

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 = 10¹⁵ 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 CO₂ (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 CO₂ 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 CO₂ 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, CO₂ and CH₄ 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**

Table 1.	Continental subsurface	Subseafloor	Aquatic	Soil	Plants
Biomass, Pg C					
With plants (pre-human)	20–200 ^{a,b,c}	10 ^{c,d}	3–8.5 ^e	15 ^f	980 ^{g,h,i}
Before plants (<2.0 Ga)	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*
264 *al.*, 2012). Given that plants proliferated so recently and are expected to die out with declining
265 CO₂ 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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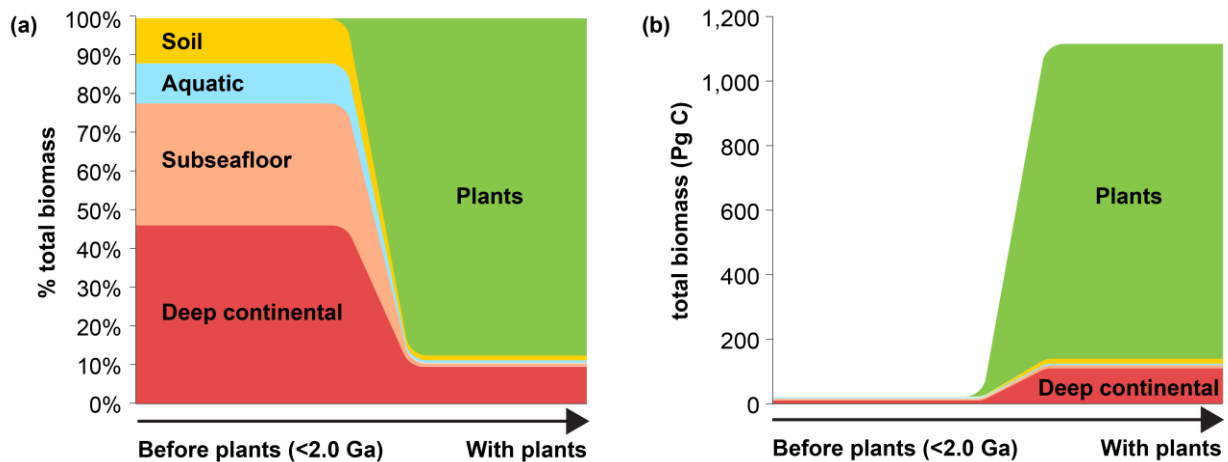
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Figure 1



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