Planetary regulation on the test tube: a synthetic Daisyworld

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Abstract

The idea that the Earth system self-regulates itself in a habitable state was proposed in the 1970s by James Lovelock, later on formalized as the Daisyworld model using a two-species system interacting with their environment. The potential for testing this conceptual framework in an experimental way is limited by its scale. To fill this gap, here we propose an explicit test tube-scale implementation for a microbial synthetic Daisyworld using an engineered community where pH as the external, abiotic control parameter. The computational modelling of this system shows robust self-regulation within a broad range of conditions, limited by tipping points, This synthetic Daisyworld allows exploring multiple scenarios of self-regulation that include the role of parasites, fluctuations or biodiversity and can help developing an experimental path to Earth Systems Science.

Introduction

The Biosphere has been shaped by millions of years of evolution, experiencing significant biotic changes due to external triggers (1; 2). Life has transformed Earth's geosphere (3) and this idea was substantiated by James Lovelock and Lynn Margulis (4; 5), suggesting that a life-free planet would have experienced runaway effects as those experienced by Mars or Venus (6), later on formalized in terms of the so called *Daisy World Model* (DWM) where two species with different albedos were shown to stabilize an ildealized planetary climate across varying solar luminosities (7). The DWM (Fig. 1), has been instrumental within Earth System Sciences from a theoretical viewpoint (8).

The planetary scale of the problem seems to exclude any experimental replication. However, synthetic biology advances in the modeling and implementation of engineered ecosystems (9) provides a potential scenario for implementing a DWM. Here we show how to build a Synthetic Microbial Daisy World (SMDW) that could offer novel insights and a rich context to explore the role of lower-scale features in global regulation processes (10). Instead of the temperature/luminosity formulation of the original DWM, we consider acidity as the key driving parameter: acidity (11). In this context, ocean pH has remained stable over millions of years (5; 12; 13; 14).

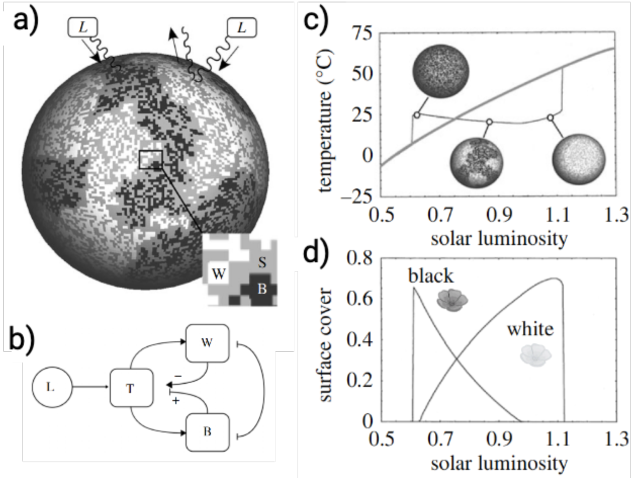

Figure 1: **The Daisy World Model (DWM)**. Using a two-dimensional surface (a), increasing levels of solar luminosity L trigger the growth of two populations of plants that share the same optimal growing temperature (here B and W stand for black and white daisies, shown as white and black squares) grey squares stand for bare soil S. In (b) the feedbacks between temperature and daisies are summarized. These feedbacks As a consequence of these nonlinear couplings, as shown in (c), the planet temperature can be stabilized (instead of just simply growing with L, grey line) for a wide range of L values, thus indicating a homeostatic response due too the biosphere-climate system. Such stabilization is obtained by means of population arrangements between W and B states (d).

In our SMDW, pH is regulated by two populations acting as daisies, enabling a straightforward microcosm/mesocosm implementation. We propose using two engineered cell types: acid-producing X_a and base-producing X_b strains in a chemostat (Fig. 2a). They can self-regulate the environment. This regulation stems from inherent feedback mechanisms: acidification favours the growth of base producers, while alkalinization provides an advantage to acid producers (Fig. 2b). Our proposed synthetic circuits include X_a, carrying *ldhA* gene to convert pyruvate to lactic acid, lowering pH, and X_b, carrying *kivd* gene to decarboxylate 2-keto-acids to aldehydes, overproducing ammonia and reducing

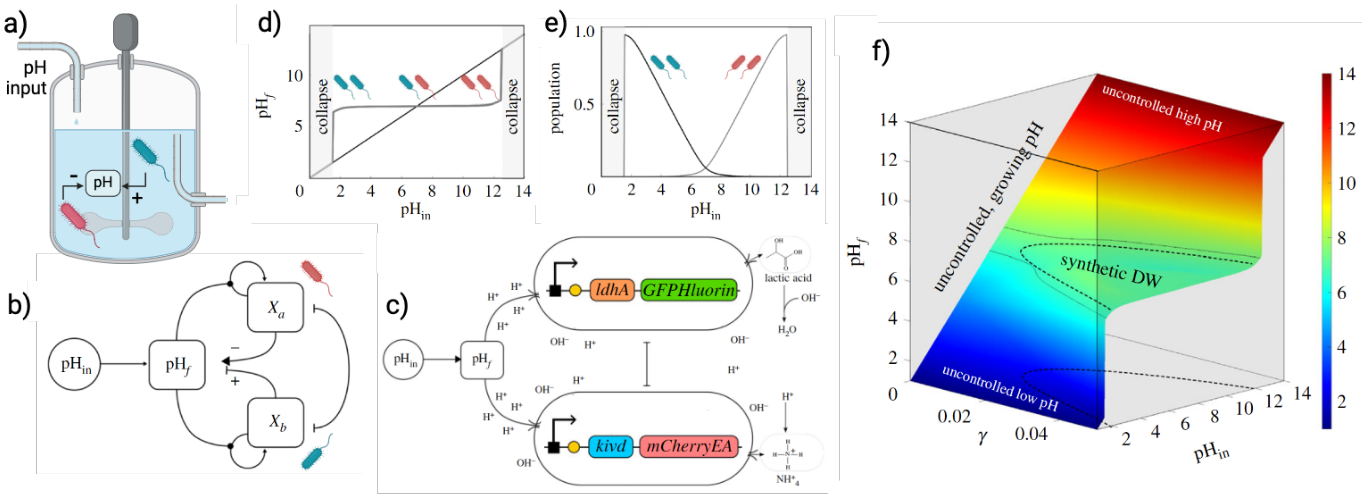

Figure 2: A synthetic, pH-driven microbial Daisyworld. (a) using a bioreactor where an external input with increasing pH (pH_{in}) enters a medium where two different strains of engineered bacteria increase or decrease the pH_f of the tank. The feedbacks are summarized in (b) and the genetic constructs are depicted in (c). A broad domain of self-regulation surrounded by the collapse domains emerges (d). The corresponding abundances of each synthetic strain are displayed in (e). X_a stands for acid-producing species and X_b for base-producing, see (b). Steady state surface for the SMDW is depicted using equations (1-2). In (f) the internal pH_f is plotted against pH_{in} and γ (acid and base production rates). As γ increases, a diverse range of controlled pH values emerges, expanding the homeostatic region (flat surface) of optimal pH.

medium acidity by forming ammonium ions (Fig. 2c). Such dynamics can be implemented under a basic model and the equations read:

$$\frac{dX_k}{dt} = \mu_{X_k} X_k \left[\beta(\mathrm{pH}_{X_k})\left(1-\frac{X_a+X_b}{X_{\mathrm{max}}}\right)-\delta\right] \qquad (1)$$

where $k = a, b$, μ_i is the growth rate of population X_i, X_{max} is the carrying capacity, and δ is the dilution rate. The function β describes the change in growth rate depending on the pH that each strain locally perceives,

$$\beta(\mathrm{pH}_i) = 1 - \frac{(\mathrm{pH}_{\mathrm{opt}}-\mathrm{pH}_i)^2}{(\mathrm{pH}_{\mathrm{opt}}\pm\mathrm{pH}_{\mathrm{lim}})^2} \qquad (2)$$

β is a symmetric, single-peaked function with its maximum located at the optimal growth pH, denoted as $\mathrm{pH}_{\mathrm{opt}}$, and positivity maintained across the interval $\mathrm{pH}_{\mathrm{opt}} \pm \mathrm{pH}_{\mathrm{lim}}$. The perceived pH of each population deviates from the environmental pH; slightly shifted by the acid or base production of the corresponding strain. Despite receiving external inputs of either acid or base, the environmental pH remains close to its optimum through the reorganization of relative populations (Fig. 2d-f). This adjustment regulates the production of acid and base, counteracting any deviations in pH caused by external perturbations, achieving a wide range of systemic homeostasis.

The previous two-species design can be generalized to include more complex communities, using cheaters (parasites) that could break down the homeostatic balance, as predicted by theoretical models of cooperation. However, the computational analysis of the extended synthetic Daisyworld reveals that the self-regulatory properties of the system are able to keep the homeostatic domain. Moreover, by extending the model into multiple species, using a model:

$$\frac{dX_i}{dt} = X_i\left[\beta(pH_i)\left(1-\sum_{j}^{n} X_j\right)-\delta\right], \qquad (3)$$

a rich space of dynamical states is found, including oscillations and chaos in population dynamics coexisting with a global stable control. Now the equation for the pH_f state would read:

$$\frac{dpH_f}{dt} = \left(\sum_{i=1}^{n} X_i \frac{\gamma_i \omega}{\delta}\right)\left(\frac{pH_f}{b}(2b-pH_f)\right) \qquad (4)$$

Most importantly, it is shown that increasing diversity acts as a firewall against fluctuations in the internal pH_f values, thus suggesting that a diverse biosphere will favour the presence of self-regulation. Future developments should consider the role played by space (using connected bioreactors), the response of diverse communities to external shocks and the recovery patterns (as it occurs with major extinction events) or different design principles involving other sources of control (such as niche construction). Finally, we believe that extensions of our models could be helpful to explore relevant issues related with astrobiology.

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