. Characterisation of  
358 yeasts isolated from deep igneous rock aquifers of the Fennoscandian Shield. *Microbial*  
359 *Ecology*, v. 46, p. 416-428.
- 360 24. Eriksson, P.G., Simpson, E.L., Eriksson, K.A., Bumby, A.J., Steyn, G.L., & Sarkar, S.,  
361 2000. Muddy roll-up structures in siliciclastic interdune beds of the c. 1.8 Ga Waterberg  
362 Group, South Africa, *Palaios*, v. 15, p. 177–183.
- 363 25. Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O. &  
364 Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. *Science*, v. 305,  
365 p. 354-360.
- 366 26. Fisk, M.R. & Giovannoni, S.J. 1999. Sources of nutrients and energy for a deep  
367 biosphere on Mars. *Journal of Geophysical Research*, 104, E11805-E11815.
- 368 27. Fry, J.C., Parkes, R.J., Cragg, B.A., Weightman, A.J. & Webster, G., 2008. Prokaryotic  
369 biodiversity and activity in the deep seafloor biosphere. *FEMS Microbial Ecology*, v.  
370 66, p. 181-196.
- 371 28. Gallardo, A. and Schlesinger, W.H., 1992. Carbon & nitrogen limitations of soil  
372 microbial biomass in desert ecosystems. *Biogeochemistry*, v. 18, p. 1-17.
- 373 29. Garcia-Pichel, F., Belnap, J., Neuer, S. & Schanz, F., 2003. Estimates of global  
374 cyanobacterial biomass and its distribution. *Algological Studies*, v. 109, p. 213-227.
- 375 30. Gleeson, T., Befus, K.M., Jasechko, S., Luijendijk, E. & Cardenas, M.B., 2016. The  
376 global volume and distribution of modern groundwater. *Nature Geoscience*, v. 9, p. 161-  
377 167.
- 378 31. Hayes, J.M. & Waldbauer, J.R., 2006. The carbon cycle and associated redox processes  
379 through time. *Philosophical Transactions of the Royal Society, B*, v. 361, p. 931-950.
- 380 32. Heberling, C., Lowell, R.P., Liu, L. & Fisk, M.R., 2010. Extent of the microbial  
381 biosphere in the oceanic crust. *Geochemistry Geophysics Geosystems*, v. 11,  
382 doi:10.1029/2009GC002968.
- 383 33. Herman, R.P., Provencio, K.R., Herrera-Matos, J. & Torrez, R.J., 1995. Resource islands  
384 predict the distribution of heterotrophic bacteria in Chihuahuan Desert soils. *Applied and*  
385 *Environmental Microbiology*, v. 61, p. 1816-1821.
- 386 34. Jennings, S., Mélin, F., Blanchard, J.L., Forster, R.M., Dulvy, N.K. & Wilson, R.W.,  
387 2008. Global-scale predictions of community and ecosystem properties from simple  
388 ecological theory. *Proceedings of the Royal Society B*, v. 275, p. 1375-1383.

- 389 35. Kallmeyer, J., Pockalny, R., Adhikari, R.R., Smith, D.C. & D'Hondt, S., 2012. Global  
390 distribution of microbial abundance and biomass in subseafloor sediment. *Proceedings of*  
391 *the National Academy of Sciences*, v. 109, p. 16213-16216.
- 392 36. Kasting, J.F. & Siefert, J.L., 2002. Life and the evolution of Earth's atmosphere. *Science*,  
393 v. 296, p. 1066-1068.
- 394 37. Kieft T.L., 2016. *Microbiology of the Deep Continental Biosphere*. In: Hurst C. (eds)  
395 *Their World: A Diversity of Microbial Environments. Advances in Environmental*  
396 *Microbiology*, v. 1. Springer, Cham.
- 397 38. Kenrick, P., Wellman, C.H., Schneider, H., & Edgecombe, G.D., 2012. A timeline for  
398 terrestrialization: consequences for the carbon cycle in the Palaeozoic. *Philosophical*  
399 *Transactions of the Royal Society B*, v. 367, p. 519-536.
- 400 39. Knauth, L.P. & Kennedy, M.J. 2009. The late Precambrian greening of the Earth. *Nature*,  
401 v. 460, p. 728-732.
- 402 40. Knoll, A.H., Bergmann, K.D. & Strauss, J.V., 2016. Life: the first two billion years. *Phil.*  
403 *Trans. R. Soc. B*, v. 371, p. 20150493.
- 404 41. Lalonde, S.V. and Konhauser, K.O., 2015. Benthic perspective on Earth's oldest  
405 evidence for oxygenic photosynthesis. *Proceedings of the National Academy of*  
406 *Sciences*, v. 112, p. 995-1000.
- 407
- 408 42. Lenton, T.M. & Daines, S.J., 2017. Matworld—the biogeochemical effects of early life on  
409 land. *New Phytologist*, v. 215, p. 531-537.
- 410 43. Lenton, T.M. & Watson, A.J., 2000. Redfield revisited 2. What regulates the oxygen  
411 content of the atmosphere? *Global Biogeochemical Cycles*, v. 14, p. 249-268.
- 412 44. Lin, L.H., Hall, J., Lippmann-Pipke, J., Ward, J.A., Sherwood Lollar, B., DeFlaun, M.,  
413 Rothmel, R., Moser, D., Gihring, T.M., Mislouck, B. & Onstott, T.C., 2005. Radiolytic  
414 H<sub>2</sub> in continental crust. Nuclear power for deep subsurface microbial communities;  
415 *Geochemistry, Geophysics, Geosystems*, v. 6, Q07003, doi:10.1029/2004GC000907.
- 416 45. Lipp, J.S., Morono, Y., Inagaki, F. & Hinrichs, K. U. 2008. Significant contribution of  
417 Archaea to extant biomass in marine subsurface sediments. *Nature*, v. 454, p. 991-994.
- 418 46. Lyons, T.W., Reinhard, C.T. & Planavsky, N.J., 2014. The rise of oxygen in Earth's early  
419 ocean and atmosphere. *Nature*, v. 506, p. 307-315.
- 420
- 421 47. Magnabosco, C., Moore, K.R., Wolfe, J.M. & Fournier, G.P., 2018. Dating phototrophic  
422 microbial lineages with reticulate gene histories. *Geobiology*, v. 16, p.179-189.
- 423
- 424 48. Magnabosco, C., Ryan, K., Lau, M.C., Kuloyo, O., Lollar, B.S., Kieft, T.L., Van  
425 Heerden, E. & Onstott, T.C., 2016. A metagenomic window into carbon metabolism at 3  
426 km depth in Precambrian continental crust. *The ISME journal*, v. 10, p.730-741.
- 427

- 428 49. Magnabosco, C., Tekere, M., Lau, M.C., Linage, B., Kuloyo, O., Erasmus, M., Cason, E.,  
429 van Heerden, E., Borgonie, G., Kieft, T.L. & Olivier, J., 2014. Comparisons of the  
430 composition and biogeographic distribution of the bacterial communities occupying  
431 South African thermal springs with those inhabiting deep subsurface fracture water.  
432 *Frontiers in Microbiology*, v. 5, p. 679.  
433
- 434 50. Martin, R.E., 1996. Secular increase in nutrient levels through the Phanerozoic:  
435 implications for productivity, biomass, and diversity of the marine biosphere. *Palaios*,  
436 209-219.
- 437 51. Martin, W., Baross, J., Kelley, D. & Russell, M.J., 2008. Hydrothermal vents and the  
438 origin of life. *Nature Reviews in Microbiology*, v. 6, p. 805-814.
- 439 52. Mason, O.U., Nakagawa, T., Rosner, M., Van Nostrand, J.D., Zhou, J., Maruyama, A.,  
440 Fisk, M.R. & Giovannoni, S.J., 2010. First investigation of the microbiology of the  
441 deepest layer of ocean crust. *PLoS one*, 5, p.e15399.
- 442 53. McMahon, S., O'Malley-James, J. & Parnell, J., 2013. Circumstellar habitable zones for  
443 deep terrestrial biospheres. *Planetary and Space Science*, v. 85, p. 312-318.
- 444 54. McMahon, S. & Parnell, J., 2014. Weighing the deep continental biosphere. *FEMS*  
445 *Microbiology Ecology*, v. 87, p. 113-120.
- 446 55. McMahon, W.J. & Davies, N.S., 2018. Evolution of alluvial mudrock forced by early  
447 land plants. *Science*, v. 359, p.1022-1024.
- 448 56. Michalski, J.R., Cuadros, J., Niles, P.B., Parnell, J., Rogers, A.D. & Wright, S.P. 2013.  
449 Groundwater activity on Mars and implications for a deep biosphere. *Nature Geoscience*,  
450 v. 6, p. 133-138.
- 451 57. Neaman, A., Chorover, J., Brantley, S.L., 2005. Element mobility patterns record organic  
452 ligands in soils on early Earth. *Geology*, v. 33, p. 117-120.
- 453 58. Olson, J.S., Watts, J.A. & Allison, L.J. 1983. Carbon in live vegetation of major world  
454 ecosystems. Oak Ridge National Laboratory Environmental Sciences Division  
455 Publication No. 1997. Washington D.C., U.S. Department of Energy.
- 456 59. O'Malley-James, J.T., Greaves, J.S., Raven, J.A. and Cockell, C.S., 2013. Swansong  
457 biospheres: refuges for life and novel microbial biospheres on terrestrial planets near the  
458 end of their habitable lifetimes. *International Journal of Astrobiology*, 12), pp.99-112.
- 459 60. Onstott, T.C., Phelps, T.J., Kieft, T., Colwell, F.S., Balkwill, D.L., Fredrickson, J.K., &  
460 Brockman, F.J. 1999. in: *Enigmatic Microorganisms and Life in Extreme Environments*  
461 (ed. J. Seckbach) p. 489-499. Kluwer, 1999.
- 462 61. Onstott, T.C., Magnabosco, C., Aubrey, A.D., Burton, A.S., Dworkin, J.P., Elsila, J.E.,  
463 Grunsfeld, S., Cao, B.H., Hein, J.E., Glavin, D.P. and Kieft, T.L., 2014. Does aspartic  
464 acid racemization constrain the depth limit of the subsurface biosphere?. *Geobiology*, v.  
465 12, p.1-19.

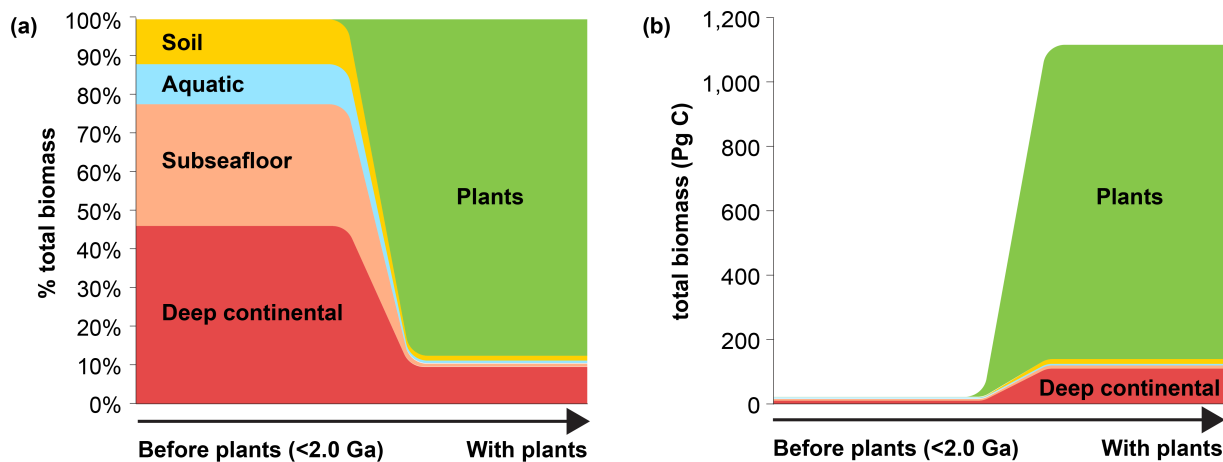
- 466 62. Orcutt, B.N., Sylvan, J.B., Knab, N.J. & Edwards, K.J., 2011. Microbial ecology of the  
467 dark ocean above, at, and below the seafloor. *Microbiology and Molecular Biology*  
468 *Reviews*, 75, 361-422.
- 469 63. Orsi, W.D., Edgcomb, V.P., Christman, G.D. & Biddle, J.F. 2013. Gene expression in the  
470 deep biosphere. *Nature*, v. 499, p. 205-208.
- 471 64. Parkes, R.J., Cragg, B., Roussel, E., Webster, G., Weightman, A. & Sass, H., 2014. A  
472 review of prokaryotic populations and processes in sub-seafloor sediments, including  
473 biosphere: geosphere interactions. *Marine Geology*, v. 352, p. 409-425.
- 474 65. Parnell, J., Boyce, A.J. & Blamey, N.J.F., 2010. Follow the methane: the search for a  
475 deep biosphere, and the case for sampling serpentinites, on Mars. *International Journal of*  
476 *Astrobiology*, v. 9, p. 193-200.
- 477 66. Pedersen, T.F. & Calvert, S.E. 1990. Anoxia vs. productivity: what controls the formation  
478 of organic-carbon-rich sediments and sedimentary rocks? *AAPG Bulletin*, v. 74, p. 454-  
479 466.
- 480 67. Peters, S.E. & Husson, J.M. 2017. Sediment cycling on continental and oceanic crust.  
481 *Geology*, doi:10.1130/G38861.1
- 482 68. Pinto, J.P. & Holland, H.D., 1988. Paleosols and the evolution of the atmosphere; Part II.  
483 *Geological Society of America Special Paper* v. 216, p. 21-34.
- 484 69. Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity  
485 and the distribution of biomass. *Oikos*, v. 86, p. 3-15.
- 486 70. Prave, A.R., 2002. Life on land in the Proterozoic: evidence from the Torridonian rocks  
487 of northwest Scotland. *Geology*, v. 30, p. 811-814.
- 488 71. Rasmussen, B., 2000. Filamentous microfossils in a 3,235-million-year-old volcanogenic  
489 massive sulphide deposit. *Nature*, v. 405, p. 676-679.
- 490 72. Reinhard, C.T., Planavsky, N.J., Gill, B.C., Ozaki, K., Robbins, L.J., Lyons, T.W.,  
491 Fischer, W.W., Wang, C., Cole, D.B. and Konhauser, K.O., 2017. Evolution of the global  
492 phosphorus cycle. *Nature*, v. 541, p. 386-389.
- 493  
494 73. Riding, R., 2006. Microbial carbonate abundance compared with fluctuations in  
495 metazoan diversity over geological time. *Sedimentary Geology*, v. 185, p. 229-238.
- 496 74. Ronov, A.B., Khain, V.E., Balukhovskiy, A.N. & Seslavinsky, K.B. 1980. Quantitative  
497 analysis of Phanerozoic sedimentation. *Sedimentary Geology*, v. 25, p. 311-325.
- 498 75. Rosing, M.T. & Frei, R., 2004. U-rich Archaean sea-floor sediments from Greenland –  
499 indications of >3700Ma oxygenic photosynthesis. *Earth and Planetary Science Letters*, v.  
500 217, p. 237-244.
- 501 76. Rothschild, L.J. & Mancinelli, R.L., 1990. Model of carbon fixation in microbial mats  
502 from 3,500 Myr ago to the present. *Nature*, v. 345, p. 710-712.

- 503  
504 77. Salas, E.C., Bhartia, R., Anderson, L., Hug, W.F., Reid, R.D., Iturrino, G. & Edwards,  
505 K.J., 2015. In situ detection of microbial life in the deep biosphere in igneous ocean  
506 crust. *Frontiers in microbiology*, v. 6, p.1260.  
507
- 508 78. Saltzman, M.R., 2005. Phosphorus, nitrogen, and the redox evolution of the Paleozoic  
509 oceans. *Geology*, v. 33, p. 573-576.
- 510 79. Saugier, B., Roy, J. & Mooney, H.A. 2001. Estimations of global terrestrial productivity:  
511 Converging toward a single number? In; Roy, J., Saugier, B. & Mooney, H.A. (eds)  
512 *Terrestrial Global Productivity*. Academic Press, New York, 543-557.
- 513 80. Schrenk, M.O., Huber, J.A. & Edwards, K.J., 2010. Microbial provinces in the  
514 seafloor. *Annual Reviews of Marine Science*, v. 2, p. 279-304.
- 515 81. Serna-Chavez, H.M., Fierer, N. & van Bodegom, P.M. 2013. Global drivers and patterns  
516 of microbial abundance in soil. *Global Ecology and Biogeography*, 22, 1162-1172.
- 517 82. Shen, Y., Farquhar, J., Masterson, A., Kaufman, A. J., & Buick, R., 2009. Evaluating the  
518 role of microbial sulfate reduction in the early Archean using quadruple isotope  
519 systematics. *Earth and Planetary Science Letters*, v. 279, p. 383–391.
- 520 83. Sherwood Lollar, B., Voglesonger, K., Lin, L.-H., Lacrampe-Couloume, G., Telling, J.,  
521 Abrajano, T.A., Onstott, T.C. & Pratt, L.M., 2007. Hydrogeologic controls on episodic  
522 H<sub>2</sub> release from Precambrian fractured rocks – energy for deep subsurface life on Earth  
523 and Mars. *Astrobiology*, v. 7, p. 971-986.
- 524 84. Sleep, N.H. & Bird, D.K., 2007. Niches of the pre-photosynthetic biosphere and geologic  
525 preservation of Earth's earliest ecology. *Geobiology*, v. 5, p. 101-117.
- 526 85. Smil, V., 2003. *The Earth's biosphere: Evolution, dynamics, and change*. MIT Press.
- 527 86. Stolper, D.A. and Keller, C.B., 2018. A record of deep-ocean dissolved O<sub>2</sub> from the  
528 oxidation state of iron in submarine basalts. *Nature*, 553, 323–327.
- 529 87. Stüeken, E.E., Catling, D.C. & Buick, R., 2012. Contributions to late Archaean sulphur  
530 cycling by life on land. *Nature Geoscience*, v. 5, p. 459-462.
- 531 88. Trumbore, S.E., 1997. Potential responses of soil organic carbon to global environmental  
532 change. *Proceedings of the National Academy of Sciences*, v. 94, 8284-8291.  
533
- 534 89. Ueno, Y., Yamada, K., Yoshida, N., Maruyama, S., & Isozaki, Y., 2006. Evidence from  
535 fluid inclusions for microbial methanogenesis in the early Archaean era. *Nature*, v. 440,  
536 p. 516–519.  
537
- 538 90. Wallace, M.W., Shuster, A., Greig, A., Planavsky, N.J. & Reed, C.P., 2017. Oxygenation  
539 history of the Neoproterozoic to early Phanerozoic and the rise of land plants. *Earth and  
540 Planetary Science Letters*, 466, 12-19.  
541

- 542 91. Wardle, D.A., 1992. A comparative assessment of factors which influence microbial  
 543 biomass carbon and nitrogen levels in soil. *Biological reviews*, v. 67, p. 321-358.  
 544  
 545 92. Watanabe, Y., Martini, J.E. & Ohmoto, H., 2000. Geochemical evidence for terrestrial  
 546 ecosystems 2.6 billion years ago. *Nature*, v. 408, p. 574-578.  
 547  
 548 93. Weiss, B.P., Yung, Y.L. & Neelson, K.H. 2000. Atmospheric energy for subsurface life  
 on Mars? *Proceedings National Academy of Sciences*, 97, 1395-1399.  
 549  
 550 94. Whitman, W.B., Coleman, D.C. & Wiebe, W.J., 1998. Prokaryotes: The unseen majority:  
*Proceedings of the National Academy of Sciences USA*, v. 95, p. 6578-6583.  
 551  
 552 95. Wolfe, J.M. and Fournier, G.P., 2018. Horizontal gene transfer constrains the timing of  
 methanogen evolution. *Nature Ecology & Evolution*, v. 2, p. 897.

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**Figure 1**



565  
 566 **Figure 1.** Earth's biomass carbon in different reservoirs pre- and post-vegetation, based on the  
 567 values (and mid-values of ranges) shown in Table 1, (a) as percentages of the total, and (b) as  
 568 absolute values.

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