The role of closed ecological systems in carbon cycle modelling

Alexandru Milcu & Martin Lukac & Phil Ineson

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

1 Background

As a species we are effectively "trapped" on a planet which, for all practical purposes, is materially closed, but energetically open (Fuller and Snyder [1969\)](#page-6-0). With the exception of the cosmic debris that falls into the atmosphere and the negligible quantities of matter in satellites and the light gases that escape into outer space, the Earth is materially closed (Morowitz et al. [2005\)](#page-6-0). We have no real choice other than to survive within this closed system and, more critically, to ensure that it remains sustainable. From cells to ecosystems and through to biomes, there is no other biological or ecological scale besides the Biosphere (Vernadsky [1926](#page-7-0)) at which life is able to persist in the absence of significant matter

A. Milcu $(\boxtimes) \cdot M$. Lukac

NERC Centre for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK e-mail: a.milcu@imperial.ac.uk

M. Lukac School of Agriculture, Policy and Development, University of Reading, RG6 6AR Reading, UK

exchange; the consequences of limiting material exchange for ecological systems at scales below the planetary scale are enormous (see section 2).

To date, our inability to replicate the Earth as an experimental system has considerably hindered our understanding of how the Earth functions. Indeed, the consequences of increasing atmospheric concentrations of greenhouse gases, arguably the most challenging environmental issue of today, are extremely difficult to predict (Solomon et al. [2007\)](#page-7-0). The urgent need for trustworthy predictions of the future climate, together with an improved understanding of the way in which the Earth functions, has fuelled the rapid development of computer-based climate-carbon cycle coupled models, also known as Earth System Models (ESMs) (Lenton [2000;](#page-6-0) Friedlingstein et al. [2006\)](#page-6-0). However, there are concerns associated with embedded parameterisation and conflicting model outputs (Friedlingstein et al. [2006](#page-6-0)). The ESMs results included in the latest IPCC report (Solomon et al. [2007\)](#page-7-0) indicate large uncertainties in predicting even the relatively short term temperature increase by the end of the century. With the future climate of the Earth becoming a major concern to governments, policymakers and citizens alike throughout the world (Solomon et al. [2007](#page-7-0)), we need all the available tools to help predict and mitigate future climate related threats. However, somewhat worryingly, ESMs are currently the only available tool to make future predictions.

In most areas of science and technology, at some point, use has been made of analogue (physical) models to force progress (Frigg and Hartmann [2006](#page-6-0)). For example, the wind tunnel was and still is an essential tool in aeronautical and structural design despite extremely complex and well-tested computer simulations. When dealing with complex systems, an analogue is frequently constructed at an early stage. We believe that in the scientific dash to provide climate change predictions this initial step of potential importance has been omitted. For example, an analogue approach could provide an alternative and independent tool capable of assessing the impacts of future $CO₂$ concentrations and temperatures on biotic C feedback. Established in materially closed, energetically open systems (just as the Earth), we argue that such physical/analogue models of the C cycle are well suited to model biotic C feedbacks. This is due to two essential features: i) ability to continuously and simultaneously allow the two-way feedbacks between the biotic and abiotic components to take place and ii) ability to perform detailed mass balance analyses.

Studying the characteristics and behaviour of systems which have been physically isolated from the surrounding space has proved to be a fundamental step in many fields of research; physics (in thermodynamics) and chemistry (Miller and Urey [1959](#page-6-0), testing for the occurrence of chemical evolution) being the most obvious examples. Thus, we contend that using CES as analogue model systems for climate change research holds promise of answering some fundamental questions about the functioning of ecosystems and, more specifically, about the carbon (C) cycle which underpins them. In ecology, CES represent the only materially closed systems we have available for study below the scale of the whole planet! But do we actually have the ecological, biological and technological expertise to establish to establish CESs as model systems for climate change research?

2 Lessons from the past

It could be argued that the history of CES started with Joseph Priestley's experiments with mice, candles and the green alga, Chlorella (Priestley [1772](#page-6-0))—which eventually led to the discovery of oxygen. Much more recently, CES have been primarily used in attempts to establish bioregenerative life support systems that aim to supply and regenerate the air,

food, water and waste recycling required for human survival in space such as Bios 3 (Salisbury, et al. [1997\)](#page-7-0) and Laboratory Biosphere (Nelson et al. [2003a](#page-6-0)). Infrequently, CES have been used as a basic tool in aquatic ecology (Taub [1974](#page-7-0); Taub [2009\)](#page-7-0). However, our understanding of what makes a closed system self sustainable is still poor. Winogradsky's columns (Winogradsky [1887\)](#page-7-0) or Folsome's (Folsome and Hanson [1986\)](#page-6-0) small and rather simple aquatic systems (airtight vials containing algae and microorganisms) stayed 'alive' more than 30 years, whilst the largest and most sophisticated attempt to create an Earth analogue—Biosphere 2 project (Nelson et al. [1993\)](#page-6-0)—reached dangerous levels of O_2 and $CO₂$ in less than a year (Cohen and Tilman [1996](#page-6-0)). This suggests a lack of mechanistic understanding of the basic principles that govern the behaviour of CES.

The most frequent outcome of longer term closure is a collapse of the ecological system due to imbalances in the autotrophic and heterotrophic gas fluxes $(O_2 \text{ vs. } CO_2)$ and/or the nutrient release and uptake cycles (waste decomposition vs. nutrient absorption) (Nelson et al. [2003b;](#page-6-0) Nitta [2003](#page-6-0)). The Biosphere 2 project drew attention to the fact that species diversity alone is not sufficient to induce a homeostatic and self-regulating (i.e. the system remains within bounds of environmental variables compatible with life) Gaian effect (Lovelock and Margulis [1974;](#page-6-0) Wilkinson [2003\)](#page-7-0). It did signal, however, that if the amounts of elements [(e.g. C and nitrogen (N)] in the main pools (atmosphere, biomass, soil and ocean) and the mass ratios between the pools are departing from those of the Earth, there might be severe consequences for the homeostatic capability of the system; the extensive use of highly fertile soil (high in C and N) in the setup of Biosphere 2 led to the accumulation of dangerous levels of $CO₂$ and $N₂O$ in the atmosphere accompanied by a drastic decrease in atmospheric $O₂$ (Cohen and Tilman [1996\)](#page-6-0).

In the attempts to use CES as bioregenerative life support systems for space exploration it became increasingly evident that some of the challenges facing the these systems—such as renewal of water and atmosphere, nutrient cycling and waste recycling—are strikingly similar to those of maintaining a sustainable global biosphere (Nelson et al. [2003b](#page-6-0)). Notably, CES proved to be ideal for mass balance studies, but also for detecting subtle effects and feedbacks, largely because of the amplification effect via accumulation over time, which allows detecting changes that remain beyond the resolution of materially open systems (Nelson et al. [2003b;](#page-6-0) Dempster [2008\)](#page-6-0). For example, this feature has made CES the right tool for detecting unwanted trace compound accumulations with potential major effects on the stability of the systems (e.g. damaging accumulation of $Na⁺$ in the soil or ethylene in the air; Wheeler et al. [1996\)](#page-7-0).

Early days of CES found that achieving a hermetic sealing is a non-trivial technical challenge (Wheeler et al. [1991;](#page-7-0) Corey and Wheeler [1992;](#page-6-0) Dempster [2008\)](#page-6-0) for the establishment of reliable CES. Meanwhile, the introduction of gas tracers (N_2O) and helium) and less gas permeable materials allowed to reduce the contamination rates in the more recent attempts to create CES (Kliss et al. [2003;](#page-6-0) Lukac et al. [2010\)](#page-6-0). This should permit the establishment of smaller scale but replicated CES (Lukac et al. [2010](#page-6-0)), previously avoided due to the larger surface per volume ratio where minute physical leaks or permeation through the wals could lead to very high atmospheric contamination rates.

3 CESs as physical models for global carbon cycle modelling

Currently we have reliable estimates of the global carbon (C) pools (Albritton et al. [2001](#page-6-0)), which allows for establishment of CES with precisely the same ratios of C in the main pools as on Earth. Recent work showed that by combining the technological know-how

gained through the construction of life-support CES with the estimates of the global C pools and fluxes, it is technologically feasible to set up small-scale materially closed systems as analogue models whilst continuously and non-invasively monitoring the relevant environmental parameters (Lukac et al. [2010](#page-6-0)). Such systems do not have to be indefinitely self-sustainable, but need to realistically emulate the global C polls and fluxes for the duration of the experimental runs.

A simple terrestrial only analogue model of the pre-industrial C cycle with total volume of \sim 120 L could represent (*pro rata*) the 2011 GtC in soil, 900 GtC in vegetation and 560 GtC in the pre-industrial atmosphere by adding e.g. 2.85 g of dry arable soil $(2.13\% \text{ C})$, 0.53 g with 0.528 g FW (14% DW) plant biomass and adjusting the atmospheric CO_2 at 280 ppm. Light intensity can then be adjusted in order to balance the $CO₂$ uptake and release and maintain the atmospheric $CO₂$ concentration ~280 p.p.m.v., thus simulating the preindustrial atmospheric $CO₂$ concentrations. Using the aforementioned (*pro rata*) representation of the terrestrial C pools and the setup of Lukac et al. [\(2010](#page-6-0)) we found that, the atmospheric CO_2 concentration tends to stabilise (i.e. weekly slope of CO_2) concentration was not different from zero) near the preindustrial atmospheric $CO₂$ concentrations within a couple of weeks post-closure (Fig. 1). Moreover, the presence or absence of light resulted in average daily $CO₂$ oscillations of ~9 p.p.m.v., of similar magnitude to the seasonal oscillations observed in the Keeling curve (up to \sim 7 p.p.m.v.), and which is mainly driven by the terrestrial biosphere (Keeling and Shertz [1992\)](#page-6-0).

Fig. 1 Average atmospheric CO₂ concentrations trends (a, c) and daily rate of CO₂ change (b, d) in two independent experimental runs setup with scaled-down ratios of the terrestrial C cycle; $n=5$

Such systems can thus be designed to address a multitude of key questions that have never been tackled except in computer simulations. For example, a less explored angle of CES is their use for detecting biotic feedbacks, which have became pivotal in understanding the relationship between the $CO₂$ concentration in the atmosphere and global temperature change (Cox et al. [2000](#page-6-0)). Recently, the ESMs started to include biological feedbacks however, the magnitude of the modelled responses, and even their direction, are highly dependent on the sensitivity of plant growth and soil respiration to temperature, which in turn are often the output from another computer simulation (Jones et al. [2003\)](#page-6-0). In climate-carbon cycle coupled ESMs the strength of the C cycle feedbacks is summarised as the relative gain (g) in atmospheric CO₂ concentrations in relation to the runs not including biotic C feedbacks (uncoupled runs) and depends on three parameters: i) β , the sensitivity of land and ocean carbon uptake to $CO₂$ (GtC/p.p.m.v. CO₂), ii) γ , the sensitivity of land and ocean carbon uptake to temperature (Gt C/ $^{\circ}$ C) and iii) α , the GCM temperature sensitivity to CO₂ (Friedlingstein et al. [2003](#page-6-0); [2006](#page-6-0)). Analogue models of the C cycle designed with good temperature control capabilities and a dynamic system of temperature control depending on the $CO₂$ concentrations according to different climate sensitivities (i.e. mimicking the α) could thus focus on estimating the global biotic responses (β and γ). Any observed changes in C pools will thus not be a result of the very simplistic temperature dependence equations $(Q_{10}$ values; Davidson et al. [2006\)](#page-6-0), but of real biological processes driven by the continuous two-way feedback between biotic (plant and rhizosphere) and abiotic components (atmosphere and soil). Currently, global biotic C responses to climate change are mainly parameterised on the basis of data originating from warming and Free-Air CO₂ Enrichment (FACE) experiments. However, these approaches do not fully incorporate the continuous two-way feedbacks between the biotic and abiotic components since the parameterisation of the $CO₂$ fertilisation effect has never been derived from an experimental system where the plant response directly impacts on the ambient $CO₂$ concentration and temperature, which in turn is known to feed back on the photosynthesis rate. The feedback loop can be closed both in computer simulations and in analogue models however, we argue that not having to reconstruct and parameterize fluxes and feedbacks is a major advantage of analogue models.

The still arguable role of nitrogen (N) availability for the terrestrial biosphere's potential to slow the global atmospheric $CO₂$ build up (Reich et al. [2006](#page-7-0)) could also be tested in analogue models. Another intriguing opportunity is largely facilitated by the fact that, in *pro rata* systems, the daily C (as p.p.m.v $CO₂$) uptake and release during the daytime and night time in stabilised, (i.e. C neutral systems as those presented in Fig. [1d](#page-3-0)) systems is comparable to the estimated annual terrestrial C uptake. This information can be used as proxy for devising multiple IPCC $CO₂$ emissions scenarios which could be simulated over a shorter period of time. By simultaneously running scenarios with control (no $CO₂$ emissions) and emissions, with and without physically forcing a climate sensitivity (α) , the difference between the reached atmospheric $CO₂$ concentrations would allow to quantify the gain due to biotic C feedbacks (g).

4 Challenges and limitations

Several challenges still have to be overcome if we are to use CES as reliable model systems for climate change research. Leaving aside the cost factor, we argue that the system size or the biological diversity included in the systems (considering Folsome's 1–5 L flasks and over 4000 species of plants and animals in Biosphere 2) have already proved not to be the most critical aspects. The lack of replication and/or unrealistic amounts and mass ratios of the main C and N pools proved to be the major drawback for the Biosphere 2 project and this alone makes a strong argument for smaller but replicated systems. One possible limitation of this approach is that certain processes observed in smaller scale systems might show different sensitivities relative to the larger ones. The existence and eventual strength of such a relationship, however, remain unexplored. At present this issue also affects the ESMs and could be tackled by setting up analogue models of different sizes to verify if the observed processes scale up linearly with size. In addition, the choice of species and the artificial nature of the assembled communities could potentially affect the functioning of the analogue models, a criticism which has often put forward to explain the failure of the Biosphere 2 to sustain the ecosystem services within the boundaries of human habitation (Cohen and Tilman [1996\)](#page-6-0). We acknowledge that the construction of analogue models that incorporate elements of global biotic and climatic heterogeneity represents a major challenge, but we argue that this is achievable.

Evidently, some aspects of the C cycle cannot be captured in analogue models. It has been a challenge so far to design systems which permit realistic transfer of matter and energy between adjacent sub-systems (e.g. between the terrestrial and aquatic components). Furthermore, there is little information whether including both terrestrial and aquatic components leads to an increase or has no effect on the homeostatic capability and viability of such systems in the long-term. Whilst the analogue models are reasonably good at emulating the short-term C cycle (which includes photosynthesis, respiration, atmosphere– ocean exchange of $CO₂$), the long-term C cycle (Berner [2003\)](#page-6-0) and the associated processes that occur over millions of years such as the C exchange between the bedrock and the surficial system or aspects of the biogeochemical cycles which are closely tied to physics, especially in the ocean (high pressure and depth), can only be addressed by computer simulations. Over geological timescales, the concentration of atmospheric $CO₂$ is regulated by biogeochemical processes such as carbonate and silicate weathering (Walker et al. [1981\)](#page-7-0) where the oceans ultimately play an important role. However, over ecological timescales, which happens to be the scale at which our anthropogenic impact is manifested, the level of atmospheric $CO₂$ is predominantly controlled by biological C uptake and release via photosynthesis and respiration (e.g. seasonal variation in the Mauna Loa curve; Keeling et al. [1976](#page-6-0)). In this respect, a physical model emulating the short-term C cycle should still be informative depending on the addressed question.

5 Conclusions

Currently, we can only speculate what would happen in a CES setup as physical model for biotic C feedbacks (as described in section [3](#page-2-0)) if we increase the temperature or if we simulate the greenhouse effect by controlling the temperature depending on the atmospheric $CO₂$ concentration under different climate sensitivity scenarios. We deem CES as crucial in their role as analogue models for climate change research, since they offer the possibility of studying some of the mechanisms and process that otherwise would be almost impossible to detect in materially open systems or could be masked at the global scale. Although still riddled with challenges, the use of CES as analogue/physical models for climate change research is the only available approach to sit alongside, validate and challenge the increasingly complex computer simulations. Whilst the development of analogue modelling for climate change research is still at an early stage, we argue that this approach has the potential to uncover key properties of the processes that drive global biotic feedbacks which will ultimately help to improve the ESMs.

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