

**Sequential selection produces self-regulation in model
biospheres**

Multi-level selection meets Ashby's ultrastability

or

New theoretical support for the Gaia hypothesis

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Background

Lovelock, J. E. and L. Margulis, 1974. Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis. *Tellus* **26**:2–10.

- Title summarizes the claim.

Lovelock, J. E., 1979. *Gaia: A New Look at Life on Earth*, Oxford University Press.

- Most criticism of the Gaia hypothesis appeared after this book.

(among many...)

Two key criticisms of the Gaia hypothesis

Empirical: where's the evidence for homeostasis?

Theoretical: why should we expect the biosphere to be homeostatic?

W. F. Doolittle, 1981. Is Nature really motherly?
CoEvolution Quarterly, Spring 1981:58–63.

By analogy to the “selfish gene”, problem of “selfish species”.

“I do not doubt that some of the feedback loops which Lovelock claims exist *do* exist, but I do doubt that they were created by natural selection, or that they are anything but accidental.”

R. Dawkins, 1982. *The Extended Phenotype*, Oxford University Press.

Lovelock rightly regards homeostatic self-regulation as one of the characteristic activities of living organisms, and this leads him to the daring hypothesis that the whole Earth is **equivalent to a single living organism** . . . The fatal flaw in Lovelock's hypothesis would have instantly occurred to him if he had wondered about the **level of natural selection process** which would be required in order to produce the Earth's supposed adaptations. Homeostatic adaptations in individual bodies evolve because individuals with improved homeostatic apparatus pass on their genes more effectively than individuals with inferior homeostatic apparatuses. For the analogy to apply strictly, there would have to have been a set of rival Gaias, presumably on different planets. Biospheres which did not develop efficient homeostatic regulation of their planetary atmospheres tended to go extinct. The Universe would have to be full of dead planets whose homeostatic regulation systems had failed, with, dotted around, a handful of successful, well-regulated planets of which Earth is one. Even this improbable scenario is not sufficient to lead to the evolution of planetary adaptations of the kind Lovelock proposes. In addition we would have to postulate some kind of reproduction, whereby successful planets spawned copies of their life forms on new planets.

... He might dispute that it does entail those assumptions, and maintain that Gaia could evolve her global adaptations by the ordinary processes of Darwinian selection acting within the one planet. I very much doubt that a model of such a selection process could be made to work: it would have all the notorious difficulties of 'group selection'. For instance, if plants are supposed to make oxygen for the good of the biosphere, imagine a mutant plant which **saved itself the costs** of oxygen manufacture. Obviously it would outreproduce its more public-spirited colleagues, and **genes for public-spiritedness would soon disappear**. It is no use protesting that oxygen manufacture need not have costs: if it did not have costs, the most parsimonious explanation of oxygen production in plants would be the one the scientific world accepts anyway, that oxygen is a byproduct of something the plants do for their own selfish good.

... Entities that pay the costs of furthering the well-being of the ecosystem as a whole will tend to reproduce themselves less successfully than rivals that exploit their public-spirited colleagues, and contribute nothing to the general welfare. Hardin (1968) summed the problem up in his memorable phrase '**The tragedy of the commons**', and more recently (1978) in the aphorism, 'Nice guys finish last'.

Two competing hypotheses:

Gaia

The biosphere maintains a good climate for itself

Tragedy of the commons

climate control = the common good

contributing to the common good is costly

self-interest → don't contribute, be a free rider

⇒ the common good can't be maintained.

Research question: investigate these competing possibilities using model biospheres

- Can an ecosystem regulate its planet's climate?
- Is climate regulation undermined by “exploiters”? Does it fail for other reasons?
- If they can succeed in “cooperating” — even occasionally — how do they do it and what can we learn from them?

What this project is not

- a General Circulation Model
- helping figure out what to do about the current climate crisis
- realistic

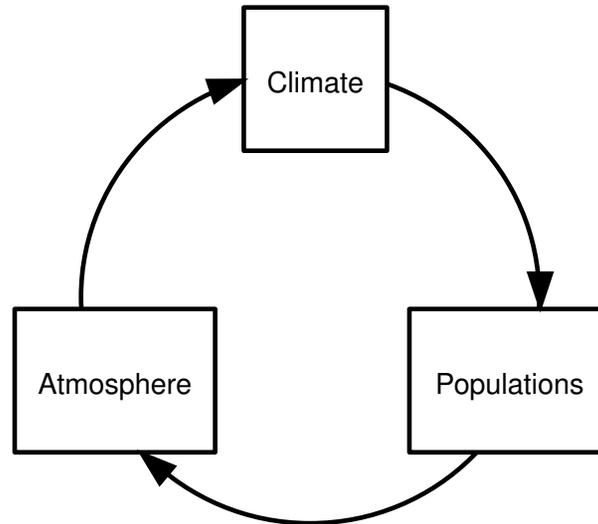
What it is

- investigating how an ecosystem can self-regulate
- taking on some basic questions about evolutionary theory
- helping develop the mathematical theory of coevolutionary dynamics
- looking for clues about cooperation, coexistence, and how diverse communities can manage themselves

To come:

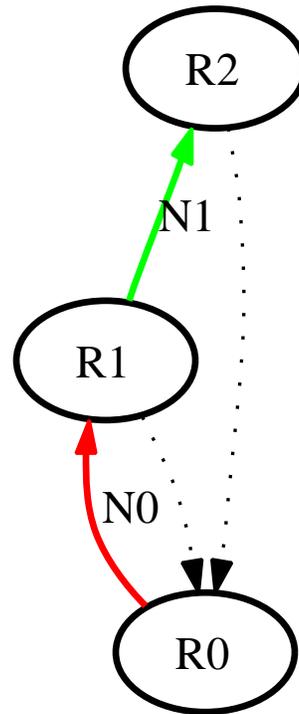
1. Model description
2. Results: stable “cooperation” without natural selection between planets
3. Analysis: how it happens
4. Philosophical discussion about natural selection and other ways to get the job done

“Greenhouse world” model design



In Daisyworld models, plants moderate the climate through their albedo; here it's by changing the balance of greenhouse and non-greenhouse gases.

An example model community



Model equations: population dynamics

Population N_i consumes resource R_c , produces resource R_p .

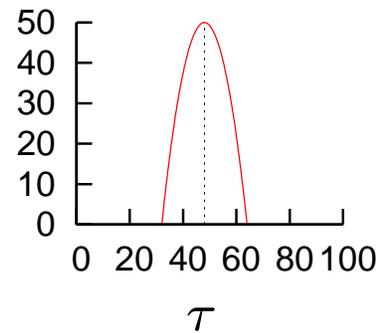
$$\frac{dN_i}{dt} = \gamma N_i R_c r(\tau_i, T) - m N_i$$

Resource R_j is consumed by some populations, produced by some. Resources reduce spontaneously to simpler resources.

$$\begin{aligned} \frac{dR_j}{dt} = & \sum_{N_i \text{ produces } R_j} (1 - \gamma) N_i R_c r(\tau_i, T) \\ & - \sum_{N_i \text{ consumes } R_j} (N_i R_c r(\tau_i, T) - m N_i) \\ & + \sum_{R_k \text{ reduces to } R_j} R_k - R_j \end{aligned}$$

Model equations: climate

Global temperature
determines
populations' survival



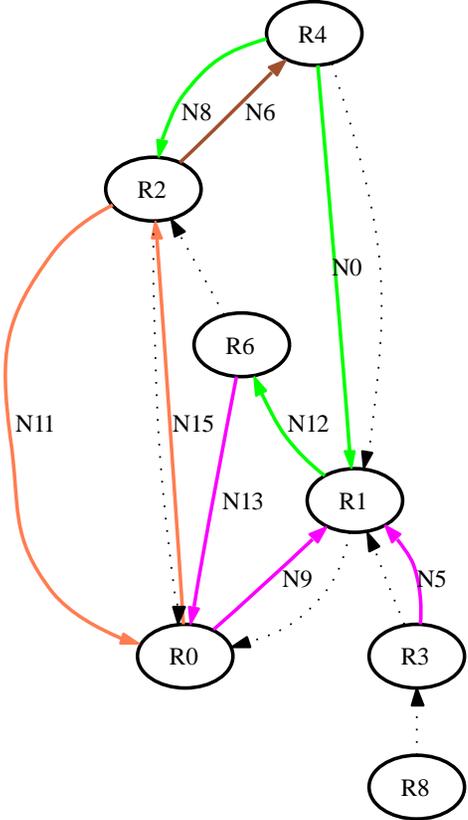
Population dynamics determine temperature, via atmospheric concentrations

$$\frac{dT}{dt} = \Lambda (T^* - T)$$

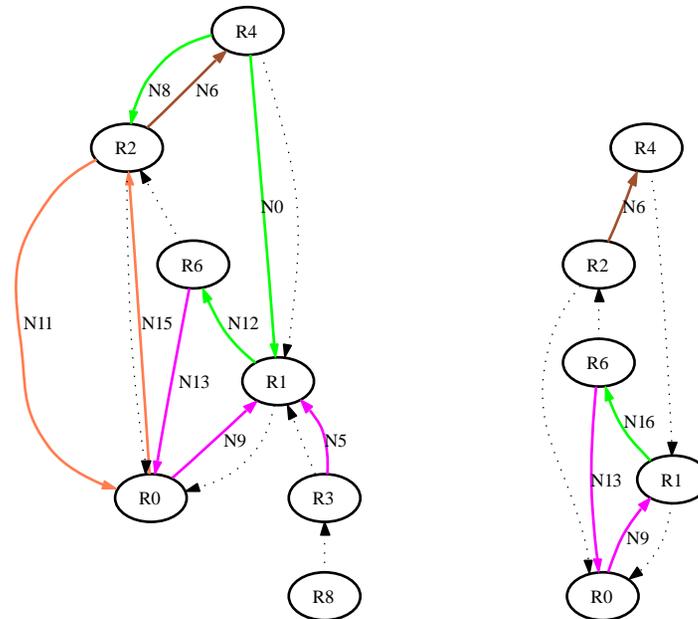
$$T^* = 100 \frac{\sum h_j R_j}{M}$$

“Heating” h_j (from 0 to 1) is how much resource R_j contributes to raising the temperature.

When I throw together a randomly assembled community

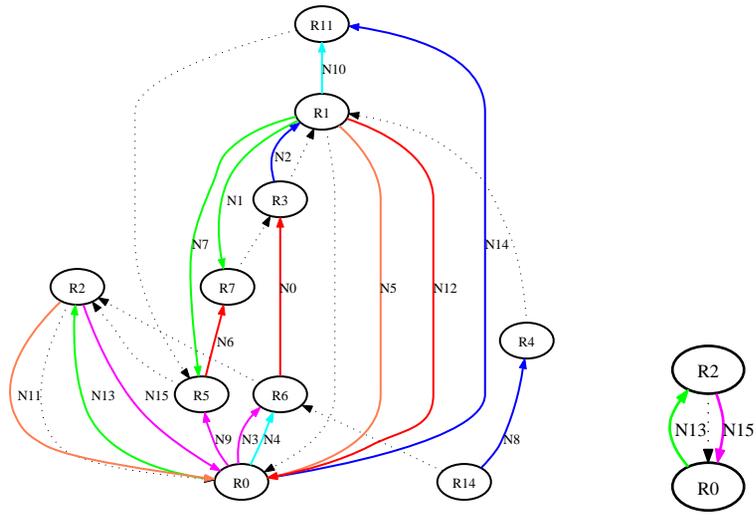


Typically some species come to an equilibrium

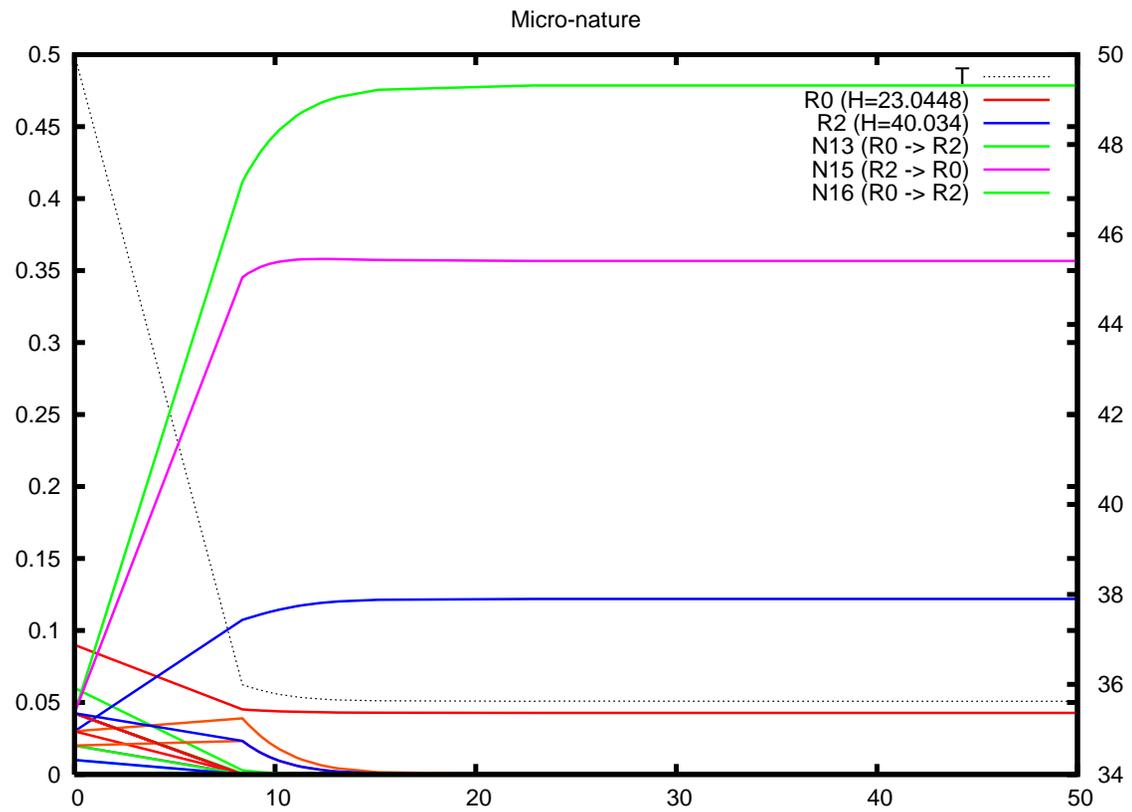


Many of them go extinct before the whole community finds stability.

Afterward, it is a Gaia-like planet, at least in the short term.



Model dynamics



Coevolutionary change

At long intervals, mutations happen:

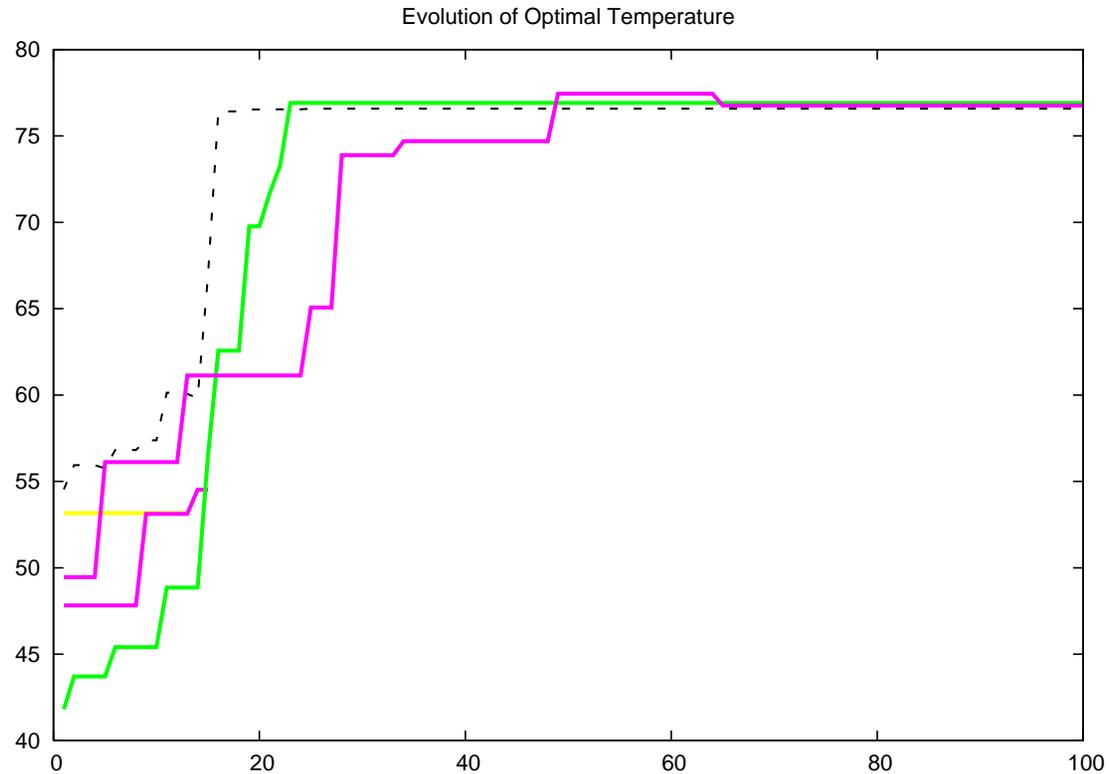
- a few individuals appear with a slightly different desired temperature (τ).

The ecological dynamics takes care of the rest: if the new type out-reproduces the old type, it will replace it.

The result: gradual change in desired temperature, toward the actual temperature.

But when the organisms change, they change the temperature too.

Coevolution changes the community - for better or worse



Some populations go extinct along the way.

At the end, an Evolutionarily Stable State (ESS).

The endpoint of the process: no tragedy

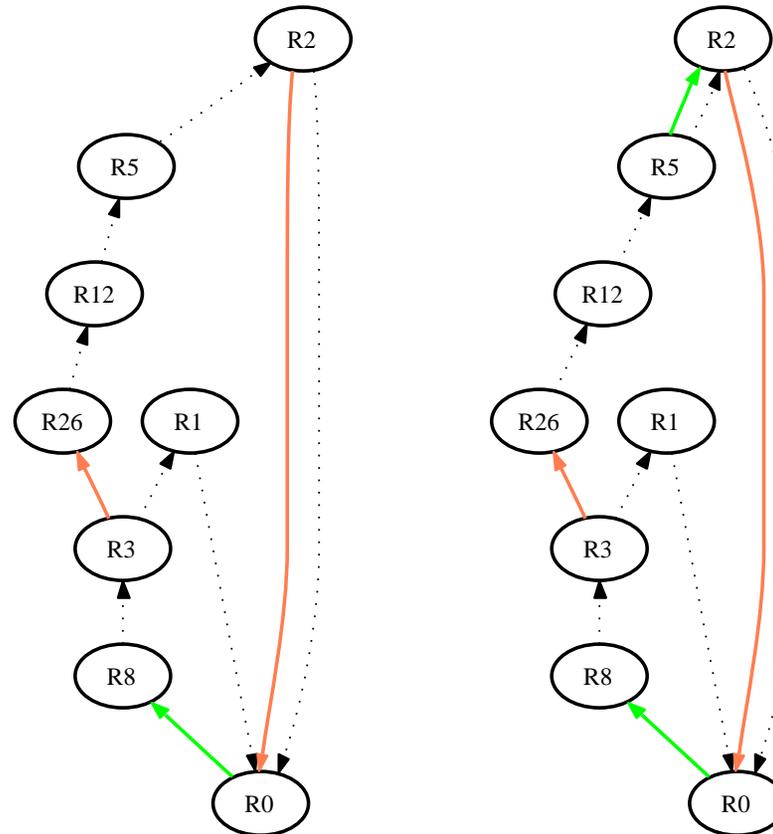
The result: **Stable “cooperation” without “free riders”**, i.e. **Gaia**.

In two ways:

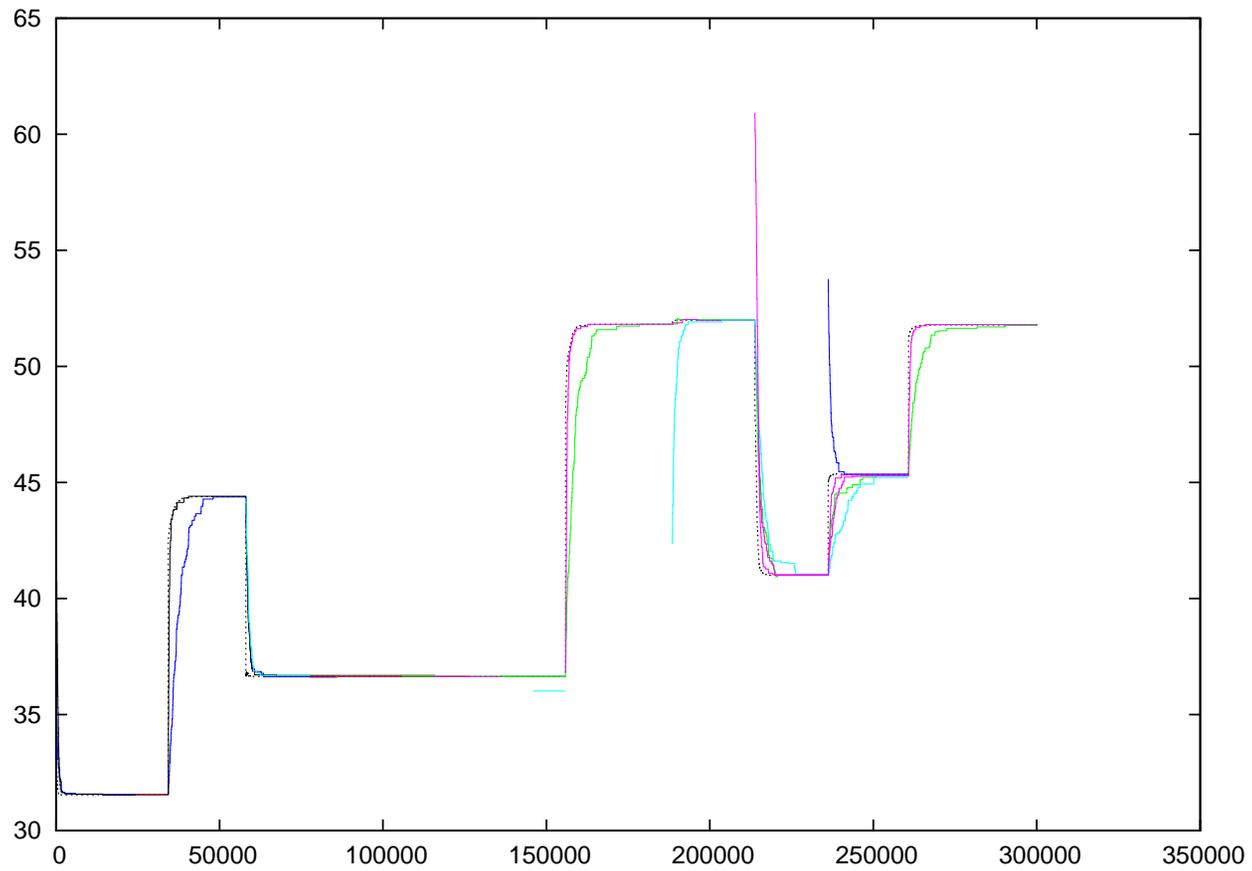
1. the community maintains the climate at an equilibrium that it likes. (could be persistent fluctuation, but it's generally equilibrium.)
2. when variants arise, they don't undermine that homeostatic process.

Long-term changes in model community structure

When everything stops evolving, introduce a new species type



Long-term coevolution of populations and climate



Periods of stability, punctuated by changes in structure

Introduction of a new species usually causes

- sudden change in climate
- one or more extinctions
- discovery of a new equilibrium

When the new type is added, the community often no longer has the Gaia property. After its crisis (if some populations survive), it regains the Gaia property.

What's going on?

Community structures that can't negotiate an agreeable climate can't last.

The system's dynamics always finds a stable attractor.

That's all it takes to **weed out non-Gaian community structures** and **select Gaian ones**.

Sequential Selection

Richard Betts and Timothy Lenton

...In the case where evolution produces **an antiregulatory system** ... As global conditions approached the limits of habitability, heterogeneity in surface conditions would provide some more favorable sites where extinction would be more gradual than elsewhere. Sparse life would cease to influence the global environment and the **antiregulatory mechanism would be removed**. ... Life could then begin to spread once more. Evolution would almost certainly take a different pathway to that previously followed, and it would be possible for the biota to evolve new properties of which a by-product is **regulation**; if not, the system would again destabilize and life would approach extinction, “re-setting” the system again and allowing evolution to explore yet another pathway.

(Lenton, T. M., K. G. Caldeira, and E. Szathmáry, 2004. What does history teach us about the major transitions and role of disturbances in the evolution of life and of the earth system? *Earth System Analysis for Sustainability*, Dahlem Workshop Report, volume 91, MIT Press, pp. 29–52.)

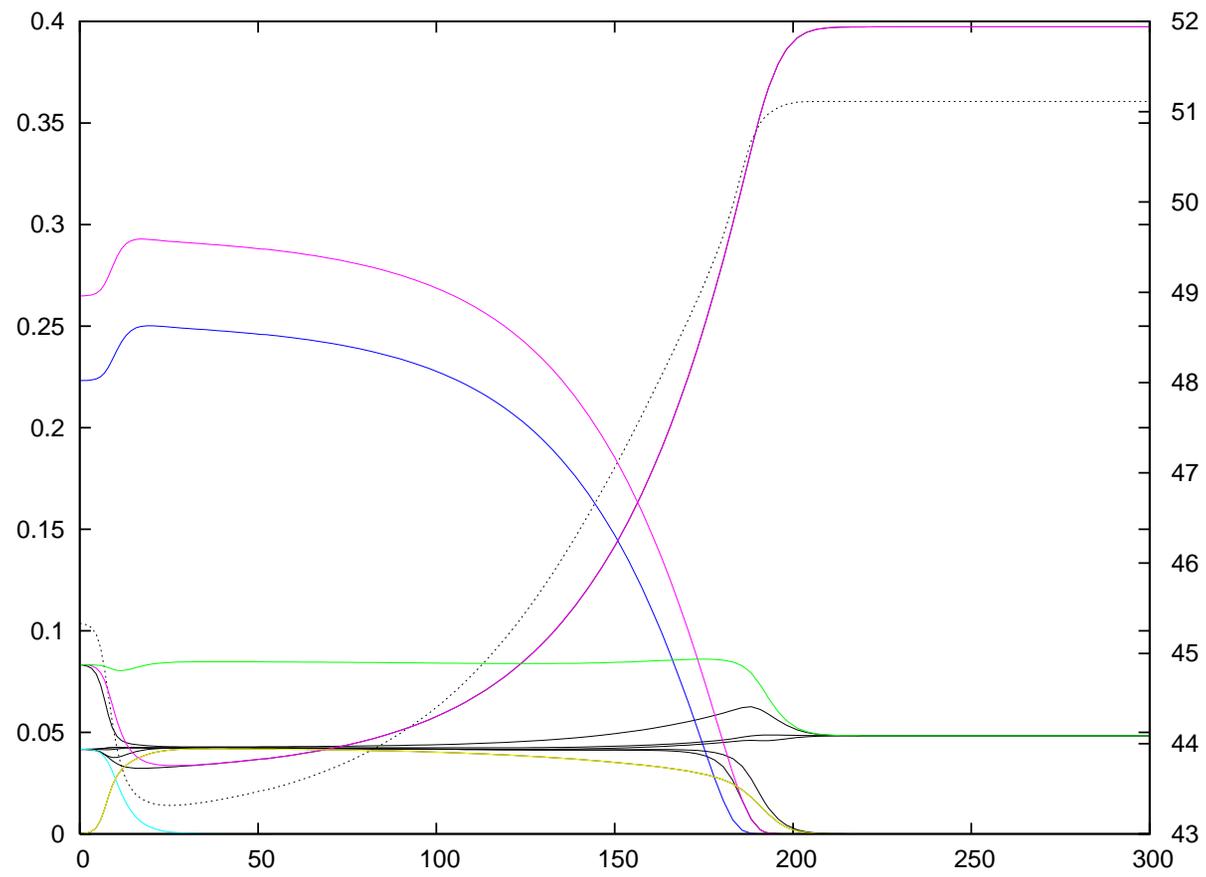
Sequential selection here is a little different

No need for near extinction

Antiregulatory system → extinction of some populations →
different dynamics

Keep restructuring until stability emerges

It's simpler, but basically the same idea



Recap

In the Greenhouse World models, **Gaian homeostasis is consistently observed**, and “tragic” situations are transient.

A newly identified **sequential selection** process causes the biosphere to adapt, producing self-regulating planets without “free riders” — simply because self-regulation is identified with the attractors of the system.

Sequential selection does what Dawkins said only Darwinian selection could do.

*** INTERMISSION ***

What is sequential selection?

Doolittle and Dawkins say since natural selection can't act on planets, what will prevent it from being destabilized by “free riders” ?

Sequential selection takes the place of natural selection, and produces stable homeostasis — an “adaptation” on the scale of the entire planet.

Sequential selection is something like natural selection. But it's not natural selection or any other “level of selection” — this is a different kind of adaptation acting on the whole system.

Unlike natural selection, it doesn't require a population of coexisting planets.

Darwinian selection is one kind of adaptation

Dawkins in particular is adamant that without natural selection you can't have adaptations.

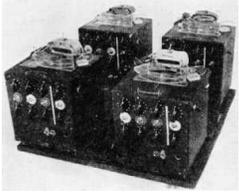
Plants might produce oxygen, but without evolution it can't be “for the good of the system” — the whole system can't have adaptations — it must be “for their own selfish good” (an adaptation of the components of the system).

But this is wrong — Darwinian selection is **not** the only way a whole system can become adapted.

Natural selection is one of many kinds of adaptation. Sequential selection is a fundamentally different kind of adaptation process, but it can do the job. (Learning is another example.)

Ashby's Homeostat





What the Homeostat does

- a simplistic, schematic model of a learning animal.
- a system of feedbacks “trying” to keep the “essential variables” within acceptable range as its “environment” changes.
- when that self-regulation fails, it rewires itself in hope of becoming a more effective system of feedbacks.

Ashby calls this process **ultrastability**.

It's an ultra-simple model for animal learning.

A way of **adapting** to unexpected circumstances.

How these model biospheres are like the homeostat

- “try” to keep the temperature within survivable range.
- if that regulation fails, one or more species go extinct, creating a different network.
- if that one fails...

Sequential selection is more similar to Ashby's ultrastability than to Darwinian selection. (So one could say it's less like the planet evolves to be self-regulating, and more like it **learns** to.)

“The argument is simple enough in principle. We start with the fact that systems in general go to equilibrium. Now most of a system’s states are non-equilibrial. So in going from any state to one of the equilibria, the system is going from a larger number of states to a smaller. In this way, it is performing a selection, in the purely objective sense that it rejects some states, by leaving them, and retains some other state, by sticking to it. Thus, as every determinate system goes to equilibrium, so does it select. We have heard ad nauseam the dictum that a machine cannot select; the truth is just the opposite; **every machine, as it goes to equilibrium, performs the corresponding act of selection.**”

W. R. Ashby in W. Buckley (ed.), *Modern Systems Research for the Behavioral Scientist*, p.115

from *Principia Cybernetica Web*,
http://pespmc1.vub.ac.be/ASC/PRINCI_SELF-.html

. . . the presence and the products of life inevitably and inexorably modify the environment. The options then open to life as a whole are constrained by its past activities. It is not a big step for loops to then begin to close and for life to become included within a larger yet tenuous entity. It may be difficult from deep within the dogma of molecular biology to think of the **cybernetic consequences of evolution** but the loop is not open, it is closed, and Gaia may not after all be inconsistent with natural selection.

J. Lovelock, 1981. James Lovelock Responds [to Doolittle's review]. *CoEvolution Quarterly*, Spring 1981:62–63.

Future. . .

Deconstruction of the Gaia controversy in cultural context

What can second-order cybernetics tell us about these ideas?

Most of the “tragedies” are not Hardinesque, they involve various kinds of inequities of power

Developing theory of sequential selection and sequential evolution. Design of the Homeostat II. . .

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