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1 Word count with references and figure legends: 3661

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4 **The role of closed ecological systems in carbon cycle modelling**

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20 **Abstract**

21 Acquiring a mechanistic understanding of the role of the biotic feedbacks on the links
22 between atmospheric CO₂ concentrations and temperature is essential for trustworthy climate
23 predictions. Currently, computer based simulations are the only available tool to estimate the
24 global impact of the biotic feedbacks on future atmospheric CO₂ and temperatures. Here we
25 propose an alternative and complementary approaches by using materially closed and
26 energetically open analogue/physical models of the carbon cycle. We argue that there is
27 potential in using a materially closed approach to improve our understanding of the
28 magnitude and sign of many biotic feedbacks, and that recent technological advance make
29 this feasible. We also suggest how such systems could be designed and discuss the
30 advantages and limitations of establishing physical models of the global carbon cycle.

31

32 **1 Background**

33 As a species we are effectively “trapped” on a planet which, for all practical purposes, is
34 materially closed, but energetically open (Fuller and Snyder 1969). With the exception of the
35 cosmic debris that falls into the atmosphere and the negligible quantities of matter in satellites
36 and light gases that escape into outer space, the Earth is materially closed. We have no real
37 choice other than to survive within this closed system and, more critically, to ensure that it
38 remains sustainable. From cells to ecosystems and through to biomes, there is no other
39 biological or ecological scale besides the Biosphere (Vernadsky 1926) at which life is able to
40 persist in the absence of significant matter exchange; the consequences for ecological
41 systems at scales below the planetary scale are enormous (see section 2).

42 To date, our inherent inability to replicate the Earth as an experimental system has
43 considerably hindered our understanding of how the Earth functions. Indeed, the
44 consequences of increasing atmospheric concentrations of greenhouse gas emissions,
45 arguably the most challenging environmental issue of today, are extremely difficult to predict
46 (Solomon et al. 2007). The urgent need for trustworthy predictions of the future climate,
47 together with an improved understanding of the way in which the Earth functions, has fuelled
48 the rapid development of computer-based climate-carbon cycle coupled models, also known
49 as Earth System Models (ESM) (Lenton 2000, Friedlingstein et al. 2006). However, there are
50 concerns associated with embedded parameterisation and conflicting model outputs
51 (Friedlingstein et al. 2006). The ESM results presented in the latest IPCC report (Solomon et
52 al. 2007) indicated large uncertainties in predicting even the relatively short term temperature
53 increase by the end of the century. With the future climate of the Earth becoming a major
54 concern to governments, policymakers and citizens alike throughout the world (Solomon, et
55 al. 2007), we need all the available tools to help predict and mitigate future climate related
56 threats. However, somewhat worryingly, ESM are currently the only available tool to make
57 future predictions.

58 In most areas of science and technology, at some point, use has been made of
59 analogue (physical) models to force progress (Frigg 2006). For example, the wind tunnel was
60 and still is an essential tool in aeronautical and structural design despite extremely complex
61 and well-tested digital models of air flow. When dealing with complex systems, an analogue
62 is frequently constructed at an early stage. We believe that in the scientific dash to provide
63 climate change predictions this initial step of potential importance has been omitted. An
64 analogue approach could provide an alternative and independent tool capable of assessing the
65 impacts of future CO₂ concentrations and temperatures on biotic C feedback. Established in

66 materially closed but energetically open systems (just as the Earth), we argue that such
67 physical/analogue models of the C cycle are well suited to model biotic C feedbacks. This is
68 due to two essential features: i) ability to continuously and simultaneously allow two-way
69 feedbacks between the biotic and abiotic components to take place and ii) ability to provide
70 detailed mass balance. Moreover, studying the characteristics and behaviour of systems
71 which have been physically isolated from the surrounding space has proved to be a
72 fundamental step in many fields of research; physics (in thermodynamics) and chemistry
73 (Miller and Urey 1959, testing for the occurrence of chemical evolution) being the most
74 obvious examples. Thus, we contend that using CES as analogue model systems for climate
75 change research holds promise of answering some fundamental questions about the
76 functioning of ecosystems and, more specifically, about the carbon (C) cycle which underpins
77 them. In ecology, CES represent the only materially closed systems we have available for
78 study below the scale of the whole planet! But do we actually have the ecological, biological
79 and technological expertise to establish to establish CESs as model systems for climate
80 change research?

81 **2 Lessons from the past**

82 It could be argued that the history of CES started with Joseph Priestley's experiments with
83 mice, candles and the green alga, Chlorella (Priestley 1775) - which eventually led to the
84 discovery of oxygen. Much more recently, CES have been primarily used in attempts to
85 establish bioregenerative life support systems to supply and regenerate the air, food, water
86 and recycling waste required for human survival in space such as Bios 3 (Salisbury, et al.
87 1997) and Laboratory Biosphere (Nelson et al. 2003a) and, secondarily, as a basic tool in
88 aquatic ecology (Taub 1974, Taub 2009). However, our understanding of what makes a
89 closed system self sustainable is still poor. Winogradsky's columns (Winogradsky 1887) or

90 Folsome's (Folsome and Hanson 1986) small and rather simple aquatic systems (airtight vials
91 containing algae and microorganisms) stayed 'alive' more than 30 years, whilst the largest
92 and most sophisticated attempt to create an Earth analogue - Biosphere 2 project (Nelson et
93 al. 1993) reached dangerous levels of O₂ and CO₂ in less than a year (Cohen and Tilman
94 1996). This suggests a lack of mechanistic understanding of the basic principles that govern
95 the behaviour of CES.

96 The most often outcome of longer term closure is a collapse of the ecological system
97 due to imbalances in the autotrophic and heterotrophic gas fluxes (O₂ vs. CO₂) and/or the
98 nutrient release and uptake cycles (waste decomposition vs. nutrient absorption) (Nelson et
99 al. 2003b, Nita 2003). The Biosphere 2 project drew attention to the fact that species diversity
100 alone is not sufficient to induce a homeostatic and self-regulating (which implies that the
101 system remains within bounds of environmental variables compatible with life) Gaian effect
102 (Lovelock and Margulis 1974; Wilkinson 2003). It did signal, however, that if the amounts of
103 elements (e.g. carbon and nitrogen) in the main pools (atmosphere, biomass, soil and ocean)
104 and the mass ratios between the pools are departing from those of the Earth, there might be
105 severe consequences for the homeostatic capability of the system; the extensive use of highly
106 fertile soil (high in C and N) in the setup of Biosphere 2 led to the accumulation of dangerous
107 levels of CO₂ and N₂O in the atmosphere accompanied by a drastic decrease in atmospheric
108 O₂ (Cohen and Tilman 1996).

109 In the attempts to use CES as bioregenerative life support systems for space
110 exploration it became increasingly evident that some of the challenges facing the these
111 systems - such as renewal of water and atmosphere, nutrient cycling and waste recycling -
112 are strikingly similar to those of maintaining a sustainable global biosphere (Nelson, et al.
113 2003b). Notably, CES proved to be ideal for mass balance studies, but also for detecting

114 subtle effects and feedbacks, largely because of the amplification effect via accumulation
115 over time and which would otherwise be beyond the resolution of our materially open
116 experimental approaches (Nelson, et al. 2003b, Dempster 2008). For example this feature has
117 made CES the right tool for detecting unwanted trace compound accumulations with potential
118 major effects on the stability of the systems (e.g. damaging accumulation of Na⁺ in the soil or
119 ethylene in the air; Wheeler et al. 1996). Such subtle effects could not be detected in
120 materially open systems (Dempster 2008).

121 Early days of CES found that achieving a hermetic sealing is a non-trivial technical
122 challenge (Wheeler et al 1991, Corey and Wheeler 1992, Dempster 2008) for the
123 establishment of reliable CES. Meanwhile, the introduction of gas tracers (N₂O and helium)
124 and less gas permeable materials allowed to reduce the contamination rates in the more recent
125 attempts to create CES (Kliss et al. 2003 Lukac et al. 2010). This should permit the
126 establishment of smaller scale but replicated CES (Lukac et al .2010), previously avoided due
127 to the larger surface per volume ratio where minute physical leaks or permeation through the
128 wals could lead to very high atmospheric contamination rates.

129 **3 CESs as physical models for global carbon cycle modelling**

130 Currently we have reliable estimates of the global carbon (C) pools (Albritton, et al. 2001),
131 which allows for establishment of closed systems with precisely the same ratios of C in the
132 main pools as on Earth. Recent work showed that by combining the technological know-how
133 gained through the construction of life-support CES with the estimates of the global C pools
134 and fluxes, it is technologically feasible to set up small-scale materially closed systems as
135 analogue models for C modelling which allow a continuous and detailed monitoring of the
136 relevant environmental parameters (Lukac *et al.* 2010). Such systems do not have to be

137 indefinitely self-sustainable, but need to realistically emulate the global C pools and fluxes for
138 the duration of the experimental runs.

139 A simple terrestrial only analogue model of the pre-industrial C cycle with total
140 volume of ~120L could represent (*pro rata*) the 2011 GtC in soil, 900 GtC in vegetation and
141 560 GtC in the pre-industrial atmosphere by adding e.g. 2.85 g of dry arable soil (2.13% C),
142 0.53 g with 0.528 g FW (14% DW) plant biomass and adjusting the atmospheric CO₂ at 280
143 ppm. Light intensity can then be adjusted in order to balance the CO₂ uptake and release and
144 maintain the atmospheric CO₂ concentration ~ 280ppm, thus simulating the preindustrial
145 atmospheric CO₂ concentrations. Using the aforementioned (*pro rata*) representation of the
146 terrestrial C pools and the setup of Lukac et al. (2010) we found that, the atmospheric CO₂
147 concentration tends to stabilise (i.e. weekly slope of CO₂ concentration was not different
148 from zero) near the preindustrial atmospheric CO₂ concentrations a couple of weeks from the
149 onset (Fig. 1). Moreover, the presence or absence of light resulted in average daily CO₂
150 oscillations of ~ 9 p.p.m.v., of similar magnitude to the seasonal oscillations observed in the
151 Keeling curve (up to ~7 p.p.m.v.) and driven by the terrestrial biosphere (Keeling and Shertz
152 1992).

153 Such systems can thus be designed to address a multitude of key questions that have
154 never been tackled except in computer simulations. For example, a less explored angle of
155 CES is their use for detecting biotic feedbacks, which have become pivotal in understanding
156 the relationship between the CO₂ concentration in the atmosphere and global temperature
157 change (Cox, et al. 2000). Recently, the ESMs started to include biological feedbacks,
158 however, the magnitude of the modelled responses, and even their sign, are highly dependent
159 on the sensitivity of plant growth and soil respiration to temperature, which in turn are often
160 the output from another digital model (Jones, et al. 2003). In climate-carbon cycle coupled

161 ESModel the strength of the C cycle feedbacks is summarised as the relative gain (g) in
162 atmospheric CO₂ concentrations in relation to the uncoupled runs and depends on three
163 parameters: i) β , the sensitivity of land and ocean carbon uptake to CO₂ (GtC/p.p.m.v. CO₂),
164 ii) γ , the sensitivity of land and ocean carbon uptake to temperature (Gt C/°C) and iii) α , the
165 GCM temperature sensitivity to CO₂ (Friedlinstein et al. 2003, 2006). Designed with good
166 temperature control capabilities and a dynamic system of temperature control depending on
167 the CO₂ concentrations according to different climate sensitivities (i.e. mimicking the α) such
168 systems could focus on estimating the global biotic responses (β and γ). Any observed
169 changes in C pools will thus not be a result of the very simplistic temperature dependence
170 equations (Q10 values; Davidson et al. 2006), but of real biological processes driven by the
171 continuous two-way feedback between biotic (plant and rhizosphere) and abiotic components
172 (atmosphere and soil). Currently, global biotic C responses to climate change are mainly
173 parameterised on the basis of data originating from warming and Free-Air CO₂ Enrichment
174 (FACE) experiments. However, these approaches do not fully incorporate the continuous
175 two-way feedbacks between the biotic and abiotic components. The feedback loop can be
176 closed both in computer and in analogue models, however we argue that not having to
177 digitally reconstruct and parameterize all feedbacks is a major advantage of materially closed
178 analogue models.

179 The still arguable role of nitrogen availability and deposition in the terrestrial
180 biosphere's potential to slow the global atmospheric CO₂ build up (Reich, et al. 2006) could
181 also be tested for the first time outside a digital model. Another intriguing opportunity here, is
182 largely facilitated by the fact that, in *pro rata* systems, the daily C (as p.p.m.v. CO₂) uptake
183 and release during the daytime and night time in stabilised and C neutral systems (as those
184 presented in Fig. 1d) is similar to the estimated annual terrestrial C uptake. This information

185 can be used as proxy for devising multiple IPCC CO₂ emissions scenarios which could be
186 simulated over a shorter period of time. By simultaneously running scenarios with control (no
187 emissions) and emissions and without physically forcing a climate sensitivity (α), the
188 difference between the reached atmospheric CO₂ concentrations would allow to quantify the
189 gain due to biotic C feedbacks (g).

190 **4 Challenges and limitations**

191 Several challenges still have to be overcome if we are to use CES as reliable model
192 systems for climate change research. Leaving aside the cost factor, we argue that the system
193 size or the biological diversity included in the systems (considering Folsome's 1-5L flasks
194 and over 4000 species of plants and animals in Biosphere 2) have already proved not to be
195 the most critical aspects. The lack of replication and/or unrealistic amounts and mass ratios
196 of the main C and N pools proved to be the major drawback for the Biosphere 2 project and
197 this alone makes a strong argument for smaller but replicated systems. One possible
198 limitation of this approach is that certain processes observed in smaller scale systems might
199 show different sensitivities relative to the larger ones. The existence and eventual strength of
200 such a relationship, however, remain unexplored. At present this issue also affects the ESMs
201 and could be tackled by setting up analogue models of different sizes to verify if the observed
202 processes scale up linearly with size. In addition, the choice of species and the artificial
203 nature of the assembled communities could potentially affect the functioning of the analogue
204 models, a criticism which has often been put forward to explain the failure of the Biosphere 2 to
205 sustain the ecosystem services within the boundaries of human habitation (Cohen and Tilman
206 1996). We acknowledge that the construction of analogue models that incorporate elements
207 of global biotic and climatic heterogeneity represents a major challenge, but we argue that
208 this is achievable.

209 Evidently, some aspects of the carbon cycle cannot be captured in analogue models. It
210 has been a challenge so far to design systems which permit realistic transfer of matter
211 between separated sub-systems (e.g. between the terrestrial and aquatic components) short-
212 term C cycle (which includes photosynthesis, respiration, atmosphere–ocean exchange of
213 CO₂). The long-term C cycle (Berner 1993) and the associated processes that occur over
214 millions of years such as the C exchange between the bedrock and the surficial system or
215 aspects of the biogeochemical cycles which are closely tied to physics, especially in the
216 ocean (high pressure or depth), can only be addressed by digital models. Further, at the
217 present there is little information whether including both terrestrial and aquatic components
218 leads to an increase or has no effect on the homeostatic capability and viability of such
219 systems in the long-term. Over geological timescales, the concentration of atmospheric CO₂
220 is regulated by biogeochemical processes such as carbonate and silicate weathering (Walker,
221 et al. 1981) where the oceans ultimately play an important role. However, over ecological
222 timescales, which happens to be the scale at which our anthropogenic impact is manifested,
223 the level of atmospheric CO₂ is predominantly controlled by biological C uptake and release
224 via photosynthesis and respiration (e.g. seasonal variation in the Mauna Loa curve; Keeling
225 1976). In this respect, a physical model without an aquatic compartment should still be
226 informative depending on the addressed question.

227 **5 Conclusions**

228 Currently, we can only speculate what would happen in a CES setup as physical model for
229 biotic C feedbacks (as described in section 3) if we increase the temperature or if we simulate
230 the greenhouse effect by controlling the temperature depending on the atmospheric CO₂
231 concentration under different climate sensitivity scenarios. We deem CES as crucial in their
232 role as analogue models for climate change research, since they offer the possibility of

233 studying some of the mechanisms and process that otherwise would be almost impossible to
234 detect in materially open systems or could be masked at the global scale. Although still
235 ridden with challenges, the use of CES as physical (analogue) models for climate change
236 research is the only available approach to sit alongside, validate and challenge the
237 increasingly complex digital models. Whilst the development of analogue modelling for
238 climate change research is still at an early stage, we argue that this approach has the potential
239 to uncover key properties of the processes that drive global biotic feedbacks which will
240 ultimately help to predict future Earth system changes using ESMs with greater certainty.

241 *Acknowledgements*

242 We thank all the participants to the Workshop on Closed Ecological Systems organised by
243 the NERC Centre for Population Biology: Tim Benton, Mike Dixon, Larissa Hendrickx,
244 Andreas Heinemeyer, Oscar Monje, Mark Nelson, Frieda B. Taub, Tyler Volk, Raymond M.
245 Wheeler and Mathew Williams. Special thanks to David M. Wilkinson and Dennis Wildman
246 for their comments on the manuscript.

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248 **References**

249 Albritton D, Allen M, Baede A, Church J, Cubasch U, Xiaosu D, Yihui D, Ehhalt D, Folland
250 C, Giorgi F (2001) of Book: Climate Change 2001: The Scientific Basis. Contributions of
251 Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate
252 Change. Cambridge University Press.

253 Berner R (2003) The long-term carbon cycle, fossil fuels and atmospheric composition.
254 Nature 426:323-326.

- 255 Cohen J, Tilman D (1996) Biosphere 2 and Biodiversity--The Lessons So Far. *Science*
256 274:1150-1151.
- 257 Corey K, Wheeler R (1992) Gas exchange in NASA's biomass production chamber.
258 *BioScience* 42:503-509.
- 259 Cox P, Betts R, Jones C, Spall S, Totterdell I (2000) Acceleration of global warming due to
260 carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184-187.
- 261 Davidson E, Janssens I, Luo Y (2006) On the variability of respiration in terrestrial
262 ecosystems: moving beyond Q10. *Glob Change Biol* 12:154-164.
- 263 Dempster W (2008) Tightly closed ecological systems reveal atmospheric subtleties--
264 experience from Biosphere 2. *Adv Space Res* 42:1951-1956.
- 265 Folsome C, Hanson J (1986) The emergence of materially closed system ecology. *Ecosystem*
266 *Theory and Application*: 269-288.
- 267 Friedlingstein P, Bopp L, Rayner P, Cox P, Betts R, Jones C, Von Bloh W, Brovkin V,
268 Cadule P, Doney S (2006) Climate-carbon cycle feedback analysis: results from the C4MIP
269 model intercomparison. *Journal of Climate* 19:3337-3353.
- 270 Friedlingstein P, Dufresne J, Cox P, Rayner P (2003) How positive is the feedback between
271 climate change and the carbon cycle? *Tellus B* 55:692-700.
- 272 Frigg R, Hartmann S (2006) Models in science. *Stanford Encyclopedia of Philosophy*.
- 273 Fuller R, Snyder J (1969) Operating manual for spaceship earth. Southern Illinois University
274 Press Carbondale, Illinois.
- 275 Jones C, Cox P, Huntingford C (2003) Uncertainty in climate-carbon-cycle projections
276 associated with the sensitivity of soil respiration to temperature. *Tellus B* 55:642-648.
- 277 Keeling C, Bacastow R, Bainbridge A, Ekdahl Jr C, Guenther P, Waterman L, Chin J (1976)
278 Atmospheric carbon dioxide variations at Mauna Loa observatory, Hawaii. *Tellus* 28:538-
279 551.

- 280 Kliss M, Blackwell C, Zografos A, Drews M, Macelroy R, Mckenna R, Heyenga A (2003)
281 Initial closed operation of the CELSS test facility engineering development unit. *Adv Space*
282 *Res* 31:263-270.
- 283 Lenton T (2000) Land and ocean carbon cycle feedback effects on global warming in a
284 simple Earth system model. *Tellus* 52:1159-1188.
- 285 Lovelock J, Margulis L (1974) Atmospheric homeostasis by and for the biosphere- The Gaia
286 hypothesis. *Tellus* 26:2-10.
- 287 Lukac M, Milcu A, Wildman D, Anderson R, Sloan T, Ineson P (2010) Non intrusive
288 monitoring of atmospheric CO₂ in analogue models of terrestrial carbon cycle. *Methods in*
289 *Ecology and Evolution*. doi: 10.1111/j.2041-210X.2010.00058.x
- 290 Miller S, Urey H (1959) Organic Compound Synthes on the Primitive Eart Several questions
291 about the origin of life have been answered, but much remains to be studied. pp. 245-251.
- 292 Nelson M, Allen J, Ailing A, Dempster Wf, Silverstone S (2003) Earth applications of closed
293 ecological systems: Relevance to the development of sustainability in our global biosphere.
294 *Adv Space Res* 31:1649-1655.
- 295 Nelson M, Burgess T, Alling A, Alvarez-Romo N, Dempster W, Walford R, Allen J (1993)
296 Using a closed ecological system to study Earth's biosphere. *BioScience* 43:225-236.
- 297 Nelson M, Dempster Wf, Alling A, Allen Jp, Rasmussen R, Silverstone S, Van Thillo M
298 (2003) Initial experimental results from the laboratory biosphere closed ecological system
299 facility. *Adv Space Res* 31:1721-1730.
- 300 Nitta K (2003) New problems to be solved for establishing closed life support system. *Adv*
301 *Space Res* 31:63-68.
- 302 Priestley J (1772) *Experiments and Observations on Different Kinds of Air*. *J Phil Trans*
303 62:147-264 .

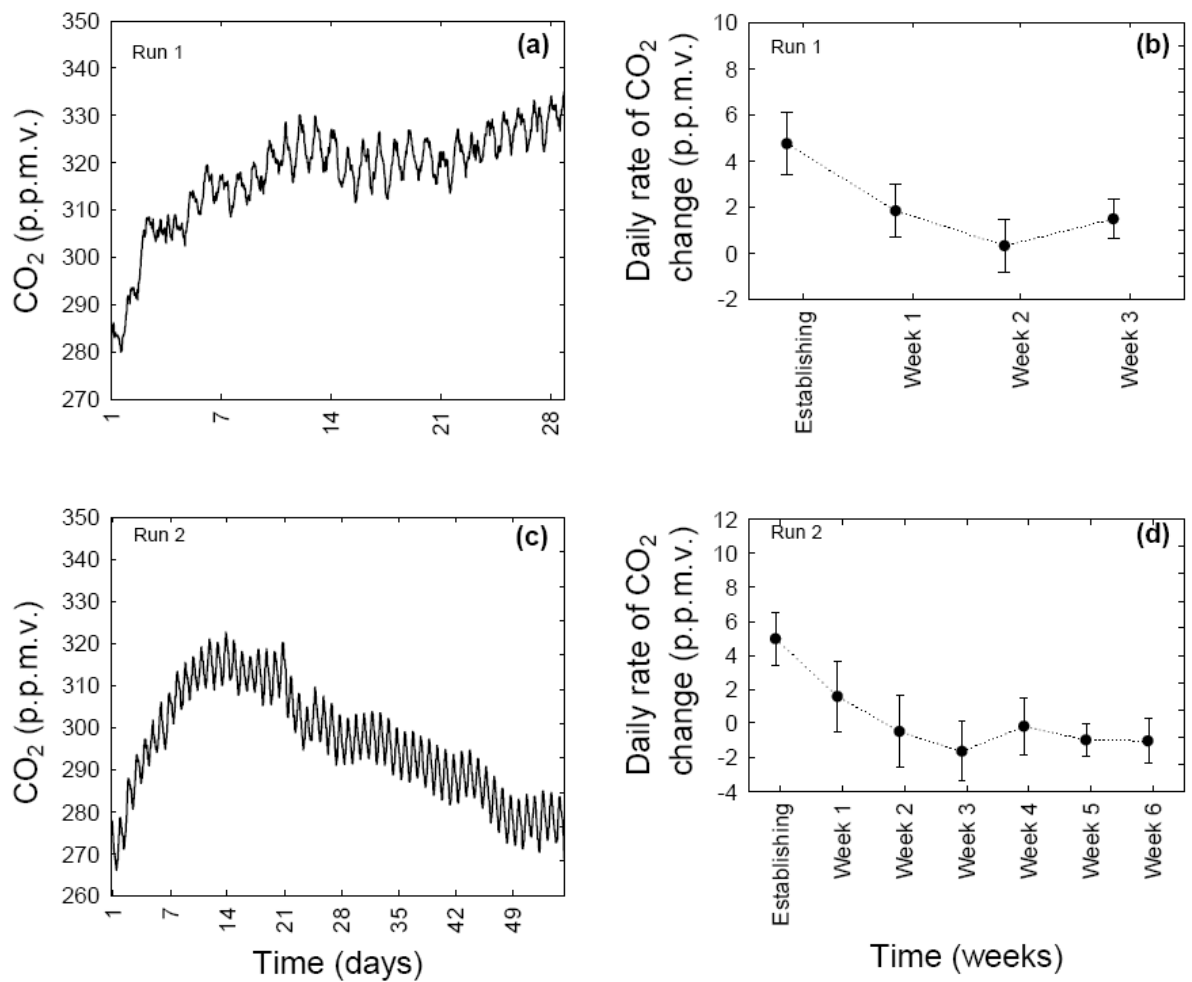
- 304 Reich P, Hobbie S, Lee T, Ellsworth D, West J, Tilman D, Knops J, Naeem S, Trost J (2006)
305 Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440:922-
306 925.
- 307 Salisbury F, Gitelson J, Lisovsky G (1997) Bios-3: Siberian Experiments in Bioregenerative
308 Life Support. *BioScience* 47:575-585.
- 309 Solomon S, Qin D, Manning M, Marquis M, Averyt K, Tignor Mmb, Miller Hlj, Chen Z
310 (2007) *Climate change 2007: the physical science basis; Contribution of Working Group I to*
311 *the fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge
312 Univ. Press.
- 313 Taub F (2009) Community metabolism of aquatic Closed Ecological Systems: Effects of
314 nitrogen sources. *Adv Space Res* 44:949-957.
- 315 Taub F (1974) Closed ecological systems. *Annual Reviews of Ecology and Systematics*
316 5:139-160.
- 317 Vernadsky V (1926) *The Biosphere*. Abridged English edition published in 1986 by
318 Synergetic Press, Oracle, Arizona.
- 319 Wheeler R, Drese J, Sager J (1991) Atmospheric leakage and condensate production in
320 NASA's biomass production chamber. Effect of diurnal temperature cycles. John F. Kennedy
321 Space Center . NASA Technical Memorandum 103819.
- 322 Wheeler R, Peterson B, Sager J, Knott W (1996) Ethylene production by plants in a closed
323 environment. *Adv Space Res* 18:193-196.
- 324 Wilkinson D (2003) The fundamental processes in ecology: a thought experiment on
325 extraterrestrial biospheres. *Biol Rev* 78:171-179.
- 326 Winogradsky S (1887) *Über Schwefelbakterien*. *Bot. Zeitung* 45:489-610.
- 327
- 328

329 **Figure legend**

330 Average atmospheric CO₂ concentrations trends (a, c) and daily rate of CO₂ change (b, d) in
 331 two independent experimental runs setup with scaled-down ratios of the terrestrial C cycle; n
 332 = 5.

333

334 **Figure 1**



335