



## **Daisyworld is Darwinian: Constraints on Adaptation are Important for Planetary Self-Regulation**

TIMOTHY M. LENTON\*† AND JAMES E. LOVELOCK‡

\* *Centre for Ecology and Hydrology-Edinburgh, Bush Estate, Penicuik, Midlothian EH26 0QB, U.K. and*  
‡ *Coombe Mill Experimental Station, St. Giles on the Heath, Launceston, Cornwall PL15 9RY, U.K.*

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The Daisyworld model demonstrates that self-regulation of the global environment can emerge from competition amongst types of life altering their local environment in different ways. Robertson & Robinson (1998. *J. theor. Biol.* **195**, 129–134) presented what they describe as a “Darwinian Daisyworld” in which the ability of organisms to adapt their internal physiology in response to environmental change undermines their ability to regulate their environment. They assume that there are no bounds on the environmental conditions that organisms can adapt to and that equal growth rates can potentially be achieved under any conditions. If adaptation could respond sufficiently rapidly to changes in the environment, this would eliminate any need for the environment to be regulated in the first place, because all possible states of the environment would be equally tolerable to life. However, the thermodynamics, chemistry and structure of living organisms set bounds on the range of environmental conditions that can be adapted to. As these bounds are approached, environmental conditions limit growth rate, and adaptations necessary for survival can also cost energy. Here we take account of such constraints and find that environmental regulation is recovered in the Daisyworld model. Hence, we suggest that constraints are an important part of a self-regulating planetary system.

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### **Introduction**

The Gaia theory proposes that the Earth’s biota and its surface environment (atmosphere, oceans, land surface and crustal rocks) form a self-regulating system that keeps the planet in a habitable state (Lovelock, 1995; Lenton, 1998). Daisyworld is a parable, invented to demonstrate that such self-regulation can occur without teleology (conscious foresight or planning on the part of unconscious organisms), from a tight feedback coupling between life and its environment (Watson & Lovelock, 1983). Daisyworld is also a Darwinian

model in that it contains competition (for space and hence light) between different types of life (“daisies”) with heritable variation in a trait (their colour or albedo) that affects their fitness (by altering their local temperature and hence their growth rate), generating a rudimentary form of natural selection. Subsequent versions of the model show that mutation of the environment-altering trait (albedo) and subsequent evolution by natural selection can generate environmental regulation and extend its range (Stöcker, 1995; Von Bloh *et al.*, 1997; Lenton, 1998), whilst adaptively plausible alterations of optimum growth temperature can narrow the range of environmental regulation (Saunders, 1994).

† Author to whom correspondence should be addressed.  
E-mail: [tlenton@ceh.ac.uk](mailto:tlenton@ceh.ac.uk)

Robertson & Robinson (1998) argue that both Daisyworld and the Gaia theory lack attention to biological evolution, in particular, the internal, physiological adaptation of organisms to prevailing environmental conditions. Hence, they introduce a “Darwinian Daisyworld” in which the organisms’ growth response adapts to the conditions prevailing in their environment. As the rate of adaptation is increased, regulation of the environment is impaired and then eliminated. However, Robertson & Robinson (1998) assume there are no limits on the environmental conditions that can be adapted to and that equal growth rates can potentially be achieved under any conditions. We argue that this is biologically unrealistic and develop the model to include bounds on adaptation and reduction of growth rate as these bounds are approached. We find that with these constraints, planetary self-regulation is recovered.

### Daisyworld

Daisyworld is an imaginary world orbiting a star like our Sun that gets more luminous with time. The environment of Daisyworld is reduced to one variable, temperature, and the biota to two types of life, “black” and “white” daisies, which differ in their reflectivity to solar radiation (albedo) and hence their local temperature. The planet has a grey surface of intermediate albedo. Hence, the black daisies are always warmer than their surroundings and the white daisies are always cooler. The local temperature of each daisy type,  $T_l$  (in °C) is given by

$$T_l = \sqrt[4]{((T_e + 273)^4 + q(A_p - A_l))} - 273, \quad (1)$$

where  $T_e$  is the effective temperature of the planet (in °C),  $A_p$  the albedo of the planet,  $A_l$  the albedo of the daisy type (0.25 for black, 0.75 for white) and  $q = 2.06425 \times 10^9 \text{ K}^4$  is a measure of the degree of insulation between regions of the planet’s surface. The growth rate of each daisy type,  $\beta_l$ , is a function of its local temperature,  $T_l$ :

$$\beta_l = \max(0, m(1 - ((T_{opt} - T_l)/17.5)^2)), \quad (2)$$

where  $m = 1$  is the peak growth rate and  $T_{opt} = 22.5^\circ\text{C}$  is the optimum growth temperature,

which is the same for both daisy types in the original model, giving limits to growth of 5 and 40°C. The planet has a negligible atmospheric greenhouse, so its surface temperature is simply determined by its overall albedo and, therefore, the amount of solar radiation absorbed. This depends on the fractional coverage of black daisies, white daisies and bare ground. The other equations of the model can be found in Watson & Lovelock (1983). Here we follow Robertson & Robinson (1998) in using the increase of the Sun’s luminosity with time to force the model (Caldeira & Kasting, 1992), starting at 4 Gyr ago, shortly before the earliest evidence of life on Earth (3.85 Gyr ago) (Mojzsis *et al.*, 1996). The solar constant for Daisyworld is  $\sim 2.8$  times that for the Earth, corresponding to a planet  $\sim 0.6$  AU from our Sun (Earth’s mean distance from the Sun is 1 AU =  $149.6 \times 10^6$  km), but this is partially counteracted by Daisyworld’s higher initial albedo and lack of greenhouse effect.

We use our own coded version of Daisyworld, rather than the spreadsheet version adopted by Robertson & Robinson (1998). The differential equations for the daisy populations are solved by iteration (Euler’s method). Time is increased in increments of 40 Myr and after each corresponding increase in luminosity we allow 100 iterations of the equations to ensure that the populations remain close to equilibrium with the forcing. We find that we can best reproduce the results of Robertson & Robinson (1998) by only iterating the equations once per time step, but in this case the populations do not remain close to equilibrium with the forcing. We consider this to be unrealistic, because populations change many orders of magnitude faster than solar luminosity.

In the original Daisyworld model the planetary temperature is regulated [Fig. 1(a)], in contrast to the warming predicted without life. Black daisies dominate initially [Fig. 1(b)] because they are locally warmer and grow faster under the low initial solar forcing. They spread and warm the planet. As solar luminosity increases, the white daisies gradually take over, and this actually cools the planet. When only white daisies remain, the planet warms until they overheat and disappear. Daisyworld’s self-regulation involves both positive and negative feedback, and the system is stable against rapid perturbations as well as

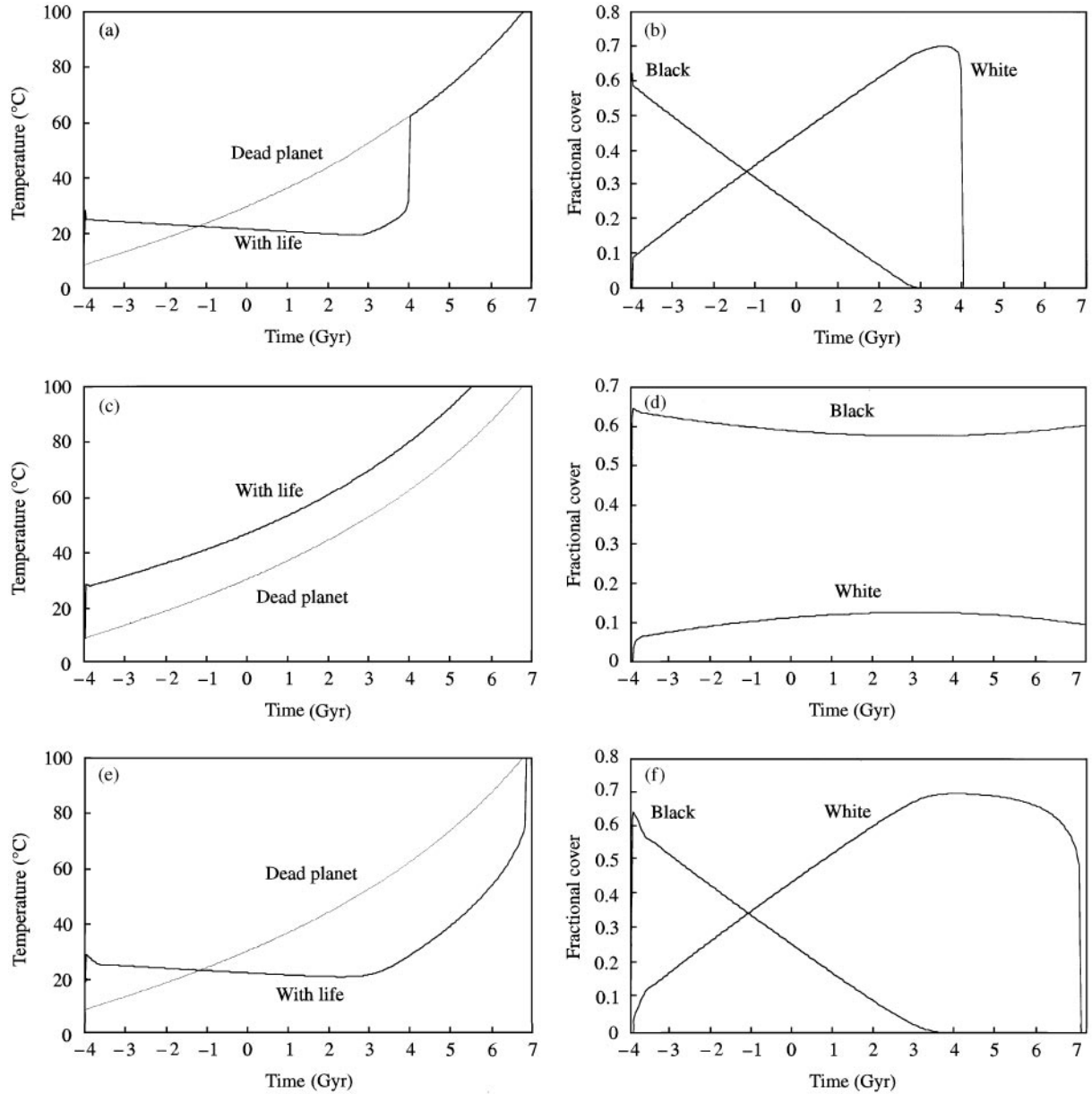


FIG. 1. Daisyworld without adaptation (a and b), with unconstrained adaptation (c and d) and with constrained adaptation (e and f), of optimum growth temperature toward local temperature. The system is forced with increasing solar luminosity. Panels a, c and e show planetary temperature in the presence of daisies (“with life”) contrasted with that without life (“dead planet”). Panels b, d and f show the black and white daisy populations, expressed as fractional cover of the planet’s surface (corresponding to the temperature with life). The rate of adaptation,  $a = 0.5$ , is the same in the constrained and unconstrained cases. Methods are described in the text.

gradual changes in the forcing parameter. Hence, Daisyworld is not “simply a restatement of a well-established principle”, “that negative feedback can keep a system stable in the face of outside perturbation” (Robertson & Robinson, 1998).

### Unconstrained Adaptation

Saunders (1994) first suggested that as the black daisies are always warmer and the white daisies are always cooler than the mean planetary temperature, which is stable over long periods of time, one might expect the optimum growth

temperature of the daisies to evolve towards their local temperatures. Robertson & Robinson (1998) introduced a continuous adaptation of the optimum growth temperature ( $T_{opt}$ ) of each daisy population towards its local temperature ( $T_l$ ):

$$T_{opt,t} = T_{opt,t-1} + a(T_{l,t-1} - T_{opt,t-1}), \quad (3)$$

where  $a$  is the rate of adaptation,  $t$  the current time step and  $t - 1$  denotes the value at the previous time step. This approach assumes that adaptation occurs without any penalty to growth rates, which means that in principle, the daisies can adapt to grow equally well at any temperature, including well below freezing and above boiling point. The optimum growth temperatures adapt once each time step, based on the local and optimum temperatures at the previous time step. In our simulations, where the populations are then run close to equilibrium with the forcing, we find that we must adopt larger values of  $a$  than Robertson & Robinson (1998), in order to reproduce similar results.

If we choose a high rate of adaptation,  $a = 0.5$ , which causes the difference between optimum growth temperature and local temperature to be halved every 40 Myr, there is no planetary temperature regulation [Fig. 1(c)]. The black daisies rapidly dominate the world at low solar luminosity, being the fastest growing from the cool starting temperature [Fig. 1(d)]. As the solar forcing increases, the black daisies adapt to progressively warmer conditions, eventually driving the planetary temperature over  $100^\circ\text{C}$ . The system “chases its tail”—as increasing solar luminosity heats the planet the black daisies adapt to the warmth maintaining a high growth rate and fractional coverage that keeps the temperature well above that of a dead planet.

### Critique

In our view, Robertson & Robinson’s (1998) variant of Daisyworld is flawed in that it pays no attention to the constraints on adaptation that exist for all carbon-based, cellular life forms, including plants (DeDuve, 1995). Overheat or overcool a living system and its order breaks down. The limits are to some degree set by the structural stability of cell membranes and the

fixed thermodynamics of key chemical reactions. The membranes of most living cells have an upper temperature limit of  $\sim 50^\circ\text{C}$  set by the chemical and physical properties of the lipids that form them.

Although the “daisies” of Daisyworld should not be taken too literally, it is instructive to consider the responses of higher plants to temperature (Mohr & Schopfer, 1995). Heating plants over  $40^\circ\text{C}$  can cause irreversible damage due to enzymes denaturing. Heat shock proteins have evolved that increase the ability to survive at  $40\text{--}50^\circ\text{C}$ , and the temperature optima of photosynthesis in some desert plants can reach  $\sim 45^\circ\text{C}$ . However, even in the most heat-tolerant desert plants, rates of net photosynthesis drop steeply to zero at  $\sim 55^\circ\text{C}$ . Plant respiration rates increase with temperature (typically following an Arrhenius equation) such that the upper temperature limit for net primary productivity (plant growth) is lower than that for net photosynthesis, and growth is restricted towards this limit. Environmental constraints linked to temperature, in particular, lack of water, can limit plant growth (Lovelock & Kump, 1994). Drought stress has triggered adaptations including thick cuticles, sunken stomata and  $\text{C}_4$  photosynthesis. Such adaptations can cost energy in the manufacture of new structures or biochemistry necessary for survival. Regardless of adaptation, plant growth is limited in extreme natural environments such as deserts and arctic tundra.

Some simple, ancient organisms are much more tolerant of extreme temperatures than the plants and other multi-cellular eukaryotes that currently dominate the Earth. Thermophilic archaeobacteria and some eubacteria can grow in exotic environments at temperatures approaching or exceeding  $100^\circ\text{C}$ , and cease to grow below temperatures that are well above what is tolerable for “mainstream” life (Pool, 1990). The most thermophilic, photosynthesizing cyanobacterium *Synechococcus lividus* grows at  $66\text{--}73^\circ\text{C}$  (Edwards *et al.*, 1997). These “extremophiles” give outer limits for the bounds of adaptation.

### Constrained Adaptation

To account for the bounds on adaptation, and the limitation of growth rate as they are

approached, we introduce to the Daisyworld model a dependence of peak growth rate,  $m$ , on temperature:

$$m = 1 - ((22.5 - T_{opt})/c)^2, \quad (4)$$

where  $c$  determines the width of a parabolic “envelope”, within which the optimum growth temperature can adapt. We take  $c = 77.5^\circ\text{C}$  as a generous upper limit, which gives bounds of  $-55$  and  $100^\circ\text{C}$ . As the growth curve adapts away from  $22.5^\circ\text{C}$  the peak growth rate declines, gradually at first but quite steeply near the limits of the growth envelope. We keep  $a = 0.5$ .

The system now once again exhibits planetary temperature regulation [Fig. 1(e)] with a characteristic transition from black “daisy” dominance to white “daisy” dominance [Fig. 1(f)]. The revised model contains an additional negative feedback whereby solar-driven warming, which causes the optimum growth temperature of the black “daisies” to increase, now also reduces their overall growth rate and fractional cover, thus preventing them from remaining dominant. When only white “daisies” remain they are able to adapt to solar warming and do not disappear until 6.9 Gyr hence, when planetary temperature exceeds  $80^\circ\text{C}$  and they near the upper end of the adaptation envelope. The persistence of life is extended relative to the original Daisyworld [Fig. 1(a) and (b)] because it is assumed that the organisms can adapt to a wider range of temperature. Furthermore, the planetary temperature is maintained within the originally assumed limits to growth of  $5$  and  $40^\circ\text{C}$  for a longer time (until 5.1 Gyr) than in the original model.

If we narrow the bounds on adaptation to give a temperature range more realistic for plants (decreasing  $c$ ) this causes regulation to collapse earlier. However, even a small degree of adaptation to warmer temperatures extends the persistence of life. We have experimented with different shapes for the adaptation envelope, for example, no penalties on growth rate until a critical threshold is reached, followed by a parabolic decline to an outer limit. In this case, black daisies remain dominant until their local temperature reaches the assumed threshold (e.g.  $40^\circ\text{C}$ ) where their growth rate begins to decline. Then there is a characteristic gradual transition from black to

white daisies that regulates the planetary temperature below this threshold. Retaining the assumption that optimum growth temperature always adapts towards the local temperature may be unrealistic because it can entail an overall drop in growth rate. This can be thought of as adaptation compromising the ability of the evolved type to compete if returned to more equable growth conditions. A better model would include variation in optimum growth temperature and not assume inevitable adaptation in one direction.

### Discussion

We acknowledge that there can be an evolutionary trade off between altering the environment and adapting to prevailing conditions (Lenton, 1998; Robertson & Robinson, 1998) and that the observed range of albedo variation in plants is modest (Robertson & Robinson, 1998). Despite this, changes in plant albedo can have beneficial environmental effects. For example, the darkness of trees in the boreal forest combined with their ability to shed and shade snow warms the region and the Northern Hemisphere in the winter (Lovelock, 1995; Lenton, 1998; Betts, 1999). Globally, a combination of plant traits, including rooting depth, roughness and evapotranspiration, alter the climate in a self-beneficial manner that increases net primary production and biomass (Betts, 1999). Over Earth history, the dominant effect of the biota has been to alter the climate rather than to internally adapt to externally driven changes. In particular, the evolution of mechanisms for the biological amplification of rock weathering has progressively reduced the carbon dioxide content of the atmosphere by an estimated (10–1000)-fold causing  $15$ – $45^\circ\text{C}$  cooling (Lovelock & Watson, 1982; Schwartzman & Volk, 1989).

### Conclusion

Internal adaptation to changes in the environment does not necessarily conflict with or undermine regulation arising from altering the environment, as has been suggested by Robertson & Robinson (1998). In Daisyworld, adaptation of the optimum growth temperature toward

the local temperature can destroy temperature regulation if it is assumed that there are no bounds on the environmental conditions that can be adapted to, that equal growth rates can potentially be achieved under any conditions, and that adaptation to changes in the environment is sufficiently rapid. If this were the case, all possible states of the environment would be equally tolerable to life, and there would be no selection for organisms that stabilized the environment. However, for life as we know it there are bounds on the range of environmental conditions that can be adapted to, and as these are approached environmental conditions limit growth rates and often demand adaptations to survive, which themselves cost energy. When these constraints are taken into account, climate regulation is recovered in the Daisyworld model. Hence, our results emphasize that constraints on adaptation are important for the existence of planetary self-regulation.

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