

1      **Stabilization of the coupled oxygen and phosphorus cycles by the**  
2  
3    **evolution of bioturbation**

4 R.A. Boyle<sup>1,7,\*</sup>, T.W. Dahl<sup>1,2</sup>, A.W. Dale<sup>3</sup>, G.A. Shields-Zhou<sup>4</sup>, M. Zhu<sup>5</sup>, M.D. Brasier<sup>6</sup>, D.E.  
5 Canfield<sup>1</sup> & T.M. Lenton<sup>7</sup>

6 <sup>1</sup> Institute of Biology and Nordic Centre for Earth Evolution, University of Southern  
7 Denmark

8 <sup>2</sup>Natural History Museum of Denmark, University of Copenhagen, Denmark

9 <sup>3</sup>GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany

10 <sup>4</sup>Department of Earth Sciences, University College London, UK

11 <sup>5</sup>Nanjing Institute of Geology and Palaeontology, State Key Laboratory of Palaeobiology and  
12 Stratigraphy, Nanjing, China

13 <sup>6</sup>Department of Earth Sciences, University of Oxford, UK

14 <sup>7</sup>College of Life and Environmental Sciences, University of Exeter, UK

15 \*Corresponding author [rboyle@biology.sdu.dk](mailto:rboyle@biology.sdu.dk)

16 **Animal burrowing and sediment-mixing (bioturbation) began during the run up to the**  
17 **Ediacaran-Cambrian boundary<sup>1,2,3</sup>, initiating a transitional interval<sup>4,5</sup> separating**  
18 **stratified Precambrian<sup>6</sup> from well-mixed Phanerozoic<sup>7</sup> sediment archetypes. This rise in**  
19 **bioturbation occurred in between oxygen increases at ~551 million years ago (Ma)<sup>8,9</sup>**  
20 **and ~400(Ma)<sup>10</sup> million years ago(Ma), whilst the global oxygen reservoir was probably**  
21 **smaller than present<sup>10,11</sup>. Phosphorus is the long-term<sup>12</sup> limiting nutrient for oxygen**  
22 **production via burial of organic carbon<sup>13</sup>, and its retention (relative to carbon) within**

22 **organic matter in marine sediments is enhanced by bioturbation<sup>14-17</sup>, probably in part**  
23 **through increased microbial polyphosphate sequestration<sup>18</sup>. Here we show in a simple**  
24 **model that introducing this link between bioturbation and organic phosphorus burial**  
25 **robustly triggers a net decrease in atmospheric oxygen- the magnitude of which is**  
26 **contingent upon the prescribed difference in C:P ratios between bioturbated and**  
27 **laminated sediments. Bioturbation also reduces steady state marine phosphate levels,**  
28 **but this effect is offset by declining Fe-adsorbed phosphate burial with lower oxygen.**  
29 **Dynamical model simulations show how introducing oxygen-sensitive bioturbation**  
30 **triggers an initial oxygen decrease, which subsequently curtails bioturbation intensity in**  
31 **a net negative feedback loop. This trajectory is consistent with evidence for changes in**  
32 **ocean oxygenation concurrent with the rise of bioturbation.**

33 The first widely accepted trace fossil evidence for locomotion at about 565 Ma<sup>1</sup> is succeeded  
34 by very shallow, three dimensional burrowing from about 555 Ma<sup>2,3</sup>. This is followed by a  
35 diversity increase in observable bioturbation traces across the Ediacaran-Cambrian  
36 boundary,<sup>19</sup> e.g. from around 540 Ma burrows tend to appear in more inshore environments,  
37 and become larger and more frequently open-ended<sup>19,20</sup>. An emerging view of this early  
38 Cambrian “substrate revolution” suggests largely unmixed sediments in some parts of the  
39 continental shelf<sup>5</sup>, during what was presumably a spatially heterogeneous ocean sediment  
40 system, undergoing a transitional phase involving progressive loss of sediment stratification.  
41 Nevertheless, it is clear that by ~530-525 Ma the intensity of bioturbation had increased  
42 significantly<sup>3</sup>. Between Cambrian stages 1 (541~529 Ma) and 2 (~529~521Ma), maximum  
43 burrow depth rose to almost modern levels of up to a metre, and the bioturbation index (a  
44 measure of the percentage of primary bedding fabric disrupted by bioturbation<sup>21</sup>) changed  
45 from 0.5 to 2.3<sup>3</sup>, a value around which it remained around until Cambrian stage 5.

46 The palaeoredox context in which this biological change occurred is depicted in figure 1,  
47 which shows a compilation of U and Mo concentration and Mo isotope data,<sup>10</sup> compared to  
48 average and maximum bioturbation index<sup>21,3</sup> between 580-490 Ma. Between approximately  
49 520 and 510 Ma, after the initial increase in the average bioturbation index, marine shale  
50  $\delta^{98}\text{Mo}$ , U and Mo content points to declining oxygen, over a time interval of around 10-15  
51 million years. We argue this is consistent with a decrease in the size of the global oxygen  
52 reservoir immediately after the first appreciable bioturbation. It is important to emphasize the  
53 need for caution in any attempt at a quantitative reconstruction of oxygen's trajectory during  
54 this time interval, and that temporal variability is implied by existing data. For example, some  
55 data from ~499 Ma point to widespread euxinia<sup>11</sup>, although, conversely, a pulse of  
56 oxygenation has also been suggested 1-2 million years later<sup>22</sup>. Nevertheless the  $\delta^{98}\text{Mo}$  proxy  
57 does specifically focus on reservoir size changes<sup>10</sup>, and does imply declining oxygen.

58 The earliest moving animals would, of course, have required organic carbon for food, which  
59 today is predominantly buried in continental shelf sediments<sup>23</sup>. Within such sediments  
60 bioturbation would have reduced stratification, and bioirrigation would have increased  
61 reactive surface area for chemical exchange with the water column. The potential  
62 significance of the impact of these sort of changes on sediment composition is illustrated by  
63 the behaviour of phosphorus. Marine shales derived from bioturbated sediments exhibit  
64 organic C:P ratios as low as 150, whereas those derived from laminated sediments can have  
65 C:P ratios of up to 3900<sup>15</sup>, with typical values in the region of 500-700<sup>16,24</sup>. There are three  
66 probable mechanistic explanations<sup>14,15</sup> for these differences: (i) microbial polyphosphate  
67 sequestration in well-mixed sediments under oxygenated conditions<sup>14,18</sup>, with subsequent  
68 accumulation of refractory organic P compounds; (ii) greater retention of phosphate via  
69 adsorption on Fe-oxyhydroxides<sup>14,15</sup> in sediments exposed to oxygenated waters by  
70 bioturbation (leading to subsequent P burial in inorganic phases); and (iii) enhanced organic

71 carbon preservation in anoxic and/or euxinic conditions<sup>14</sup> (i.e. aside from any change in P),  
72 due ultimately to the increased energy yield of aerobic respiration.

73 These mechanisms are already represented in existing models of the long-term coupling  
74 between the phosphorus and oxygen cycles, but redox-linked changes in modelled C:P ratios  
75 of buried organic matter are expressed as a function of the ocean anoxic fraction, rather than  
76 bioturbation<sup>25,26</sup>. In this work, we focus on the timing of the onset of the sensitivity of organic  
77 phosphorus burial to ocean oxygenation, making the case that this sensitivity can be  
78 attributed to bioturbation. We hypothesize that increased exposure of sediments to oxygen in  
79 overlying water, caused by bioturbation and bioirrigation, initiated an organic phosphorus  
80 sink via increased microbial polyphosphate sequestration<sup>18</sup> (i.e. mechanism (i) above) for the  
81 first time during the early Cambrian.

82 We adapted an existing model<sup>26</sup> (see Methods), describing the coupled long-term dynamics  
83 of the marine phosphate and nitrate reservoirs, and the oxygen content of the atmosphere (and  
84 surface ocean). The model includes a weak inverse dependence of organic carbon burial on  
85 water column O<sub>2</sub><sup>13</sup> ((iii) above), as well as the removal of phosphate with ferric iron (Fe<sup>3+</sup>)  
86 oxyhydroxides<sup>25</sup>, which ceases under anoxic conditions ((ii) above). The burial flux of marine  
87 organic phosphorus  $mopb$  is related to that of marine organic carbon  $mocb$  through the  
88 bioturbated fraction  $f_{biot}$  of buried organic matter, which dictates the apportioning between  
89 the low burial ratio  $C : P_{biot}$  of bioturbated sediments, and the higher value of laminated  
90 sediments  $C : P_{lam}$  :

$$91 \quad mopb = mocb \cdot \left( \frac{f_{biot}}{C : P_{biot}} + \frac{1 - f_{biot}}{C : P_{lam}} \right) \quad (1)$$

92 Mathematically this is a very simple modification to existing models, but conceptually  
93 speaking, we suggest that bioturbation is more important in determining sedimentary organic

94 C:P burial ratios than the oxygenation state of the overlying water *per se*. For example,  
95 sediments intermittently oxygenated by bioturbation exhibit C:P ratios closer to permanently  
96 oxygenated sediments than to anoxic ones<sup>17</sup>, whereas even under an oxygenated water  
97 column an undisturbed sediment will go anoxic within about 2.5cm of the sediment-water  
98 interface<sup>27</sup>. Furthermore, we suggest that even incompletely mixed sediments would have  
99 undergone an increase in propensity to support microbial P sequestration through increased  
100 bioirrigation.

101 Our central result is depicted by the steady state solutions shown in figure 2. Increasing the  
102 bioturbated fraction  $f_{biot}$  of buried organic matter leads to a reduction in the size of the global  
103 oxygen reservoir - across the range of potential C:P burial ratios for bioturbated and  
104 laminated sediments, and across various different bulk weathering rates. This is because  
105 increased marine organic phosphorus burial results from increasing  $f_{biot}$ . The feedback  
106 sequence giving rise to this result is illustrated in figure 3, which shows example dynamical  
107 runs in which we ran the model to steady-state with negligible bioturbation ( $f_{biot} = 0.01$ ),  
108 before introducing oxygen sensitive bioturbation  $f_{biot} = 1 - anox$  (where *anox* is the anoxic  
109 fraction of ocean waters (see Methods)). Bioturbation leads to increased marine organic  
110 phosphorus burial, decreasing (phosphorus-limited) new production, marine organic carbon  
111 burial, and oxygen. As oxygen drops and anoxia increases, organic carbon burial increases  
112 due to reduced remineralisation. Increased anoxia also weakens the Fe-oxyhydroxide  
113 phosphate sink, causing a secondary increase in phosphate (therefore new production and  
114 organic carbon burial). This compensating increase in phosphate as anoxia rises explains why  
115 the impact of increased  $f_{biot}$  on the phosphate reservoir is weaker than the impact on oxygen.  
116 The differing response of the phosphate reservoir to that of oxygen is also affected by how  
117 close the system is to anoxia prior to the introduction of bioturbation. With low weathering

118  $W=0.5*$  present, the lower initial oxygen reservoir size means that the bioturbation-induced  
119 phosphate sink more easily increases anoxia, feeding back negatively on the Fe-P burial flux  
120 early in the simulation, and leading to the (counter-intuitive) slight net increase in deep ocean  
121 phosphate concentration. At higher weathering rates, the initial larger  $O_2$  reservoir means a  
122 greater initial phosphate/oxygen decrease is necessary to induce anoxia, and the overall  
123 impact on the phosphate reservoir at steady state is a negative one.

124 The oxygen-sensitivity of bioturbation used in the dynamical runs (figure 3), causes  $f_{biot}$  to  
125 decline asymptotically due to the drop in oxygen that it initially causes, and the resultant  
126 decrease in the organic phosphate burial flux helps the system approach a new, lower steady  
127 state oxygen level (see also supplementary figure S1). This qualitative feedback sequence is  
128 robust to changes in bulk weathering, the introduction of alternative formulations for  
129 oxidative weathering and organic carbon burial (supplementary figures S2, S3), increased  
130 C:P ratio differences (S4), and expression of  $f_{biot}$  as a direct increasing function of the global  
131 oxygen reservoir (S5) (as opposed to a decreasing function of anoxia). The key point that we  
132 wish to emphasize here is that the introduction of this feedback to the Earth system occurred  
133 as a consequence of the spread of the first bioturbating animals.

134 Quantitative thresholds on the overall change in the global oxygen and phosphate reservoirs  
135 that likely resulted from the introduction of bioturbation, were assessed by comparing pre-  
136 and post-bioturbation steady states across a range of simulations. Figure 4 depicts the  
137 difference between the steady states with negligible bioturbation ( $f_{biot}=0.01$ ) and with anoxia  
138 sensitive bioturbation ( $f_{biot}=1-anox$ ), for various C:P ratio and weathering parameters. The  
139 magnitude of the decline in the oxygen reservoir scales with the difference in C:P ratios  
140 between bioturbated and laminated sediments (also see supplementary figure S4). The size of  
141 the change in atmospheric oxygen also increases with the weathering flux of phosphorus (up  
142 to  $\sim 70\%$  of the present flux), above which anoxia (due to high productivity, rather than low

143 oxygen, see methods) leads to loss of Fe-P burial, limiting the potential change in phosphate  
144 that can be induced by the bioturbation-driven organic P sink.

145 The nature and stability of the pre-bioturbation oxygen/phosphorus steady state is an  
146 important outstanding uncertainty. A steady state with negligible bioturbation and weaker  
147 phosphate removal (i.e. higher  $C : P_{lam}$  within the pre-bioturbation organic phosphorus burial

148 flux  $mopb \approx \frac{m o c b}{C P_{lam}}$ ), entails higher oxygen, but must nevertheless remain consistent with

149 data for appreciable anoxia<sup>11</sup>, implying that the organic phosphorus sink cannot have been too  
150 weak, even before the onset of bioturbation (this constraint is formalised analytically in the  
151 supplemental). This means that either: (a) atmospheric oxygen remained below present levels  
152 through the latest Neoproterozoic, (with inorganic P-burial changes compensating for a high  
153  $C:P_{lam}$ , keeping oxygen low), (b) there was sufficient organic P-scavenging even before  
154 bioturbation to adequately reduce  $C:P_{lam}$  or (c) widespread anoxic conditions ceased with the  
155 Neoproterozoic oxygenation event (or at least were more restricted than present), only  
156 recurring much later. Intriguingly, the final possibility (c) would imply weak to negligible  
157 regulation of the oxygen reservoir (at least by ocean biogeochemistry) prior to the rise of  
158 bioturbation.

159 Some form of qualitative reorganisation of the global phosphorus cycle is broadly consistent  
160 with phosphorite deposition across the Precambrian-Cambrian boundary<sup>28</sup>, perhaps linked to  
161 increased anaerobic remineralization connected to a bioturbation-induced oxygen decline  
162 (S6). However, substantial phosphorite deposition occurs well before the onset of  
163 bioturbation<sup>28</sup>, so bioturbation cannot provide a comprehensive explanation for this  
164 phenomenon. A bioturbation-driven organic phosphorus sink is also potentially consistent  
165 with the downward trajectory of C:P ratios around 500 Ma<sup>29</sup>, although more data is needed  
166 for the earlier Cambrian to test this supposition. Most directly, the data we present in figure 1

167 shows how, after the initial increase in bioturbation intensity during Cambrian stage 2, the  
168 trace element data is consistent with a drop in ocean oxygenation and a relative decrease in  
169 the size of the global oxygen reservoir.

170 Our results thus suggest that the earliest bioturbating animals caused a relative decline in the  
171 size of the oxygen reservoir on which they depended, initiating a net negative feedback loop  
172 through the creation of an oxygen-sensitive phosphorus sink. This strengthened the link  
173 between the oxygen and phosphorus biogeochemical cycles, and contributed to oxygen  
174 regulation across Phanerozoic time.

## 175 **Methods**

### 176 *Redox-sensitive trace element data*

177 Molybdenum is soluble as the molybdate  $\text{MoO}_4^{2-}$  anion in oxygenated conditions, which is removed slowly via  
178 adsorption onto Mn oxides. In sulphidic solutions molybdate reacts with  $\text{H}_2\text{S}$  to form reactive  
179 oxythiomolybdates  $\text{MoO}_4\text{-}_x\text{S}_x^{2-}$  that are reductively removed from solution. Distinct isotopic fractionation and  
180 burial rates are associated with (a) fully oxygenated waters, (b) low oxygen non-euxinic settings that become  
181 sulphidic at depth and (c) fully euxinic settings. All these sinks preferentially remove  $^{95}\text{Mo}$ , but the strongest  
182 fractionation is associated with oxic settings, so that increasing seawater  $\delta^{98}\text{Mo}$  indicates increasing ocean  
183 oxygenation. Because the  $\delta^{98}\text{Mo}$  of euxinic shales can be lower than that of seawater, the maximum  $\delta^{98}\text{Mo}$   
184 value in shales (rather than the mean) is generally the most reliable indicator of the Mo isotopic composition of  
185 the oceans in which they were deposited. This maximum value is set by the fraction of ocean sediments that are  
186 fully oxygenated (because these oxygenated settings impart the strongest fractionation). Because Mo's residence  
187 time (today ~400 kyrs) is much longer than the mixing time of the Earth's oceans (~1.5 kyrs), seawater is well-  
188 mixed and homogenous with respect to Mo. Similarly, Uranium has a soluble oxidised state (hexavalent  
189  $\text{U(VI)}$ , stable in oxygenated water as uranyl-tetracarbonate  $\text{UO}_2(\text{CO}_3)_3^{4-}$ ) and an immobile reduced state  
190 (tetravalent  $\text{U(IV)}$ , readily sequestered into organic rich shales in low oxygen conditions). Figure 1 shows U  
191 concentration in shales, relative to total organic carbon (which will positively correlate with ambient seawater U  
192 concentration, thus ocean oxygenation). See (for example) Dahl et al 2010<sup>11</sup> and Partin et al 2013<sup>30</sup> for detailed  
193 considerations of ancient ocean oxygenation, in relation to Mo and U respectively. We argue that the fact that a



194 downward trajectory in ocean oxygenation is implicit in two distinct trace elements lends weight to the  
 195 possibility of a net oxygen decrease in conjunction with the rise of bioturbation.

196 *Model*

197 The “Redfield revisited” model by Lenton & Watson, 2000<sup>28</sup> (incorporating key phosphorus cycle functions by  
 198 Van Capellen & Ingall 1994<sup>27</sup>) describes the change over time in the size of the global phosphorus  $PO_4$  nitrate  
 199  $NO_3$  and oxygen  $O_2$  reservoirs:

$$200 \quad \frac{dPO_4}{dt} = phosw - fepb - capb - mopb \quad (2)$$

$$201 \quad \frac{dNO_3}{dt} = nfix - monb - denif \quad (3)$$

$$202 \quad \frac{dO_2}{dt} = mocb - oxidw \quad (4)$$

203 *Normalisation and reservoir size / concentration scaling*

204 The total size (in moles) of the above three reservoirs is assumed to scale linearly with the average concentration  
 205 (in  $\text{mol kg}^{-1}$  seawater) in marine surface waters ventilating the deep ocean, via scaling factors<sup>28</sup>

206  $k_{N,P} = 7.1 \times 10^{-22} \text{ kg}^{-1}$  and  $k_O = 8.96 \times 10^{-24} \text{ kg}^{-1}$ . Thus, concentrations in moles per kilogram seawater

207 are  $O_{2CONC} = O_2 \cdot k_O$  and  $NO_{3CONC} = NO_3 \cdot k_{N,P}$ ,  $PO_{4CONC} = PO_4 \cdot k_{N,P}$ . Present day average surface

208 water concentrations used for normalisation are  $O_{2CONC0} = 331.5 \times 10^{-6} \text{ mol kg}^{-1}$ ,

209  $NO_{3CONC0} = 30.9 \times 10^{-6} \text{ mol kg}^{-1}$ ,  $PO_{4CONC0} = 2.2 \times 10^{-6} \text{ mol kg}^{-1}$ , in micromoles per kilogram of

210 seawater. Where normalised concentrations are used (denoted by an overscore) we therefore have

$$211 \quad \overline{O_{2CONC}} = \frac{O_{2CONC}}{O_{2CONC0}}, \quad \overline{NO_{3CONC}} = \frac{NO_{3CONC}}{NO_{3CONC0}}, \quad \overline{PO_{4CONC}} = \frac{PO_{4CONC}}{PO_{4CONC0}}. \text{ When normalised reservoir sizes}$$

212 are referred to this is relative to present day values (in moles) of  $O_{20} = 3.7 \times 10^{19}$ ,  $NO_{30} = 4.35 \times 10^{16}$ ,

213  $PO_{40} = 3.1 \times 10^{15}$ .

214 *Fluxes*

215 Default values for fluxes and parameters are given in tables S1 and S2 in the supplemental.  $W$  denotes the bulk  
 216 weathering forcing relative to present. Fluxes are in units of moles per year, zero subscript denotes present day

217 value. Phosphorus is added to the ocean via phosphorus weathering  $phosw = W \cdot phosw_0$ , and removed by

218 iron-adsorbed phosphate burial  $fepb = fepb_0 \left( \frac{1 - anox}{k_{ox}} \right)$ , (where the anoxic fraction is

219  $anox = MAX(0, 1 - k_{ox} \cdot \frac{O_{2CONC}}{O_{2CONC0}} \cdot \frac{newp_0}{newp})$ ,  $k_{ox} = 0.86$  is the present day ocean's oxic fraction, and new

220 production  $newp = newp_0 \cdot MIN(117 PO_{4CONC}, \frac{117}{16} NO_{3CONC})$  in units of moles organic carbon per

221 kilogram seawater, scales stoichiometrically with limiting nutrient concentration. Phosphorus also leaves the

222 marine reservoir through calcium bound phosphate burial  $capb = capb_0 \cdot \left( \frac{newp}{newp_0} \right)^2$  and marine organic

223 phosphorus burial  $mopb = mocb \cdot \left( \frac{f_{biot}}{C : P_{biot}} + \frac{1 - f_{biot}}{C : P_{lam}} \right)$ . Nitrate changes via nitrogen fixation

224  $nfix = MAX(0, nfix_0 \cdot \left( \frac{PO_{4CONC} - \frac{NO_{3CONC}}{16}}{(PO_{4CONC0} - \frac{NO_{3CONC0}}{16}) \times 10^{-6}} \right))$  when nitrate is deficient relative to Redfield

225 stoichiometry with phosphate, marine organic nitrogen burial  $monb = \frac{mocb}{37.5}$  and denitrification

226  $denif = denif_0 \cdot \left( 1 + \frac{anox}{anox_0} \right)$ , but is not directly relevant to the results discussed in this paper, beyond

227 supporting the assumption that phosphorus is limiting over long timescales. Marine organic carbon burial

228  $mocb = mocb_0 \cdot \left( \frac{newp}{newp_0} \right)^2 \cdot De^{-BO_{2CONC}}$  (with  $D = 2.127$ ,  $B = 2277 mol^{-1} kg$ ) adds to the oxygen

229 reservoir, and oxidative weathering  $oxidw = oxidw_0 W$  removes from it.

230 This work differs from the original model by use of equation (1) in the main text and (for figures 3 & 4) by

231 putting  $f_{biot} = 1 - anox$ . The model was numerically integrated in Matlab using a Runge-Kutta solver. For

232 more detailed model description see supplementary methods and supplementary figure S7.

233 Analytic solutions show how simultaneous non-zero steady state oxygen and anoxia impose constraints on the

234 scaling factor used to relate marine organic carbon and phosphorus burial

235 
$$\frac{phosw_0 - \frac{fepb_0}{k_{ox} \cdot W} - \frac{capb_0}{f_{remin}}}{oxidw_0} \leq \frac{f_{biot}}{C : P_{biot}} + \frac{1 - f_{biot}}{C : P_{lam}} < \frac{phosw_0 - \frac{capb_0}{f_{remin}}}{oxidw_0}$$
, which can be rearranged to

236 give maximum and minimum values for  $f_{biot}$  in terms of the C:P burial ratios, or (for a pre-bioturbation ocean),

237 constrain the strength of the phosphorus sink in terms of  $C : P_{lam}$ . We also find that the partial derivative of

238 steady state normalised oxygen with respect to the bioturbated fraction is always less than zero

239 
$$\frac{\partial \overline{O_{2CONC}}}{\partial f_{biot}} = -\frac{W^{\frac{3}{2}} \cdot moch_0}{fepb_0 \sqrt{f_{remin}}} \left( \frac{1}{C : P_{biot}} - \frac{1}{C : P_{lam}} \right) < 0$$
, supporting the basic result. Default flux values

240 and derivation of analytic results are given in the supplementary methods.

## 241 **References**

242 1. Liu, A.G., McIlroy, D., & Brasier, M.D. First evidence for locomotion in the Ediacara

243 biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology* **38**, 123-126

244 (2010).

245 2. Menon, L., McIlroy, D. & Brasier, M.D. Evidence for Cnidaria-like behaviour in c. 560

246 Ma Ediacaran *Aspidella*. *Geology* **41**, 895-898. (2013).

247 3. Mangano, M & Buatois, L.A. Decoupling of body plan diversification and ecological

248 structuring during the Ediacaran-Cambrian transition: Evolutionary and geobiological

249 feedbacks. *Proc. R. Soc. B.* 281. 20140038. (2014).

250 4. Buatois, L.A., Narbonne, G.M., Mangano, M.G., Carmona, M.B. & Myrow, P.

251 “Ediacaran matground persisted into the earliest Cambrian.” *Nature Communications* 5.

252 3544. doi 10.1038/ncomms4544. (2014)

253 5. Tarhan, L.G. & Droser, M. L. Widespread delayed mixing in early to middle Cambrian

254 marine shelfal settings. *Palaeogeog. Palaeoclim, Palaeoecol.* 399. 310-322. (2014).

255 6. Seilacher, A. Biomat-related lifestyles in the Precambrian. *Palaios* 14. 86-93 (1999).

256 7. Droser, M.L. & Bottjer, D.J., Trends and patterns of Phanerozoic ichnofabrics. *Ann. Rev.*

257 *Earth. Planet. Sci. Lett.* **21**, 205-225 (1993).

- 258 8. Frei, R., Gaucher, C., Poulton, S.W. & Canfield, D.E. Fluctuations in Precambrian  
259 atmospheric oxygenation recorded by Chromium isotopes. *Nature* **461**. 250-254. (2009).
- 260 9. Scott, C, Lyons, T.W., Bekker, A., Shen, Y., Poulton, S.W., Chu, X. & Anbar, A.D.  
261 Tracing the stepwise oxidation of the Proterozoic ocean. *Nature* **452**. 456-460. 2008.
- 262 10. Dahl, T.W., Hammarlund, E.U., Anbar, A.D., Bond, D.P.G., Hill, B.C., Gordon, G.W.,  
263 Knoll, A.H., Nielsen, A.T., Schovsbo, N.H. & Canfield, D.E. Devonian rise in  
264 atmospheric oxygen correlated to the radiations in terrestrial plants and large predatory  
265 fish. *Proceedings of the National Academy of Sciences* **107**, 17911-17915 (2010).
- 266 11. Gill, B.C., Lyons, T.W., Young, S.A., Kump, L.R., Knoll, A.H. & Saltzman M.R.  
267 Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* **469**,  
268 80-83 (2011).
- 269 12. Redfield, A.C. The biological control of chemical factors in the environment. *American*  
270 *Scientist* **46**, 205-221 (1958).
- 271 13. Betts, J.N. & Holland, H.D. The oxygen content of ocean bottom waters, the burial  
272 efficiency of organic carbon, and the regulation of atmospheric oxygen.  
273 *Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change*  
274 *Section)* **97**, 5-18 (1991).
- 275 14. Ingall, E. & Jahnke, R. Evidence for enhanced phosphorus regeneration from marine  
276 sediments overlain by oxygen depleted waters. *Geochimica et Cosmochimica Acta* **58**,  
277 2571-2575 (1994).
- 278 15. Ingall, E.D., Bustin, R.M., & Van Cappellen, P. Influence of water column anoxia on the  
279 burial and preservation of carbon and phosphorus in marine shales. *Geochimica et*  
280 *Cosmochimica Acta* **57**, 303-316 (1993).
- 281 16. Anderson, L.D., Delaney, M.L. & Faul, K.L. Carbon to phosphorus ratios in sediments:  
282 Implications for nutrient cycling. *Global Biogeochemical Cycles* **15**, 65-79 (2001).

- 283 17. Aller, R.C. Bioturbation and remineralization of sedimentary organic matter: effects of  
284 redox oscillation. *Chemical Geology* **114**, 331-345 (1994).
- 285 18. Kerrn-Jespersen, J.P. & Henze, M. Biological phosphorus uptake under anoxic and  
286 aerobic conditions. *Water Research*. **27**, 617-324. (1993).
- 287 19. Droser, M.L. & Bottjer, D.J. Trends in depth and extent of bioturbation in Cambrian  
288 carbonate marine environments, western United States. *Geology* **16**, 233-236 (1988).
- 289 20. McIlroy, D. & Logan, G.A. The impact of bioturbation on infaunal ecology and evolution  
290 during the Proterozoic-Cambrian transition. *Palaios* **14**, 58-72 (1999).
- 291 21. Taylor, A. Goldring, R. & Gowland, S. Analysis and application of ichnofabrics. Earth  
292 Science Reviews 60. 227-259 (2003).
- 293 22. Saltzman, M.R., Young, S.E, Kump, L.R., Gill, B.C., Lyons, T.W. & Runnegar, B. Pulse  
294 of atmospheric oxygen during the late Cambrian. *Proceedings of the National Academy  
295 of Sciences* **108**, 3876-3881 (2011).
- 296 23. Berner, R.A. 1982. Burial of organic carbon and pyrite sulphur in the modern ocean: Its  
297 Geochemical and environmental significance? Am. J. Sci. 282. 451-473.
- 298 24. Slomp, C.P., Thomson, J. & de Lange, G.J. Controls on phosphorus regeneration and  
299 burial during formation of eastern Mediterranean sapropels. *Marine Geology* **203**, 141-  
300 159 (2004).
- 301 25. Van Cappellen, P. & Ingall, E.D. Benthic phosphorus regeneration, net primary  
302 production, and ocean anoxia: A model of the coupled marine biogeochemical cycles of  
303 carbon and phosphorus. *Paleoceanography* **9**, 677-692 (1994).
- 304 26. Lenton, T.M. & Watson, A.J. Redfield revisited: 2. What regulates the oxygen content of  
305 the atmosphere? *Global Biogeochemical Cycles* **14**, 249-268. (2000).
- 306 27. Gundersen, J.K. & Jorgensen, B.B. Microstructure of diffusive boundary layers and the  
307 oxygen uptake of the seafloor. *Nature* 345. 604-607. (1993).

- 308 28. Papineau, D., Global Biogeochemical Changes at Both Ends of the Proterozoic: Insights  
309 from Phosphorites. *Astrobiology* **10**, 165-181 (2010).
- 310 29. Algeo, T.J. & Ingall, E. Sedimentary Corg:P ratios, paleocean ventilation, and  
311 Phanerozoic atmospheric pO<sub>2</sub>. *Palaeogeography, Palaeoclimatology, Palaeoecology*  
312 **256**, 130-155 (2007).
- 313 30. Partin, C.A., Bekker, A., Planavsky N.J., Scott, C.T, Gill, B.C., Li, C., Podkovyrow, V,  
314 Maslov, A., Konhauser, K.O., Lalonde, S.V., Love, G.D, Poulton, S.W. & Lyons, T.W.  
315 “Large scale fluctuations in Precambrian atmospheric and oceanic oxygen levels from the  
316 record of U in shales”. *Earth. Plan. Sci. Lett.* 369-370, 284-293. (2013).

### 317 **Acknowledgements**

318 RAB, TML & GSZ gratefully acknowledge funding from the National Environment Research  
319 Council (NE/I005978/1). TWD was sponsored from the Inge Lehmann Scholarship and the  
320 VILLUM Foundation (VKR023127). MZ is funded by the National Basic Research Program  
321 of China (2013CB835000) and the National Natural Science Foundation of China  
322 (40930211). AWD was supported by the SFB754 funded by the German DFG  
323 (www.sfb754.de).

### 324 **Author contributions**

325 RAB developed the hypothesis including ideas from all co-authors. TWD provided data.  
326 RAB modified the original model of TML. RAB wrote the paper with input from all co-  
327 authors. Correspondence and requests for materials should be addressed to  
328 [rboyle@biology.sdu.dk](mailto:rboyle@biology.sdu.dk)

329

## 330 **Figure Legends**

331 **Figure 1. Redox proxy data is consistent with decreased oxygenation of the marine**  
332 **environment following the early Cambrian increase in bioturbation.**

333 **a-b.** Bioturbation data from Mangano & Buatois, 2014<sup>3</sup>. Bioturbation index<sup>22,3</sup> refers to %  
334 of the original sediment fabric exhibiting disturbance by bioturbation: 0=0%, 1=1–4%, 2=5–  
335 30%, 3=31–60%, 4=61–90%, 5=91–99%, 6=100%. **c.** Molybdenum isotope compositions  
336  $\delta^{98}\text{Mo} = [({}^{98}\text{Mo}/{}^{95}\text{Mo})_{\text{sample}} / ({}^{98}\text{Mo}/{}^{95}\text{Mo})_{\text{NIST-SRM3134}} - 1] \cdot 1000$  [‰]. Seawater  $\delta^{98}\text{Mo}$  scales  
337 positively with ocean oxygenation. The maximum  $\delta^{98}\text{Mo}$  value (rather than the mean) is the  
338 strongest indicator of the extent of ocean oxygenation, because mildly euxinic shales have a  
339 lower  $\delta^{98}\text{Mo}$  than ambient seawater. **d.** Mo/Total organic carbon (TOC), **e.** U/TOC and **f.**  
340 sedimentary Mo and U contents. Both Mo and U are soluble in oxic waters and more  
341 efficiently removed under anoxic and sulphidic conditions. Normalisation to TOC scales out  
342 the dependence of trace metal enrichment on total organic carbon content. Anoxic settings  
343 identified by  $\text{Fe:Al} > 0.5$ , euxinic settings by  $\text{Fe}_{(\text{Highly reactive}/\text{total})} > 0.38$  and  $\text{Fe}_{(\text{pyritised}/\text{highly reactive})}$   
344  $> 0.7$  (see table S3 for further details and full references). Arrows mark intervals of proposed  
345 relative oxygen decline.

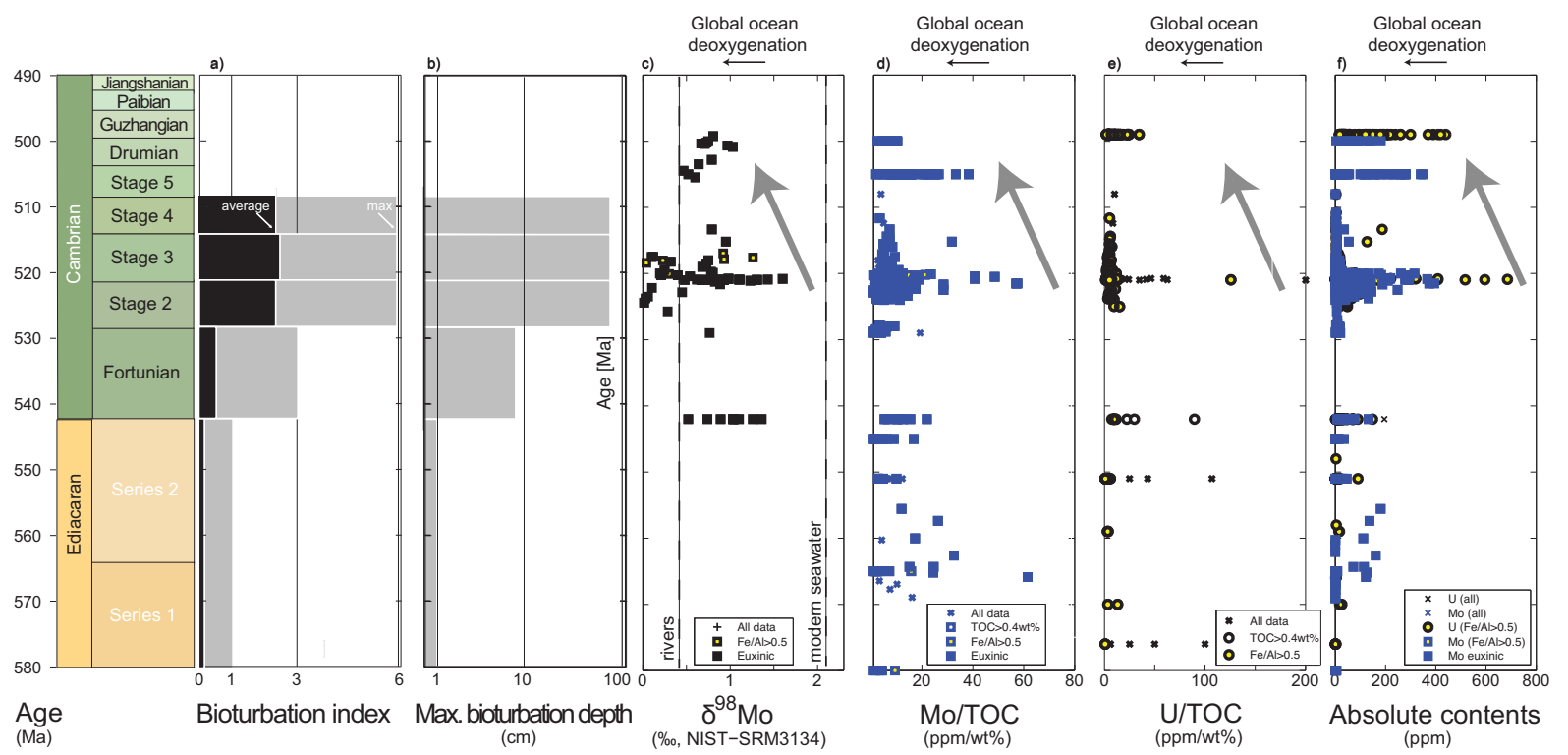
346 **Figure 2. Modelled steady-states oxygen/phosphorus reservoir sizes as a function of**  
347 **bioturbation.** Steady state size of the atmosphere/surface oxygen (blue, left) and marine  
348 phosphorus (green, right) reservoirs for different bulk weathering forcings  $W=0.5$  (a,b),  
349  $W=1.0$  (c,d),  $W=1.5$ (e,f) times the present value and different values for the organic carbon  
350 to phosphorus ratio for bioturbated  $C:P_{\text{biot}}$  and laminated  $C:P_{\text{lam}}$  sediments (different lines on  
351 each plot).

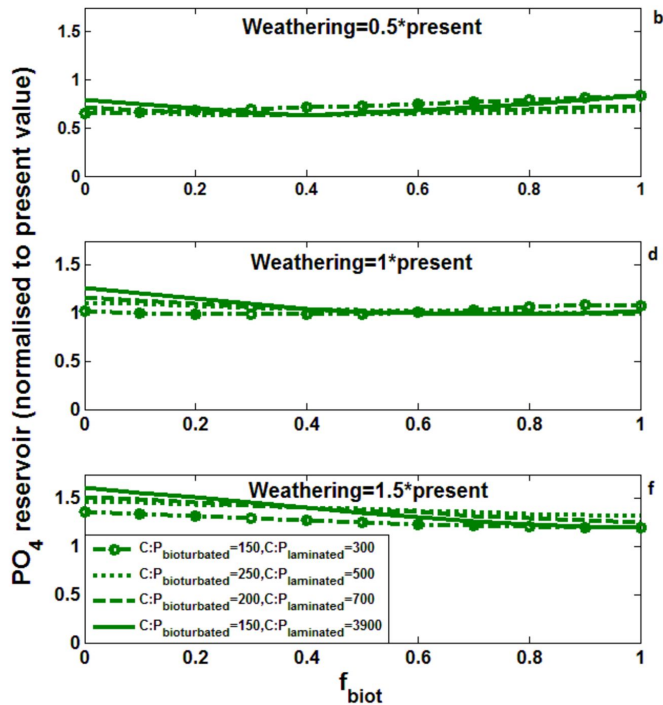
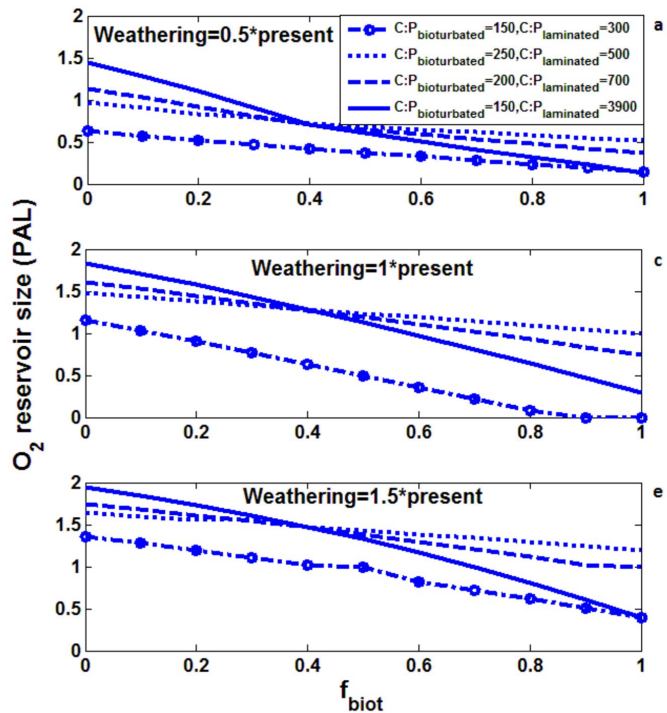
352 **Figure 3. Examples of dynamic model response to the introduction of oxygen-sensitive**  
353 **bioturbation.** Model initialised at a steady state with negligible bioturbation,  $f_{\text{biot}} = 0.01$ ,

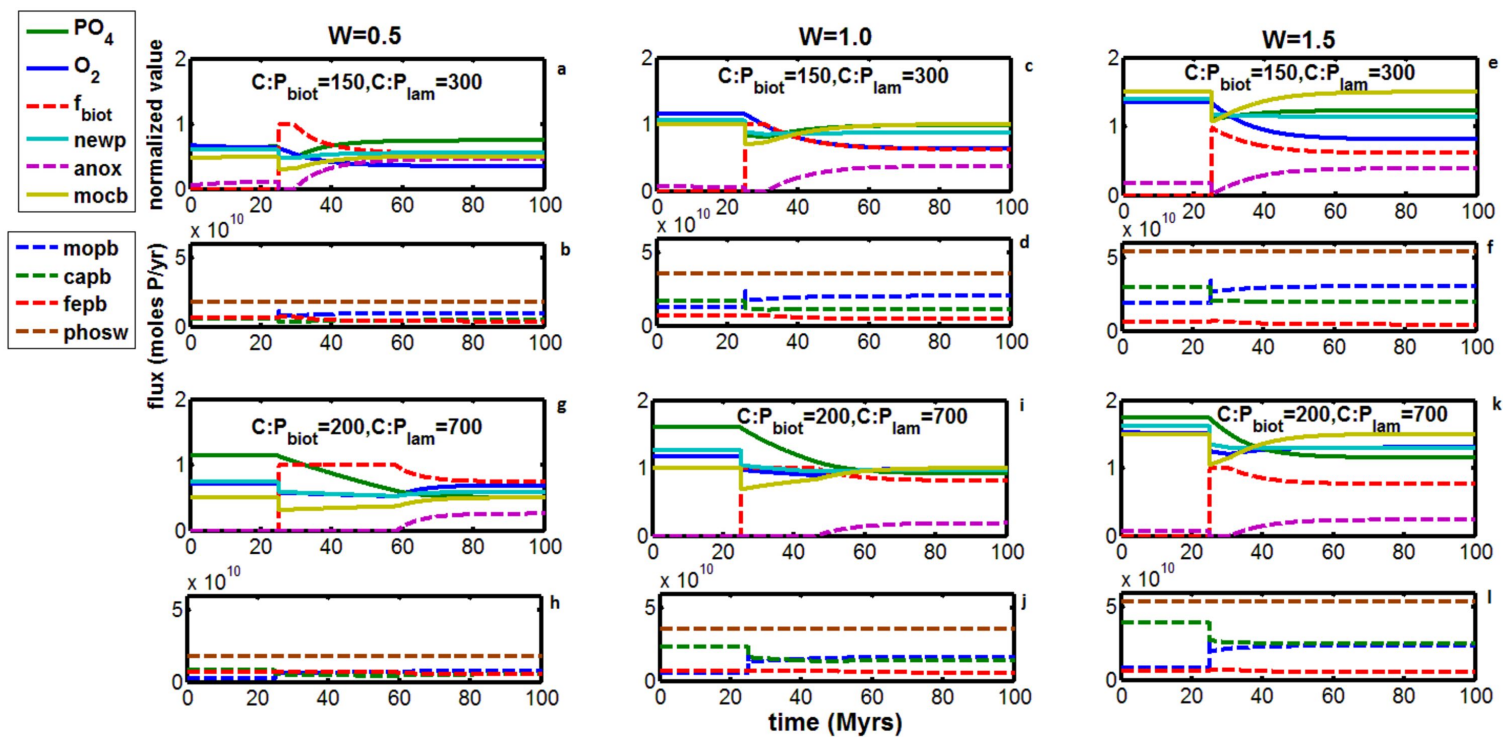
354 then dynamic bioturbation  $f_{biot} = 1 - anox$  (where *anox* is the ocean anoxic fraction) is  
355 introduced 25 million years into each 100 million year simulation. For each model run the  
356 upper panel shows the marine reservoirs (relative to their modern values) and relevant fluxes.  
357 The lower panel shows the fluxes affecting the phosphorus reservoir (in absolute values  
358 of  $10^{10}$  mol yr<sup>-1</sup>). Top two rows show a moderate difference in prescribed C:P burial ratios  
359  $C : P_{biot} = 150, C : P_{lam} = 300$  ((a,b), (c,d) and (e,f)), lower two rows a larger difference  
360  $C : P_{biot} = 200, C : P_{lam} = 700$  ((g,h), (i,j), (k,l)). Columns show different bulk weathering  
361 values  $W=0.5$  ((a,b) and (g,h)),  $W=1.0$  ((c,d) and (i,j)),  $W=1.5$  ((e,f) and (k,l)) left through  
362 right. Abbreviations:  $PO_4$ =marine phosphate reservoir,  $O_2$ =atmosphere/surface ocean  
363 oxygen reservoir,  $f_{biot}$ =bioturbated fraction of buried organic matter, *newp*=new production,  
364 *anox*=ocean anoxic fraction, *mocb*=marine organic carbon burial, *mopb*=marine organic  
365 phosphorus burial, *capb*=calcium-bound phosphate burial, *fepb*=iron adsorbed phosphate  
366 burial, *phosw*=phosphorus weathering.

367 **Figure 4. Net change in steady-state oxygen and phosphate reservoirs due to the**  
368 **introduction of dynamical oxygen-sensitive bioturbation.** The model was allowed to reach  
369 steady-state with negligible bioturbation, then dynamical bioturbation was introduced leading  
370 to a new steady-state (i.e. every point in figure 4 corresponds to a dynamical run as  
371 equivalent to figure 3). Pre-bioturbation reservoir sizes were subtracted from their respective  
372 post-bioturbation values, and the difference is expressed relative to the present-day reservoir  
373 size, i.e.  $\frac{O_{2(after)} - O_{2(before)}}{O_{20}}$  and  $\frac{PO_{4(after)} - PO_{4(before)}}{PO_{40}}$ . Results are shown as a function of bulk  
374 weathering rate (x-axis) and C:P burial ratio parameter choices (different lines, see legend). **a.**  
375 Change in atmosphere-surface-ocean oxygen reservoir. **b.** Change in marine phosphate  
376 reservoir.

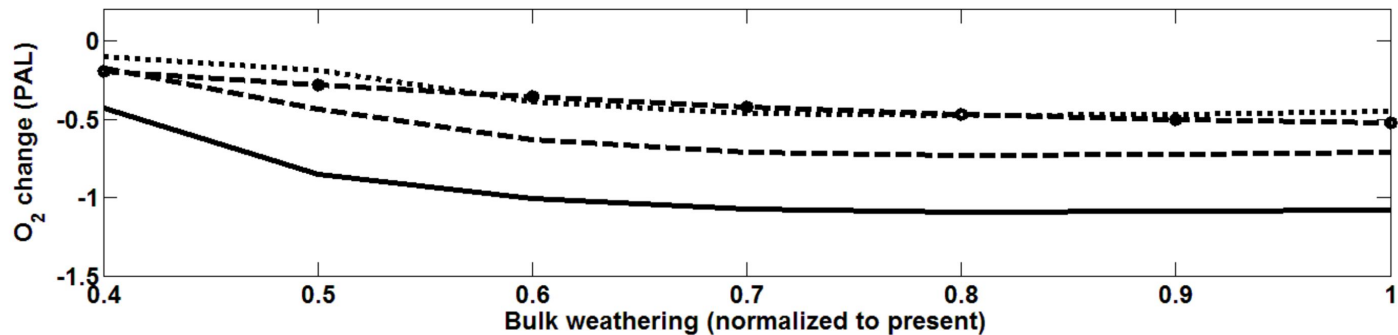




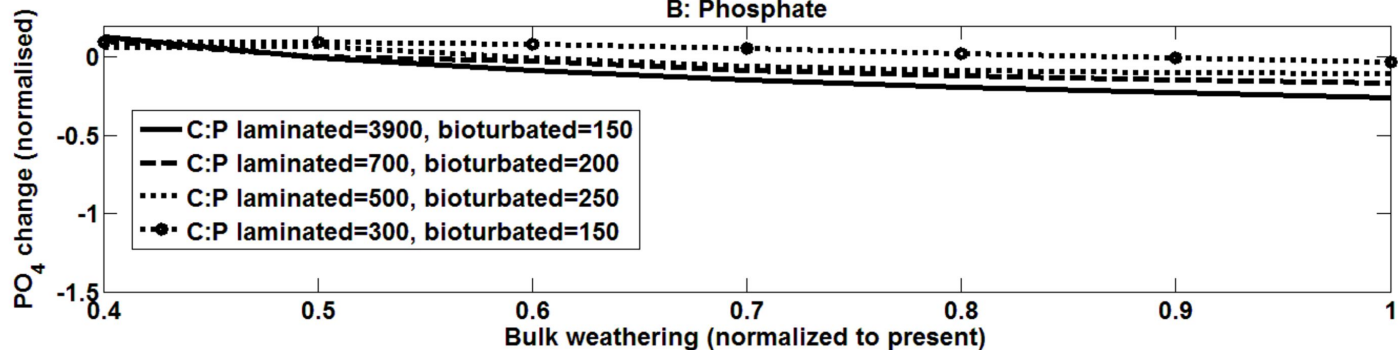


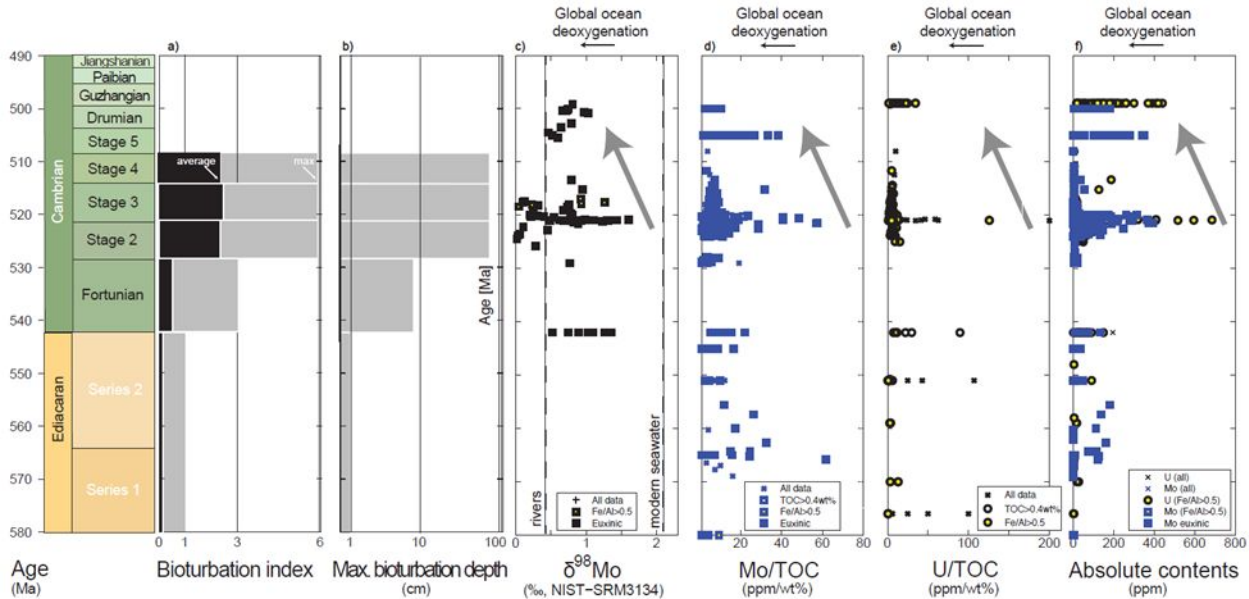


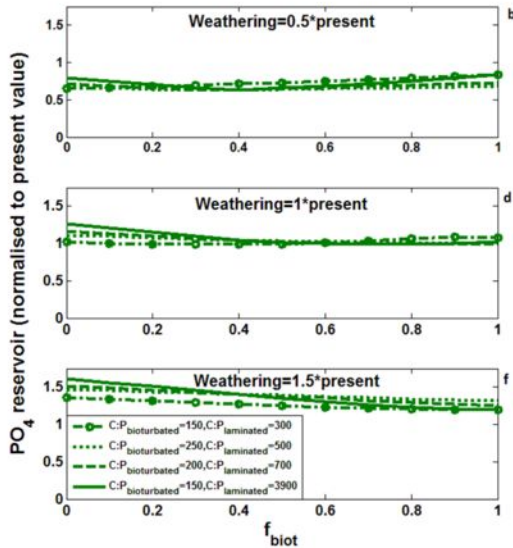
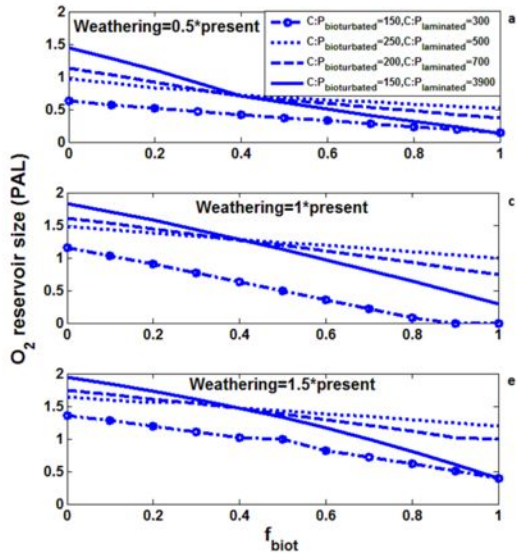
A: Oxygen

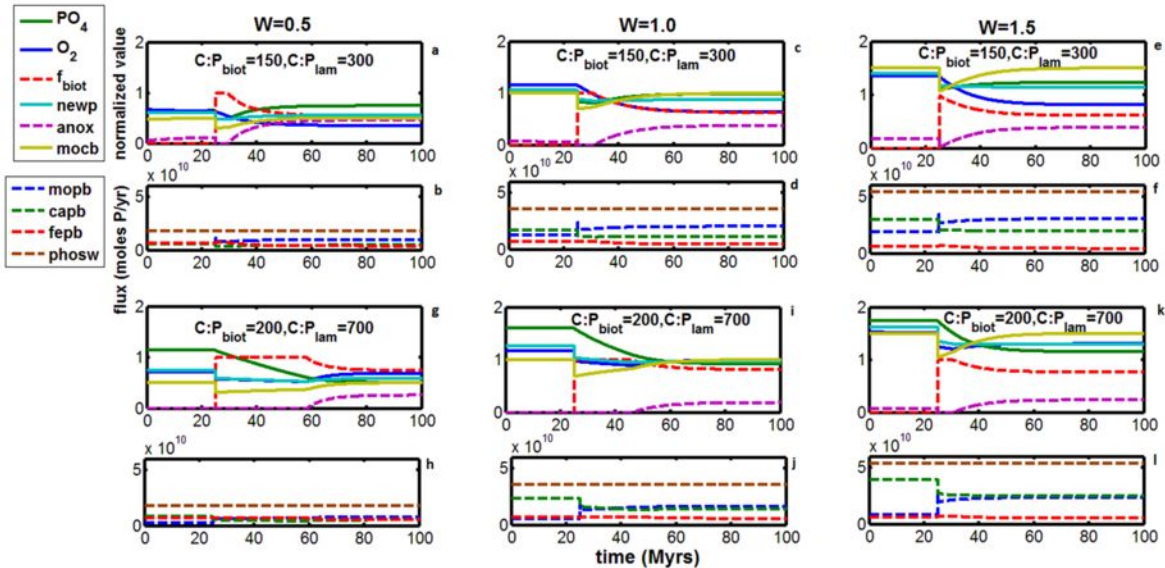


B: Phosphate

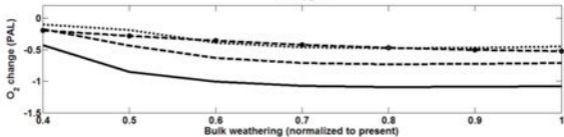








A: Oxygen



B: Phosphate

