Journal of Theoretical Biology 414 (2017) 17–34

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Multiple states of environmental regulation in well-mixed model biospheres

Arwen E. Nicholson[a,*], David M. Wilkinson[b,c], Hywel T.P. Williams[a], Timothy M. Lenton[a]

[a] Earth System Science, University of Exeter, UK
[b] Natural Science and Psychology, Liverpool John Moores University, UK
[c] School of Life Sciences, University of Lincoln, UK

ARTICLE INFO

Keywords:
Gaia
Self-regulation
Complexity
Feedback
Agent-based model

ABSTRACT

The Gaia hypothesis postulates that life influences Earth's feedback mechanisms to form a self regulating system. This provokes the question: how can global self-regulation evolve? Most models demonstrating environmental regulation involving life have relied on alignment between local selection and global regulation. In these models environment-improving individuals or communities spread to outcompete environment degrading individuals/communities, leading to global regulation, but this depends on local differences in environmental conditions. In contrast, well-mixed components of the Earth system, such as the atmosphere, lack local environmental differentiation. These previous models do not explain how global regulation can emerge in a system with no well defined local environment, or where the local environment is overwhelmed by global effects. We present a model of self-regulation by 'microbes' in an environment with no spatial structure. These microbes affect an abiotic 'temperature' as a byproduct of metabolism. We demonstrate that global self-regulation can arise in the absence of spatial structure in a diverse ecosystem without localised environmental effects. We find that systems can exhibit nutrient limitation and two temperature limitation regimes where the temperature is maintained at a near constant value. During temperature regulation, the total temperature change caused by the microbes is kept near constant by the total population expanding or contracting to absorb the impacts of new mutants on the average affect on the temperature per microbe. Dramatic shifts between low temperature regulation and high temperature regulation can occur when a mutant arises that causes the sign of the temperature effect to change. This result implies that self-regulating feedback loops can arise without the need for spatial structure, weakening criticisms of the Gaia hypothesis that state that with just one Earth, global regulation has no mechanism for developing because natural selection requires selection between multiple entities.

1. Introduction

The Gaia hypothesis postulates that life on Earth interacts with abiotic processes to form a complex self regulating system that maintains habitable conditions on the planet (Lovelock and Margulis, 1974; Lenton, 1998; Lovelock, 2000). This is evolutionary ecology at the very largest spatial and temporal scales (Wilkinson, 2006). Critics of the theory argue that any organism acting to improve the habitability of the planet would have to contend with "cheaters" who do not contribute to regulation, or that a system would be just as likely to drive itself extinct as it would to drive itself towards stability (Doolittle, 1981; Dawkins, 1982). This leads to the question: how can self-regulation evolve in a way consistent with evolutionary theory? With only one Earth, and thus a lack of data to analyse, this question has been addressed using theoretical models. Hence we describe other models to put this study into context.

The Daisyworld model (Watson and Lovelock, 1983) was the first model to present global regulation emerging by local selection of individual level traits that contribute to global regulation. In the original Daisyworld there are two species of daisy – black daisies that have a low albedo and white daisies that have a high albedo. The growth of daisies is a function of temperature and all daisies have the same ideal temperature for maximum growth rate. Incoming radiation from a 'sun' that evolves in the manner of a typical main sequence star, heats Daisyworld. Daisyworld initially starts off too cool for any daisy growth, but as the sun evolves the incoming solar radiation becomes high enough for the surface temperature to allow daisy growth. Black daisies are the first to appear. By absorbing more solar radiation they warm their local environment encouraging their own growth and warming the global environment. When the temperature increases enough, cooling high albedo white daisies appear. The balance between the number of white cooling daisies and the number of warming black

---

* Corresponding author.
E-mail address: arwen.e.nicholson@gmail.com (A.E. Nicholson).

http://dx.doi.org/10.1016/j.jtbi.2016.11.019
Received 1 August 2016; Received in revised form 27 October 2016; Accepted 21 November 2016

daisies maintains a constant habitable temperature in Daisyworld. As the solar luminosity increases the white daisies take over and keep the planet cool, until the incoming radiation is too high and all daisies die.

The Guild model (Downing and Zvirinsky, 1999), also demonstrates global regulation arising from local selection. In the Guild Model, individuals consume and excrete chemicals that appear in the system via an inflow. Which chemicals they consume and excrete are determined by an individual's genome. New ‘species’ (i.e. new genomes) arise via mutation during reproduction events. All individuals have maximum consumption levels when the ratio of chemicals is at a particular value. Individuals affect their local chemical ratios via their consumption and excretion and these effects diffuse to the global environment. As in Daisyworld, individuals that improve their local environment will be selected for, and this local selection contributes to global regulation. The Guild model finds that communities of individuals can exist together to create and regulate the preferred chemical ratios.

The Flask model (Williams and Lenton, 2007, 2008, 2010) removed a limiting assumption of Daisyworld and the Guild model that traits selected for at the individual level always improve the global environment. Instead the organisms in the system affect the abiotic environment as a byproduct of their metabolism, making these effects selectively neutral at the individual level. Instead of each individual having a distinct local environment, groups of individuals share a common local environment. During reproduction there is a small constant probability of mutation per locus P_{mut} so that over time new species arise via mutation. A spatial version of the model connected multiple local environments by inflows and outflows (Williams and Lenton, 2010, 2008). Stabilising environmental regulation still emerged and this model argues for spatial structure creating conditions where limited higher-level selection can take place. In a connected environment, locations where local communities improve their environment achieve larger populations and thus can colonise and outcompete communities that degrade their environment leading to the spread of environment-improving communities and thus global regulation.

For local selection to take place on environment-related traits, local environments must be different. However, certain environments cannot be compartmentalised in a manner that seems conducive to local selection. The obvious example is the atmosphere (with its well mixed gases) but some aquatic environments are also potentially well mixed too. In this case it is not obvious where the local environments allowing for successful communities to develop would be, leading to motivation for a homogenous model of self-regulation.

Later versions of Daisyworld (McDonald-Gibson et al., 2008) and ‘Daisystat’ (Dyke, 2010) removed the local environment and found regulation of the abiotic parameters. In these models ‘rein-control’ (Clynes, 1969; Dyke and Weaver, 2013) is responsible for the environmental regulation. In one version of these models (McDonald-Gibson et al., 2008) two main subgroups dominate the system - one group that acts to increase the abiotic parameter while preferring this parameter to be low, and another group that acts to lower the abiotic parameter, while preferring this parameter to be high. With these two groups pulling the system in opposite directions, environmental regulation is possible for significant periods of time. The Daisystat model (Dyke, 2010) features the same ‘rein-control’ in this case regulating multiple abiotic parameters with a diverse array of species instead of the system being dominated by two main groups. In Flaskworld (Williams and Lenton, 2010), the effect of allowing different microbe species to prefer different abiotic parameter values was explored and it was found that the system showed periods of stability where the abiotic parameter stayed near constant. These stable periods were interrupted with rapid transitions where the abiotic parameter would often then stabilise at a different value to before. The system was stabilised by the ‘rein-control’ mechanism present in the Daisystat model.

The Daisystat model provides global regulation with a diverse population in the absence of spatial heterogeneity. However this model lacks mutation. Species begin reproducing when the environmental parameters allow them to, and all species are present at all times even if at vanishingly low levels. This means that as the environment changes, the system does not need to evolve new species to control or adapt to these changes, the species are already present and ready to start reproducing as soon as conditions allow. Therefore in Daisystat, the system cannot go extinct. This does not reflect real world biology where the existing population must evolve to cope with a changing environment and total extinction is a possibility. For this reason we follow the Flask model implementation of microbes with selectively neutral abiotic effects that reproduce and mutate allowing new species to appear in the system.

The atmosphere taken as a single entity has a flux of energy coming in as light from the sun, heat from the mantle and various chemicals spewed forth by volcanoes similar to the nutrient and abiotic parameter inflow in the Flask model. For something like the Earth's atmosphere a single well mixed environment would be a more accurate representation than local environments interacting with a global environment. CO_2 fluxes, for example, at various points on the Earth do not vary wildly (ignoring the very small scale i.e. surrounding a currently active volcano) making a single flask Flask model a good approximation to the system.

The original Flask model (Williams and Lenton, 2007) was also a single flask environment, however the implementation of the model was quite different and the focus of the paper was on nutrient recycling and not abiotic regulation. In the original Flask model (Williams and Lenton, 2007) instead of microbes all having the same preferred value for a single abiotic parameter, there were two abiotic parameters and microbes had an encoded preference for a particular ratio of these two parameters. This ratio preference was not constant for all microbes and therefore not all microbes experienced the environment identically. When there is a universal preference for an abiotic parameter, this sets a constant target for regulation, where the preferences for abiotic parameter values differ, there is no such constant target. The target will change as the genetics within the population change. The microbes were able to evolve towards preferring the state of the current abiotic environment and exploit all the nutrients in the system. In this paper we instead focus on what happens in a system where the microbes cannot evolve towards preferring the current environment, and instead of a preferred ratio between two abiotic parameters that differs between different microbe species, we have a single abiotic parameter with a constant preferred value for this parameter, β that is the same for all microbes.

For our single flask Flask model we closely follow the implementation detailed in Williams and Lenton (2008) limiting the system to a single flask. We present a model of self-regulation of a purely global environment arising via evolution. This single Flask model allows for the possibility of rebel mutants disrupting the system, due to the lack of distinct environments and removes the issue of “cheater” species, due to the selectively neutral abiotic effects of the microbes. It is also possible for the system to drive itself to extinction - all scenarios being criticisms of the Gaia theory (Doolittle, 1981; Dawkins, 1982). The combination of assumptions presented here differs to what has been tried in previous models. The model has a shared preference for a single abiotic parameter, but lacks spatial structure as in the previous Flask models (Williams and Lenton, 2007, 2008, 2010). Mutation occurs in this model with a constant probability per reproduction event, and the system can suffer from total irreversible extinction, differing from to the Daisystat (Dyke, 2010) and models by McDonald-Gibson et al. (2008). Finally, the model lacks local environments, differing from the original Daisyworld (Watson and Lovelock, 1983), and the Guild model (Downing and Zvirinsky, 1999).

In Section 2 of this paper we give a brief outline of the model (an in depth description can be found in Appendix A). Section 3 details the