Daisyworld revisited: quantifying biological effects on planetary self-regulation

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ABSTRACT

Daisyworld demonstrates that self-regulation of the global environment can emerge from organisms altering their local environment in different ways. In Daisyworld, natural selection is directly linked to environmental effects such that what is selected for at the individual level is beneficial to the global environment. The model has been modified and extended in many studies that have highlighted the effect of biological processes on system self-regulation. Here we better quantify their effects and present new variants of the model in an attempt to resolve outstanding debates. The results confirm that Daisyworld is a remarkably robust self-regulating system and they offer some general lessons about systems where life has a strong effect on the environment, which we think are relevant to the Earth. As forcing becomes extreme, such systems can exhibit co-existing stable states with and without life (bi-stability), and rapid transitions from one to the other that are difficult to reverse. The growth response of organisms to the environment has a role in determining the range of forcing over which a system can regulate. Density-dependent ecological interactions improve Daisyworld's regulatory properties, although increased inter-species competition destabilises the environment in one interval. Self-regulation is little affected by introducing organisms that "cheat" by not altering their local environment and in so doing gain a growth advantage. Increased variation in an environment-altering trait (albedo) can weaken the negative feedback it provides on the environment. However, random mutation of this trait and subsequent natural selection can generate and extend the range of temperature regulation and improve the system's response to perturbation with time. Internal adaptation of organisms toward prevailing environmental conditions, or to tolerate extremes, can also extend the range of forcing over which life persists.

1. Introduction

The Daisyworld model (Lovelock, 1983a; Lovelock, 1983b; Watson and Lovelock, 1983) was invented to demonstrate that global regulation can emerge automatically from physically realistic feedback between life and its environment, in answer to the criticism that it demands foresight or planning on the part of unconscious organisms (Dawkins, 1983; Doolittle, 1981). As it was impossible to fully represent how the biota and its environment are coupled on Earth, a simple parable was presented of a world where the environment is reduced to one variable (global temperature) and the biota to two types of life (black and white daisies) that alter their local temperature in opposite directions by absorbing more or less solar radiation, respectively, than the bare planet surface. The planet has a negligible atmospheric greenhouse, so its surface temperature is simply determined by the total amount of solar radiation absorbed. Local temperature deter-

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mines the growth rate of the daisies. The planet orbits a star like our Sun that gives off gradually more radiation with time. However, the global temperature is maintained close to the constant optimum for daisy growth as a result of shifting coverage of black and white daisies. The whole system is described as "self-regulating" ("self" denoting that regulation is an internal property of the system).

Daisyworld has become an archetypal model for the Gaia theory, which posits that Earth is a self-regulating system in which life plays a key role (Lenton, 1998; Lovelock, 1988). This has led in some cases to critics attacking Daisyworld as a means of attacking the Gaia theory and proponents defending Daisyworld as if the Gaia theory depended on its validity. Somewhat analogous, albedo-based climate regulating mechanisms have been found to operate on Earth, particularly in boreal forest regions (Lenton, 1998; Lenton and Betts, 1998; Lovelock, 1988). However, biologically driven changes in Earth's atmospheric composition appear to be more important over geologic timescales (Lovelock, 1988; Schwartzman and Volk, 1989; Watson and Lovelock, 1983). Daisyworld cannot resolve whether, or in what ways, the Earth is self-regulating, but it can offer some general lessons about systems where life is tightly coupled to its environment that we think are relevant to the Earth. The beauty of Daisyworld is its simplicity, making it an excellent "tutorial" model (Von Bloh et al., 1997) for answering "what if ...?" questions regarding the interactions of organisms with their environment.

Our motivation for revisiting Daisyworld is a recent burst of interest in the model in the scientific literature (Cohen and Rich, 2000; Harding, 1999; Harding and Lovelock, 1996; Lenton, 1998; Lenton and Betts, 1998; Nevison et al., 1999; Robertson and Robinson, 1998; Saunders, 1994; Stöcker, 1995; Von Bloh et al., 1997; Weber, 2001). These studies have explored the effects of different biological and physical processes on system self-regulation. Some variants of the model have been claimed to undermine the original conclusions (Cohen and Rich, 2000; Robertson and Robinson, 1998), whilst others extend them (Lenton, 1998; Von Bloh et al., 1997). However, these claims have been largely qualitative. Here we present a variety of measures for the regulatory capacity of

Daisyworld that allow us to better quantify the effects of altering the model.

We focus on biological effects on system self-regulation, testing the propositions that: Growth response affects environmental regulation; Density dependent ecological interactions contribute to system stability (Hambler, 1997); Inter-specific competition destabilises the system (Cohen and Rich, 2000); "Cheats" that gain a growth advantage by not altering their environment will undermine system regulation; The degree of variation in an environment-altering trait (albedo) affects the strength of environmental feedback; Mutation and subsequent evolution can generate self-regulation (Lenton, 1998) and extend its range (Stöcker, 1995); Adaptation to prevailing conditions undermines environmental regulation (Robertson and Robinson, 1998).

Daisyworld is a special case in that the model organisms alter their immediate (local) environment and the global environment in the same way (i.e., black daisies warm themselves and the global environment, white daisies cool themselves and the global environment). This connection means that what is selected for at the individual level is also beneficial at the global level. There are a number of other possible types of interaction between the individual and the global, giving rise to different classes of feedback, which have been explored in variants of Daisyworld and other models (Lenton, 1998). In this study we restrict our attention to the class of feedback in the original model. We consider only "zero-dimensional" variants of Daisyworld with one trophic level (the daisies). A two-dimensional Daisyworld based on cellular automata (Von Bloh et al., 1997, 1999) and Daisyworlds with herbivores, carnivores and food webs (Harding, 1999; Harding and Lovelock, 1996; Lovelock, 1992) are discussed elsewhere.

Our starting point is the original Daisyworld analysed by Watson and Lovelock (1983), which is described in Section 2. Section 3 introduces measures for the self-regulation of the system. Section 4 uses these to quantify the effects of altering the growth response and ecological interactions in the model. Section 5 considers in a step-wise fashion the effects of evolution of environment-altering traits. Then these are contrasted with the effects of adapting to prevailing conditions in Section 6.

2. Daisyworld

The dynamics of the daisy populations are based on a general epidemic model (Carter and Prince, 1981):

$$\mathrm{d}a_i/\mathrm{d}t = a_i(x\beta_i - \gamma). \qquad (1)$$

Each population is expressed as its fractional cover of the planet's surface, a_i, which has a total area of 1. β_i is the growth rate per unit of time and area and γ is the death rate per unit of time (also referred to as the death fraction). $\gamma = 0.3$ in our simulations unless otherwise stated. Time is in implicit units of generations. x is the fraction of the planet's surface not covered by daisies:

$$x = 1 - \sum_{i=1}^{n} a_i. \qquad (2)$$

This determines a density-dependent reduction in growth rate due to space limitation. The daisies share the same optimum temperature for growth, 22.5°C, and limits to growth of 5°C and 40°C. The growth rate of each daisy type is an inverted parabolic function of their local temperature, T_i:

$$\beta_i = \max(0, 1 - ((22.5 - T_i)/17.5)^2). \qquad (3)$$

The effective temperature of the planet T_e (in °C) is determined by equating emitted and absorbed radiation (energy balance):

$$\sigma(T_e + 273)^4 = SL(1 - A_p). \qquad (4)$$

where σ is the Stefan–Boltzmann constant (5.67×10^{-8} Wm^{-2} K^{-4}), S is a constant energy flux such that $S/\sigma = 1.68 \times 10^{10}$ K^4, and L is a dimensionless measure of the luminosity of the star that Daisyworld orbits. A_p is the albedo of the planet, which is given by:

$$A_p = xA_g + \sum_{i=1}^{n} a_i A_i. \qquad (5)$$

In the original model there are only two daisy types ($n = 2$), with albedos (reflectivity to solar radiation) of $A_b = 0.25$ ("black") and $A_w = 0.75$ ("white"). $A_g = 0.5$ is the albedo of bare ground. The local temperature of each daisy type is determined from:

$$(T_i + 273)^4 = q(A_p - A_i) + (T_e + 273)^4. \qquad (6)$$

This satisfies the requirements of energy balance (Watson and Lovelock, 1983). $q = 2.06425 \times 10^9$ K^4 is a measure of the degree of insulation between regions of the planet's surface, which is

equivalent to $q' = 20$ used by Watson and Lovelock (1983), who approximated eq. (6).

The population eqs. (1) are solved by iteration (Euler's method) using $\Delta t = 1$ generation. The model is forced with a linear increase in L from 0.5 to 1.7 in steps of $\Delta L = 0.004$. Then the forcing is reversed. After each luminosity step the equations are iterated 100 times, so that the populations remain close to equilibrium with the forcing (because populations change much more rapidly than solar luminosity). The effective temperature of Daisyworld (T_e) is contrasted with the "dead planet" temperature, T_{dead}, which is the solution of (4) for $A_p = A_g = 0.5$.

2.1. Bi-stability of Daisyworld

Daisyworld exhibits self-regulation and bi-stability (Fig. 1). In response to increasing solar luminosity, initial conditions are too cold for either daisy type to grow until at $L_{establish} \sim 0.68$ germinating black daisies are su ciently warm for their growth rate to exceed the death fraction ($\beta_b > \gamma$) and they spread. This warms the planet, generating an environmental positive feedback on growth, until the spread of black daisies is constrained by the limited area of the planet's surface. As luminosity increases, the temperature rises to the point where white daisies begin to appear in the daisy community. Then as it increases further, the white daisies gain the selective advantage over the black daisies and gradually take over, actually cooling the planet in the process. Eventually, only white daisies are left, and the temperature starts to increase with the forcing until at $L_{max} \sim 1.5$ self-regulation collapses. Whilst the daisies are present, the solar forcing increases over a range su cient to warm a "dead planet" by 60°C, yet the surface of Daisyworld is maintained within an 11°C range around the optimum temperature for daisy growth.

Daisyworld has two regimes of bi-stability in which solutions of the system with life and without life are both stable. When the solar forcing is reversed, the white daisies cannot re-establish until luminosity has fallen to $L_{recover} \sim 1.16$, but black daisies persist down to $L_{min} \sim 0.6$. This gives a large hysteresis loop at high solar luminosities ($1.16 < L < 1.5$) and a smaller hysteresis loop at low luminosities ($0.6 < L < 0.68$). Between them lies a "comfortable" regime ($0.68 < L < 1.16$), in
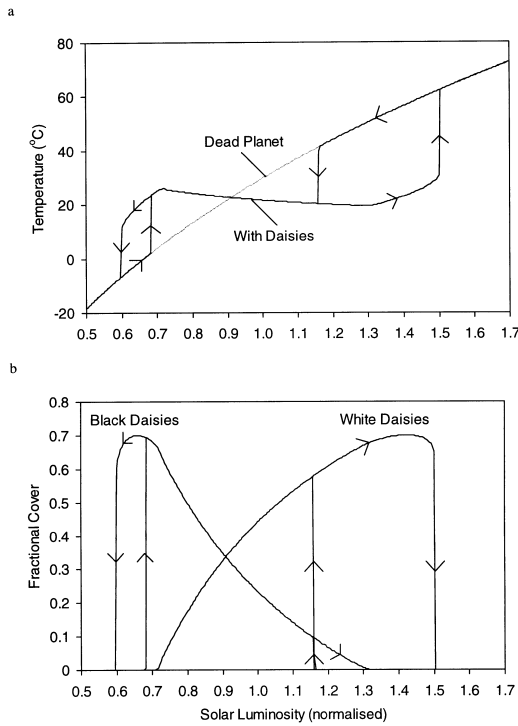
a

b

Fig. 1. Original Daisyworld. Composite results for a linear increase in solar luminosity, *L* from 0.5 to 1.7, then a linear decrease. Luminosity steps of $\Delta L = 0.004$ with $c = 100$ cycles of the population dynamics equations at each luminosity step. (a) Planetary temperature with daisies contrasted with the dead planet temperature, which is the solution of eq. (4) with constant planetary albedo, $A_p = 0.5$. (b) Fractional cover of the black and white daisy populations. The model exhibits regimes of planetary bi-stability, with the arrows indicating the directional hysteresis loops.

which the daisies can always establish from the dead planet state. In the comfortable regime, the daisies generally make the temperature closer to optimal for growth, but it would be habitable without them. In the regions of bi-stability, the daisies maintain the planet in a habitable state when otherwise it would be uninhabitable. This is an important aspect of the system's self-regulation.

2.2. Potential bi-stability of the Earth system

Life could only have arisen on Earth when the "dead" planet was in a habitable state, but once life became established there emerged the potential

for it to alter the habitability of the planet. An interesting question is whether the Earth system is now in a regime analogous to the high luminosity, bi-stable regime of Daisyworld? (Or whether it could enter such a regime in the future.) In other words, if life were deleted would the Earth revert to a hotter state from which life could not re-establish?

We suggest that the Earth system may be bi-stable, at least for eukaryotic life. The predominant effect of the contemporary biota appears to be to cool the planet (Watson and Lovelock, 1983). The biological amplification of silicate rock weathering has reduced atmospheric carbon dioxide by 10–1000 fold, causing an estimated ~ 15–$45°C$ cooling (Schwartzman and Volk, 1989; Schwartzman and Volk, 1991). Biogenic dimethyl sulphide production has been estimated to cause an increase in the average number density of cloud condensation nuclei from 5–$10\,cm^{-3}$ (without life) to $\sim 100\,cm^{-3}$ (pre-industry), and a corresponding increase in cloud albedo from 10–20% to $\sim 50\%$ causing ~ 10–$15°C$ cooling (R. J. Charlson, personal communication, 1996). These effects may not be additive because of the existence of other feedbacks in the climate system (including abiotic weathering), but they suggest that removing the responsible organisms could lead to a 25–60°C warming giving an average global temperature of 40–75°C. A global temperature in excess of 50°C would render the planet uninhabitable to most eukaryotes, and the resulting increase in water vapour in the atmosphere and loss of water from the planet due to hydrogen escape to space could eventually sterilise the Earth.

Regardless of whether the Earth system as a whole is in a bi-stable regime, model studies suggest that vegetation-climate system bi-stability exists at a regional scale. A combination of plant traits, including rooting depth, roughness and evapotranspiration, alter the climate in a self-beneficial manner that increases global net primary production and biomass. In a model without these effects on climate, the boreal, Amazonian and South-East Asian forests cannot become established (Betts, 1999). A different model suggests that the South-West Sahara could potentially exist in a "green" (vegetated) state under the present orbital

forcing, but is currently locked in a stable un-vegetated state (Claussen et al., 1998).

3. Measures of self-regulation

Daisyworld suggests some ways in which we may measure the self-regulating capacity of a planet, in response to gradual forcing or perturbation. Ideally we seek a dimensionless number somewhat akin to the Reynolds number used in fluid dynamics.

3.1. Luminosity range

Environmental feedback can extend the range of luminosity over which a planet remains habit-

able. For the case of increasing luminosity on Daisyworld, $L_{max} - L_{establish} = 0.82$. In contrast, a "neutral" daisy without any feedback to the environment, i.e., one with the same albedo as the planet's surface ($A = 0.5$), can only survive over $L_{max} - L_{establish} = 1.11 - 0.74 = 0.37$. Hence the environmental feedback in Daisyworld more than doubles the range of luminosity over which life can persist (Table 1).

3.2. Total life

The total amount of life present on Daisyworld over the whole range of luminosity provides a measure of the biological "success" of the regulatory system. This is calculated by integrating over all populations and the full range of luminos-

Table 1. *Measures of regulation in variants of the Daisyworld model*

Variant	$L_{establish}$	L_{max}	Luminosity range	Total life	Mean damping[a]	Mean temperature return time[b] (population cycles)	Reference
Neutral daisy (control)	0.74	1.11	0.37	0.204	0	—	(Watson and Lovelock, 1983)
Original Daisyworld	0.68	1.50	0.82	0.556	-3.94	2.74	(Watson and Lovelock, 1983)
Gaussian growth curve	0.72	1.45	0.73	0.461	-5.03	1.97	(Harding and Lovelock, 1996)
Density dependent death	0.65	1.53	0.88	0.603	-4.45	1.99	This study
Increased inter-specific competition	0.68	1.50	0.82	0.457	-5.65	2.42	(Cohen and Rich, 2000)
Cheats	0.68	1.50	0.82	0.576	-4.95	2.92	(Lovelock, 1989)
Albedo variation	0.68	1.50	0.82	0.570	-0.31	3.63	(Lovelock, 1989)
Mutation of albedo	0.74	1.50	0.76	0.511	-0.28	4.23	(Lenton, 1998)
Extended albedo mutation	0.74	3.20	2.46	1.712	-1.11	4.23	This study
Variance in temperature tolerance	0.60	1.57	0.97	0.657	-4.03	2.55	This study
Variance in growth optima	0.68	1.50	0.82	0.569	-5.07	2.70	This study
Constrained adaptation	0.51	2.32	1.81	1.223	-0.43	—	(Lenton and Lovelock, 2000)

[a] Derived from the amplitude of the T_{dead} (input) and T_e (output) responses to sine wave forcing of amplitude $L = 0.01$ at each luminosity step, averaged over the luminosity range in which the temperature is regulated.
[b] Defined as the time for a temperature perturbation to return to $1/e$ ($\sim 37\%$) of its initial size after halving of the daisy populations. Measured at each luminosity step then averaged over the luminosity range in which the temperature is regulated.

ity. It is increased ~2.8 fold in the original Daisyworld relative to the case without feedback to the environment (Table 1). Furthermore, despite competing for space, the area covered by each daisy type is usually greater when the other type is present (Saunders, 1994).

3.3. Resilience

Subjecting Daisyworld to instantaneous perturbations in which the fractional cover of daisies is reduced and this in turn affects the planetary temperature, tests the regulatory capacity of the system (Lovelock, 1986; Lovelock, 1988). Massive meteorite impacts or plagues could cause such extinction events, which on Earth are periodic (Raup and Sepkoski, 1986). When a system returns to its initial equilibrium after perturbation it is said to be stable in response to that perturbation, and the resilience of the system can then be measured (Pimm, 1984). Resilience describes how fast the variables of a system return towards their equilibrium following a perturbation. The characteristic "return time" is that taken for the perturbation to return to $1/e$ ($\sim 37\%$) of its initial value.

In the comfortable regime Daisyworld is stable to culls — the daisies are always able to re-establish rapidly because the temperature is never taken out of the range in which they can grow. In a bi-stable regime, if sufficient daisies are removed such that the temperature goes out of the habitable range (specifically, if $\beta_b < \gamma$ and $\beta_w < \gamma$), the remaining daisies are unable to grow and the system collapses. The cull required to cause the system to collapse gets smaller the closer one gets to the limits of temperature regulation for the unperturbed Daisyworld. We take halving the daisy populations as our standard perturbation, which causes the system to collapse at $L \sim 1.35$ (when only white daisies are present). To measure resilience we let the system approach equilibrium after each increase in luminosity, measure the temperature and populations, then halve both populations and measure the resulting change in temperature. Then we allow the system to return to equilibrium, during which we record the return time of temperature and of each population.

The temperature of Daisyworld is generally very resilient to perturbation (Fig. 2a). Over a luminos-
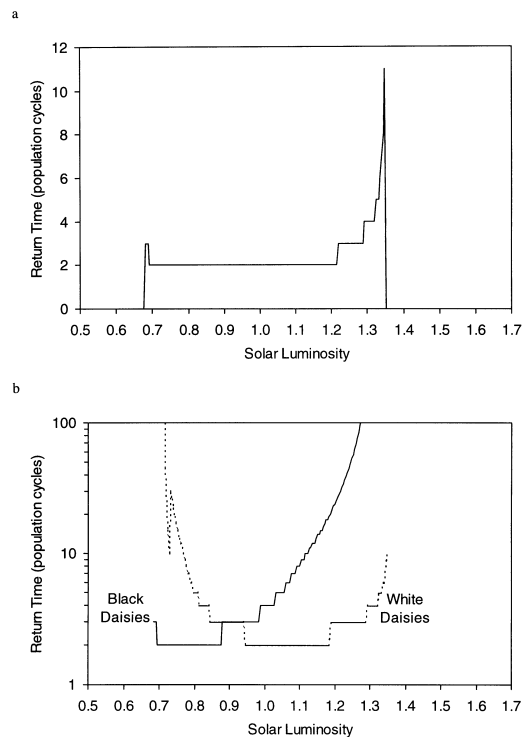

Fig. 2. Resilience of (a) temperature and (b) populations on Daisyworld, in response to halving the daisy populations at each luminosity step, measured in terms of the number of population cycles for the perturbation to be reduced to $1/e$ ($\sim 37\%$) of its initial value (the "return time").

ity range of $0.692 < L < 1.216$ the return time is only 2 cycles of the population equations. The resilience of temperature reduces markedly towards the collapse of regulation, the return time increasing to 11 cycles at the luminosity step ($L = 1.348$) just before the system collapses. We calculate a mean temperature resilience of 2.74 (Table 1) by averaging over the range of luminosities in which life is present. The resilience of the populations is high (2–3 cycles return time) when they have high fractional coverage, but decreases markedly as the fractional coverage reaches low values (Fig. 2b). For example, at $L = 1.24$ with $a_b = 0.041$ the return time for the black daisies is 45 cycles. At such low fractional coverage the black daisies have little impact on the temperature, which is basically being regulated by changes in the white daisy population. Hence, the poor resilience of the minority population does not affect the resilience

of the whole system temperature. Near the collapse of regulation at high luminosity, the resilience of the white daisy population is impaired. Just before the system collapses ($L = 1.348$), the return time of the white daisies rises to 10 cycles.

3.4. Gain, amplification and damping

The strength and sign of feedback in a system can be expressed in terms of the dimensionless measure "gain", by analogy with an electronic amplifier, with output (ω) determined by the input signal (ι) and a feedback signal proportional to output (Lashof, 1991). Gain (g) is defined as:

$$\text{gain} = \frac{\text{output} - \text{input}}{\text{output}}, \qquad g = \frac{\omega - \iota}{\omega}. \qquad (7)$$

Amplification (f) is defined as:

$$\text{amplification} = \frac{\text{output}}{\text{input}}, \qquad f = \frac{\omega}{\iota} = \frac{1}{1 - g}. \qquad (8)$$

Conventionally, ω and ι always have the same sign, g can take any real value less than 1 and f is strictly positive (Lashof, 1991). $g < 0$ ($f < 1$, $\omega < \iota$) indicates negative feedback and $0 < g < 1$ ($f > 1$, $\omega < \iota$) indicates positive feedback. The more negative g is, the stronger the negative feedback. The closer g is to 1, the stronger the positive feedback. As g tends toward 1 a system is said to be unstable. For a linear system the overall gain is the sum of the gains associated with each individual feedback loop, whereas amplification factors are neither additive nor multiplicative.

Input and output must have the same dimensions to give a dimensionless result. Hence in Daisyworld, although luminosity is the forcing parameter, we take the change in temperature of the dead planet as the input and contrast this with the change in temperature with life as the output. Through much of the luminosity range ($0.72 < L < 1.28$) the temperature with life actually decreases whilst the luminosity and the temperature of the dead planet increase. In other words, the output is of opposite sign to the input, because feedback is so strong that it over-compensates against the forcing. The term "super-negative feedback" has recently been coined to describe this phenomenon (Sardeshmukh, 2000). It poses a problem for the convention described above, because it implies $g > 1$ and $f < 0$. Allowing $f < 0$ seems a sensible indicator of overcompensation,

but values of $g > 1$ do not carry the sign of the feedback. Hence we introduce a revised measure of gain, which contrasts the *magnitude* of temperature change on the dead planet (|input|) with that in the presence of daisies (|output|). We distinguish this measure by calling it damping (d), because that is what it indicates:

$$\text{damping} = \frac{|\text{output}| - |\text{input}|}{|\text{output}|}, \qquad d = \frac{|\omega| - |\iota|}{|\omega|}. \qquad (9)$$

To measure the gain, amplification and damping of Daisyworld, after each step increase in luminosity we allow the system to approach equilibrium (100 cycles of the population equations), then vary the luminosity following a single sine wave of small amplitude ($L = 0.01$), which is divided into discreet steps of $\pi/8$ radians, at each of which we allow 100 cycles of the population equations. Then luminosity is held constant again for 100 cycles of the population equations before making the next step increase.

Fig. 3 shows the results. Through most of the luminosity range, Daisyworld is in overall negative feedback ($d < 0$). The gain is close to 1 when the black daisies first establish because a small change in forcing causes a large warming (with strong positive feedback as the daisies colonise the world). The feedback also becomes weakly positive once the white daisy population starts to decline (at $L > 1.44$) because an increase in forcing causes a decline in daisies, which amplifies the increase in temperature. Gain peaks again close to 1 as the white daisies disappear. The strongest damping, $d \sim -11$ ($f = -0.083$), occurs at $L = 1.284$, just before the temperature on Daisyworld reaches a minimum (which is also just before the black daisies disappear). The response to sinusoidal forcing at this luminosity is illustrated in Fig. 4. The anti-phase oscillations of the black and white daisy populations are characteristic of the situation whenever both populations are present. The white daisies oscillate in phase with the forcing, the black daisies oscillate out of phase with the forcing, and both effects tend to counteract the forcing. As a result the temperature with daisies oscillates in anti-phase to the dead planet temperature.

The response of Daisyworld varies through the "lifetime" of the planet, but by calculating the mean damping averaged over the range of luminosities where daisies are present, we obtain a useful
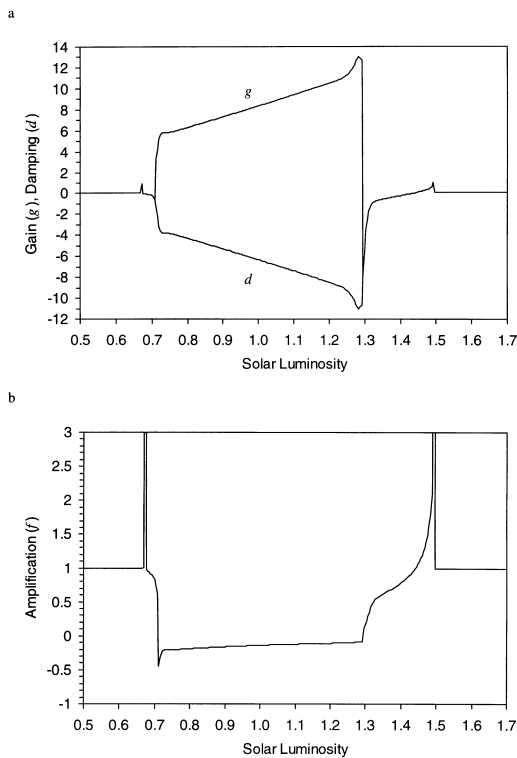
Fig. 3. Measures of the sign and strength of feedback on Daisyworld, diagnosed by small-amplitude sinusoidal forcing at each luminosity step: (a) gain, g and damping, d; (b) amplification, f.
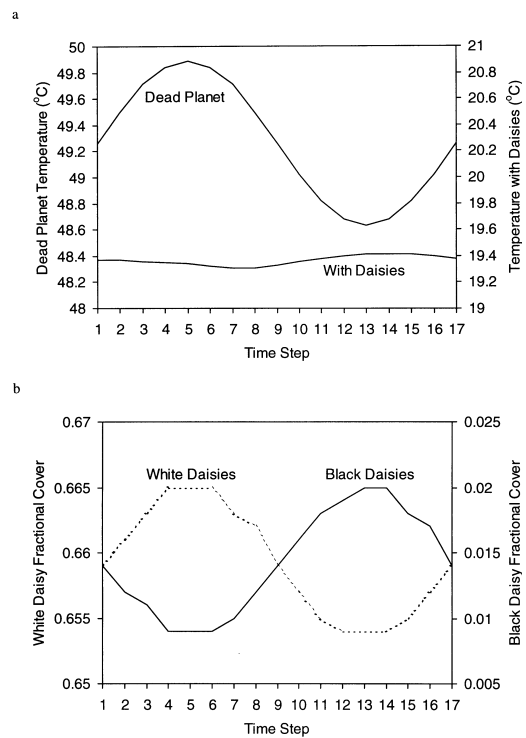

Fig. 4. Response of Daisyworld to sinusoidal forcing of solar luminosity about $L = 1.284$, where the damping is strongest (most negative). (a) Temperature change of the dead planet and the planet with daisies. (b) Fractional cover of the white and black daisies.

measure of the sign of feedback in the system and its ability to damp perturbation (Table 1). The mean damping of about -4 indicates negative feedback and strong damping. If the output of a system is constant ($\omega = 0$) despite changes in the input it is said to have infinite gain. The Daisyworld system passes through this state twice at $L \sim 0.72$ and $L \sim 1.28$ as the sign of planetary temperature change reverses. A variant of Daisyworld with infinite gain over a wide range of luminosity has been described elsewhere (Koeslag et al., 1997).

3.5. Quantifying Earth system self-regulation

The Gaia theory is often misinterpreted as suggesting that the Earth system is always dominated by stable behaviour and negative feedback. Daisyworld illustrates that "self-regulation" is not completely synonymous with "stability" or "nega-tive feedback". Although temperature is stabilised over a wide range of luminosity, the intervals when daisies colonise and later disappear from the planet are characterised by positive feedback, destabilisation of the temperature. If the Earth system is self-regulating we expect its behaviour to be characterised by relatively long periods of stability interspersed by intervals of rapid change. The measures presented for Daisyworld are potentially applicable to quantify the strength of self-regulation of the Earth system. The predominantly negative feedback in Daisyworld is much stronger than some predominantly positive, short-term Earth system feedbacks (Lashof, 1991). However, many feedbacks, including those involving biological amplification of rock weathering and dimethyl sulphide production have yet to be properly quantified.

4. Growth response and ecological interactions

We now have a suite of measures with which to assess the effects of various alterations on the regulatory capacity of Daisyworld. First we consider alterations of the growth function and population equations.

4.1. Gaussian growth curve

A peaked growth versus temperature curve may be a universal property of living things (Watson and Lovelock, 1983), but the precise shape of the curve varies considerably. For example, some extensions of the Daisyworld model with many daisy types of differing albedo have adopted a Gaussian function for the dependence of growth rate on temperature (Harding, 1999; Harding and Lovelock, 1996):

$$\beta_i = e^{-0.01(22.5 - T_i)^2}. \tag{10}$$

The function peaks at the same temperature and value as the original parabola (1 at 22.5°C), but declines more steeply with deviations in temperature from the optimum. The function remains positive, thus avoiding any mathematical discontinuities and making the low-temperature response more biologically realistic. Composite Gaussian functions for the temperature responses of marine phytoplankton and terrestrial plants fit data reasonably and have been used in a model of climate feedbacks in the Earth system, inspired by Daisyworld (Lovelock and Kump, 1994).

With the parameter values used in eq. (10), the critical condition for spread of the daisies, $\beta > \gamma$, is met over a narrower range of local temperature than the original parabola. Hence the range of temperature regulation in Daisyworld is reduced and with it the total amount of life (Table 1). However, the steeper functional response of growth to changes in local temperature improves the mean damping of the system (indicating stronger negative feedback) and the resilience of temperature (indicating more rapid response to perturbation). Thus the use of this functional response in "ecological" Daisyworlds (Harding, 1999; Harding and Lovelock, 1996) presumably contributes to their observed resilience. Other alterations of the growth response have been considered (e.g., Section 6). These confirm that

when organisms are tightly coupled to their environment, their growth range is positively correlated with the regulation range of the system, and the sensitivity of their growth response affects the strength of feedback.

4.2. Carrying capacity

Density-dependent ecological processes have been proposed as an important contributor to planetary stability (Hambler, 1997). The original Daisyworld model includes a density dependent effect on the rate of spread of the population (the birth rate) caused by the finite area of the planet — as more sites become occupied the rate of spread declines. The death rate (γ) was assumed constant. Together, the birth and death rates set the carrying capacity of the planet, K (Begon et al., 1996). This is defined as the maximum achievable cover of daisies ($a_b + a_w$), under ideal growing conditions. At steady-state, when both types are present, $\beta_b = \beta_w = \beta$ (Saunders, 1994) and from (1) and (2):

$$a_b + a_w = 1 - \frac{\gamma}{\beta}. \tag{11}$$

Using $\gamma = 0.3$ and under ideal growth conditions $\beta = 1$, gives $K = 0.7$ as the carrying capacity of Daisyworld. Throughout the time that daisies are present they are close to carrying capacity ($a_b + a_w > 0.67$), except when the black daisies are emerging and the white daisies are collapsing. Carrying capacity is reached for $1.41 < L < 1.44$, when only white daisies are present.

4.3. Density-dependent death rate

Many populations experience density dependent mortality due to intra- and/or inter-specific competition (Begon et al., 1996). Hence, to test the importance of density-dependent effects (Hambler, 1997), we make the death rate of each daisy population dependent on the total density of daisies:

$$da_i/dt = a_i \left(x\beta_i - \gamma \sum_{i=1}^{n} a_i \right). \tag{12}$$

From steady state for either population:

$$a_b + a_w = \frac{1}{\gamma/\beta + 1}. \tag{13}$$

If we adopted the original $\gamma = 0.3$, this would

give an increased carrying capacity of $K = 0.769$ and hence increase the total amount of life and the range of regulation. In order to isolate the effect of changing the functionality of the equations, we keep the carrying capacity of Daisyworld constant at $K = 0.7$, which demands that $\gamma = 0.3/0.7 = 0.429$. Density-dependent death rate introduces an additional negative feedback on changes in the size of the populations. When the total fractional cover of daisies ($a_b + a_w$) is small, the death rate is small, which helps the daisies establish. As the total cover increases then so does the death rate, buffering the increase. When the daisies are established any factor tending to decrease their fractional cover will also decrease their death rate, thus helping them re-establish.

Introducing density-dependent mortality improves the regulatory properties of Daisyworld (Table 1). The death rate is initially zero, allowing earlier establishment of the black daisies at $L \sim 0.65$. The collapse of the white daisies occurs later, at $L \sim 1.53$, because their death rate declines as over-heating causes their fractional cover to shrink. Thus the range of temperature regulation is extended and the total amount of life is increased. The additional negative feedback gives the system a more negative mean damping. The resilience of temperature and of the populations are improved because for a given cull of the populations, the overall rate of change of size of the populations is greater and hence the system returns to equilibrium faster. These results support the proposal that density-dependent ecological effects can contribute to stabilising the environment (Hambler, 1997).

4.4. Increased inter-species competition

Inter- and intra-specific competition (between and within species) are given equal weighting in the original Daisyworld and the variant above with density dependent death rate. However, in real plant communities, inter-specific competition can be stronger due to allelopathy — the secretion by plants of chemicals that inhibit the growth or reproduction of other plant species (Cohen and Rich, 2000). Cohen and Rich (2000) present a variant of the original Daisyworld with increased inter-specific competition between the two daisy types affecting the birth rate. High levels of inter-specific competition — parameter values given in

Fig. 1 of Cohen and Rich (2000) — generate mutual exclusion of the two types and a rapid change in temperature when the system switches from black daisy dominance to white daisy dominance. We find that during this interval the damping of the system is positive (indicating positive feedback), but once the white daisies are dominant it goes very negative, and the mean damping is more negative than in the original model (Table 1). Furthermore, the resilience of temperature is improved. Thus, increased inter-specific competition can improve some of the regulatory properties of the system. This is because it causes dominance of one daisy type, and a single daisy system generally has more effective damping because it does not over-compensate for changes in luminosity (temperature does not decrease as luminosity increases). Increased inter-specific competition has the detrimental effect of reducing the total amount of life, because it inhibits co-existence of the daisy types tending to make temperature and hence growth rates sub-optimal, and when both types do co-exist it reduces the carrying capacity.

5. Evolution of environment-altering traits

The Daisyworld model and the Gaia theory have both been criticised for paying insufficient attention to evolution (Robertson and Robinson, 1998). One can engineer a scenario in Daisyworld to destroy regulation (Keeling, 1991), but the question is whether such scenarios could have evolved by natural selection. There are two basic pathways for evolution in response to a changing environment — alter it or adapt to it. In the case of the daisies, altering the environment can occur through changes in albedo (Lenton, 1998; Stöcker, 1995; Von Bloh et al., 1997), whilst adaptation to the environment can occur through changes in the growth curve (Robertson and Robinson, 1998; Saunders, 1994). First we consider evolution of albedo, the environment-altering trait, taking a stepwise approach to introducing evolution to the model. Initially we increase the variation of traits at the start of the model run, which gives more for natural selection to act upon. Then we introduce random mutation, which generates variation as the model run progresses.

5.1. Cheats

Evolutionary biologists have criticised the foundations of Daisyworld, arguing first that the system would be vulnerable to "cheats" that saved the energy of producing pigment, whilst enjoying the climate modulation offered by the other daisies. It was predicted that this would destroy the system. When daisies of the same colour as the planet's surface are introduced to Daisyworld and given a 5% advantage in growth rate, this does not destroy the regulation of climate (Lovelock, 1989). These grey daisies only dominate when the solar luminosity is well within the comfortable regime. As solar luminosity warms the planet above the optimum temperature for daisy growth, the benefits to growth from producing white pigment begin to outweigh the costs. This emphasises that planetary self-regulation can only emerge from traits that are more beneficial than costly to the individuals carrying them. The introduction of cheats does not alter the regulatory range of the model but it does increase the total amount of life (Table 1), because the increase in maximum growth rate awarded to the cheats gives them a greater carrying capacity. The mean damping of the system is improved by the presence of cheats, despite the fact that there is no damping when the cheats are dominant. This is because the presence of the cheat inhibits co-existence of the black and white daisies, thus suppressing the tendency for the system to over-compensate in response to temperature perturbations. The temperature resilience is slightly impaired.

5.2. Increased albedo variation

Variation in the albedo of the daisies is present in the original model (i.e., "black" or "white") and selection amongst this variation is essential to the regulation. When a greater number of daisy types of differing albedo are included, planetary temperature is generally maintained closer to the optimum for daisy growth (Lovelock, 1989). We consider the case of eleven daisy types ($n = 11$) with albedos ranging from 0.25 to 0.75 in steps of 0.05. As luminosity increases each type dominates in turn in order of increasing albedo. At equilibrium at a given luminosity a maximum of two daisy types can co-exist, these being the best suited to the prevailing conditions (achieving the highest

growth rate when covering the planet). The range of regulation is unaltered but the total amount of life is slightly increased (Table 1), because the system is closer to carrying capacity throughout. The mean damping of the system is much less negative because, except at the extremes of the luminosity range, the dominant daisy types are now ones whose albedo differs less from the bare planet surface. Hence, the negative feedback due to changes in the area of these types is weaker. This in turn causes the system temperature to be somewhat less resilient to perturbation.

5.3. Mutation of albedo

We now consider a model world in which the albedo of the daisies is subject to random mutation, using the approach described by Lenton (1998) but here using slightly different parameter values. Mutation of albedo was independently considered by Stöcker (1995) and in a two-dimensional Daisyworld (Von Bloh et al., 1997). These studies found that when daisy albedo is allowed to mutate across a continuous spectrum (at a relatively low rate) this can significantly increase the range of temperature regulation at high luminosity, because more reflective daisies than the original "white" ones can evolve (Stöcker, 1995; Von Bloh et al., 1997).

We take a different approach, beginning with a single daisy type of the same albedo ($A_1 = 0.5$) as the planet's surface, which hence has no affect on the local or global temperature. Albedo is allowed to mutate in discrete steps of $\Delta A = 0.05$ within limits that are initially set as $A_{min} = 0.25$ and $A_{max} = 0.75$, corresponding to the "black" and "white" daisies of the original model. Solar luminosity is increased in steps of $\Delta L = 0.004$. Each time luminosity is increased there is the potential for mutation, followed by c cycles of the population dynamics equations. Mutation occurs with equal probability in either direction of increasing or decreasing albedo. The probability of mutation for any individual reproducing daisy is assumed to be constant. This is represented by the parameter, p, which varies between 0 and 1 and is scaled for the whole planet. The probability of a new type being created by mutation from an ancestral type is also proportional to the size of the ancestral population, expressed as fractional coverage, a_i. Hence, the more abundant types are

more likely to beget new types. A new daisy type is created when:

$$pa_i > \text{Rnd} \qquad (14)$$

where Rnd is a random number between 0 and 1, generated each time there is the potential for mutation. As the fractional coverage cannot exceed the carrying capacity of 0.7 there is always at least a 30% chance that mutation will not occur after a given step up in luminosity. When mutation does occur, the new type is compared with existing albedos. If that albedo type already exists, it is subsumed into the existing population (nothing happens in the program because the loss from one population and addition to the other is negligible). If a genuinely new albedo type has been created, it is represented by a new population equation (1) in the computer program.

Fig. 5 shows the result of a typical run with $p = 0.5$ and $c = 100$ (similar to Fig. 3 of Lenton 1998)). The ancestral grey type starts to grow ($\beta_1 > \gamma$) at $L = 0.74$ and as the planet warms and it becomes more abundant, a darker mutant ($A_2 = 0.45$) arises. This out-competes the ancestral type by virtue of being locally warmer (closer to the optimum temperature for growth), and its spread warms the planet. As L increases, the ancestral type re-establishes dominance and then a paler mutant ($A_3 = 0.55$) evolves and takes over. A series of successively paler mutants arise and dominate the planet as the forcing increases. The result is that the temperature of the planet is maintained a little above the optimum for daisy growth. Regulation collapses at $L = 1.5$ when the palest allowable type (with $A_{\max} = 0.75$) overheats. A sensitivity analysis for the mutation model is presented in Section 9.

The results should be compared with the model with increased albedo variation, because that contains, at the outset, all the daisy types that can potentially evolve in the mutation model. The regulatory range is less in the mutation model and hence the total amount of life is reduced (Table 1), because the evolution of dark daisies cannot occur until there is a significant population of the ancestral grey daisy. The damping and resilience of the mutation model were tested without allowing mutation in response to the perturbations. The mean damping is somewhat weaker and the resilience poorer than in the model with all variants present from the outset, because of the delays in
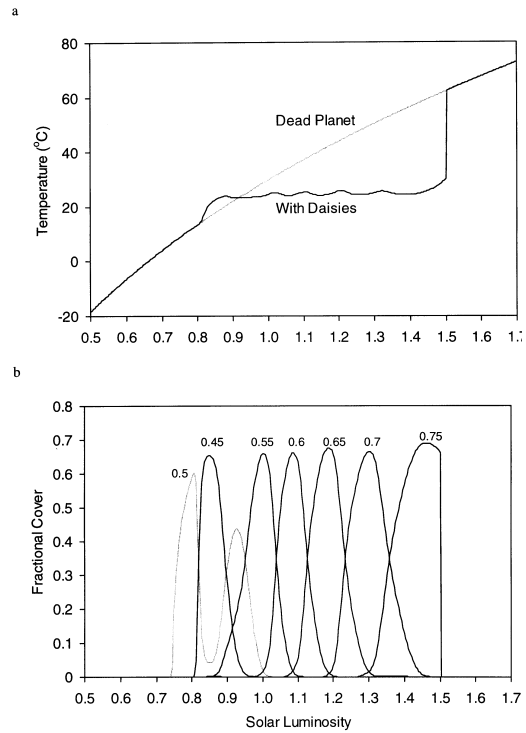

Fig. 5. Mutation of albedo generating temperature regulation. Maximum albedo is limited to $A_{\max} = 0.75$, the probability of mutation is relatively high, $p = 0.5$, and the system is run close to equilibrium with the forcing at each luminosity step, $c = 100$. (a) Temperature. (b) Evolution of daisy types labelled by their albedo. "0.5" is the ancestral neutral daisy type.

evolving each daisy type of progressively higher albedo.

If we relax the constraint on the maximum albedo and allow the daisies to mutate to become perfect reflectors, $A_{\max} = 1$, then the range of temperature regulation can be greatly extended. Fig. 6 shows the result keeping $p = 0.5$, but with slightly larger luminosity steps of $\Delta L = 0.006$ (due to constraints on array size in our computer program), and $c = 200$. Temperature regulation continues up to $L = 3.2$ corresponding to a dead planet temperature of 130°C. The total amount of life is correspondingly increased (Table 1) and the damping of the system improves considerably at the higher luminosities, indicating that the system has evolved more effective regulation.
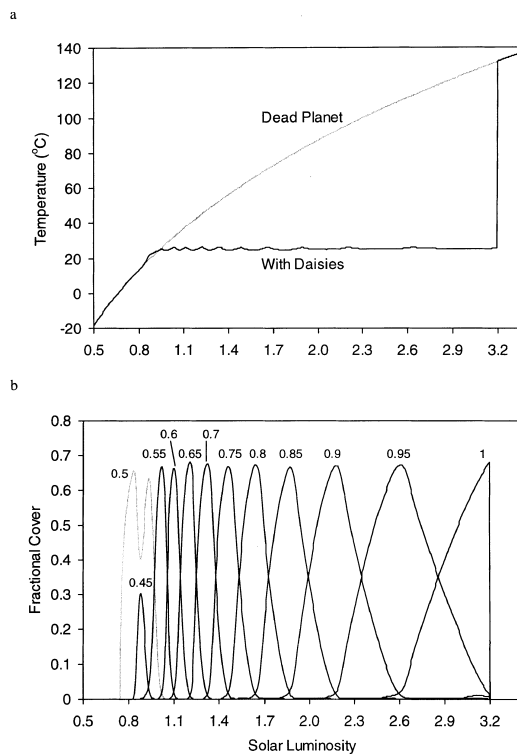
Fig. 6. Mutation of albedo extending the range of temperature regulation. The constraint on maximum albedo is relaxed so that perfect reflectors can evolve ($A_{max} = 1$). The probability of mutation remains the same $p = 0.5$, other parameters are $c = 200$, $\Delta L = 0.006$. (a) Temperature. (b) Evolution of daisy types labelled by their albedo. "0.5" is the ancestral neutral daisy type.

5.4. Effect of evolution on Earth's climate

It appears that over the history of life on Earth, evolution has generated progressively stronger cooling effects on the Earth's climate. In particular, traits that amplify the rate of rock weathering and consequently reduce the carbon dioxide content of the atmosphere have accumulated over time and have become more effective, especially with the rise of vascular plants on the land surface (Lovelock, 1988; Schwartzman and Volk, 1989, 1991). A stronger biotic amplification of weathering implies a stronger negative feedback and more responsive regulation against perturbations that tend to increase carbon dioxide and/or temperature.

An overall trend towards stronger cooling effects on Earth's climate appears superficially similar to the evolution of progressively paler daisies in the Daisyworld with albedo mutation. However, there is a much clearer connection between local natural selection and beneficial global effects on Daisyworld than in many Earth system feedback mechanisms (Lenton, 1998). Biotic weathering traits most likely evolved because they provide a source of limiting nutrients, especially phosphorus, to the responsible organisms (Lenton, 1998). They were not selected for their global effects on carbon dioxide or temperature. Cooling of the planet may have been beneficial to growth at times in the past, if the Earth was above the optimum temperature for growth, and may thus have encouraged the spread of the responsible traits, until temperatures became suboptimal. However, with the evolution of land plants, lowered carbon dioxide levels and further cooling became limiting to growth and weathering rates. Evolution thus appears to have driven the Earth system into a self-limiting negative feedback regime. Daisyworld remains in a negative feedback regime until it is nearing the limits of its operation.

6. Adaptation to prevailing conditions

Natural selection (acting on heritable variation) can drive the physiological adaptation of organisms to the conditions prevailing in their environment. It has been suggested that such internal adaptation will tend to undermine any self-regulation due to the organisms altering their environment (Robertson and Robinson, 1998). In the original Daisyworld, the response of the organisms to environmental conditions (temperature) is fixed. Here we consider potential adaptations of the growth response of the daisies to temperature, to test whether adaptation undermines self-regulation.

6.1. Variation in tolerance of extreme temperatures

First we consider variation in the tolerance of the daisies to extreme temperatures, by introducing to the original model, black and white daisies that are more tolerant of extremes in temperature, i.e., with a broader growth parabola. We reason that evolving the ability to tolerate and grow under freezing or excessively hot conditions will involve some energy investment (e.g., in novel

biochemistry or structural changes), which in turn reduces the maximum growth rate of the daisies (relative to the original types). The growth function can be expressed in general form as:

$$\beta_i = \max(0, m(1 - ((T_{\text{opt}} - T_i)/r)^2)), \qquad (15)$$

where m is the peak growth rate (which scales the whole growth function), and r determines the range of temperature tolerance (it is half of the width of the growth parabola). T_{opt} is the optimum growth temperature, which is kept constant at $22.5°C$, and T_i is the local temperature of the daisy type in question. In the original model, $m = 1$ and $r = 17.5°C$. We now introduce black and white daisy types with $r = 27.5°C$, giving a wider range of temperature tolerance of $-5°C$ to $50°C$, which is assumed to cause them a 5% growth rate penalty, $m = 0.95$.

Fig. 7 shows the result of introducing these temperature tolerant types in addition to the original types (four daisy types in all, two black, two white). The range of temperature regulation is extended to $0.6 < L < 1.57$ (Table 1), as a direct consequence of assuming a wider range of temperature tolerance of the organisms. The more cold-tolerant black daisy can establish itself at lower solar luminosity. This has the knock-on effect of creating a warm enough world that the original black daisy type (which has a higher growth rate in the range $18–27°C$) takes over, at a lower luminosity ($L = 0.632$) than it could establish in the original model. At intermediate luminosity ($0.7 < L < 1.3$), all 4 types co-exist, before the original white type becomes dominant (in the range $1.3 < L < 1.5$). As the original white daisy declines at $L = 1.5$, the more heat tolerant white daisy takes over and is able to persist up to $L = 1.57$. The wider range of temperature regulation means a greater amount of life. The mean damping of the system and the resilience of temperature are slightly improved. The appearance of a more cold-tolerant black daisy at low solar luminosity is very robust. It occurs even if these daisies are given a large growth rate penalty (e.g., $m = 0.8$). In contrast, the appearance of a heat tolerant white daisy at high luminosity is more sensitive to the parameter values chosen in the model. Reducing the growth penalty (increasing m) favours its appearance, as does running more completely to equilibrium (increasing c).
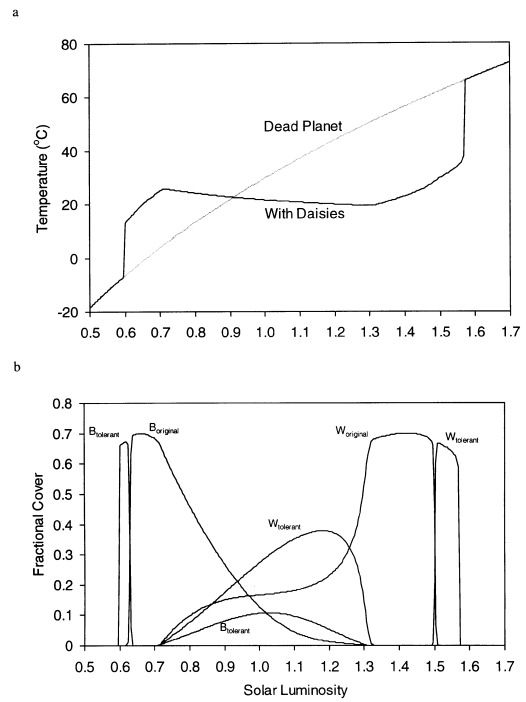
Fig. 7. Variation in tolerance of temperature extremes — new black (B_{tolerant}) and white (W_{tolerant}) daisy types with wider ranges of temperature tolerance ($r = 27.5°C$, $m = 0.95$) are introduced in addition to the original black (B_{original}) and white (W_{original}) types. There are $c = 400$ cycles of the population dynamics equations at each step up in luminosity, in order to capture the transition from original white daisy to more tolerant white daisy at high luminosity. (a) Temperature. (b) Populations.

6.2. Variation in optimum growth temperature

Saunders (1994) first reasoned that if there is variation of optimum growth temperature within each daisy population then we might expect the optimum to evolve towards the local temperature. Over the range of luminosity where black and white daisies co-exist, $T_b = 27.5°C$ and $T_w = 17.5°C$ (Saunders, 1994). To explore the effect of variation in the optimum growth temperature within the black and white daisy populations, we introduce new types of black and white daisy with these optimum growth temperatures in addition to the original types. This gives two populations of "black" daisies ($A_b = 0.25$), one with $T_{\text{opt}} = 27.5°C$, the other with $T_{\text{opt}} = 22.5°C$, and two populations of "white" daisies ($A_w = 0.75$), one with $T_{\text{opt}} = 17.5°C$, the other with $T_{\text{opt}} = 22.5°C$.

Fig. 8 shows the result. The original black type with the lower optimum growth temperature dominates first (because it is the first that is able to grow). This warms the planet to the point where the new black and white types can begin to invade, and the new black type, with high optimum growth temperature, takes over. As the solar forcing increases, the original white daisy (with higher optimum growth temperature) gradually takes over. Thus, the original daisy types dominate at the beginning and end of temperature regulation, which consequently occurs over the same range of luminosity ($0.68 < L < 1.5$) as in the original model. This contrasts with a narrowing of the range for just the two types with altered optimum growth temperature (Saunders, 1994). Thus, including variation explicitly in the model rather than assuming adaptation can alter the result. The

total amount of life is slightly increased (Table 1), in agreement with Saunders (1994). The resilience of the system is slightly improved and the mean damping is significantly improved.

6.3. Adaptation of optimum growth temperature toward local temperature

Robertson and Robinson (1998) have argued that if there were variation in the optimum growth temperature within each daisy population, this parameter should always adapt towards the prevailing local temperature. At high rates of adaptation, this is found to destroy temperature regulation on Daisyworld when it is assumed that there are no bounds on the conditions that can be adapted to and equal growth rates can potentially be achieved under any conditions (Robertson and Robinson, 1998). However, the thermodynamics, chemistry and structure of living organisms set bounds on the range of conditions that can be adapted to. As these are approached, environmental conditions limit growth rate and adaptations necessary for survival can cost energy. When bounds on the range of adaptation are added to this variant of the model and peak growth rate is limited as these are approached, temperature regulation is recovered (Lenton and Lovelock, 2000). With adaptation in the response to perturbation, the mean damping of this system is comparable to the mutating albedo model (Table 1). The range of solar forcing over which life maintains the planet in a habitable state is extended because it is assumed that organisms can adapt to tolerate a wider range of local temperatures.

6.4. Adaptation and Earth system regulation

The preceding studies suggest that the adaptation of organisms to the conditions prevailing in their environment does not necessarily conflict with regulation arising from them altering their environment. Adaptation can disrupt regulation but it operates within constraints that prevent it destroying regulation. Hence regulation is feasible in a world where organisms both alter their environment and adapt to it. Adaptation can be beneficial to the long-term survival of life, allowing it to accommodate externally forced changes in the
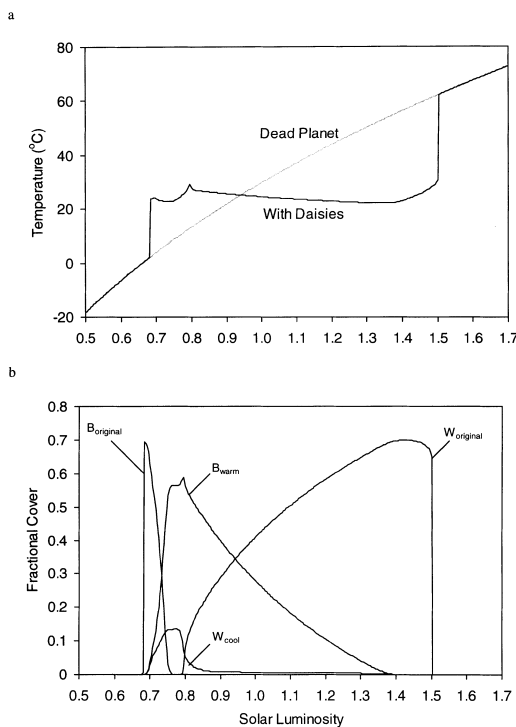
Fig. 8. Variation in optimum growth temperature — a black daisy type with a higher optimum growth temperature $T_{opt} = 27.5°C$ (B_{warm}) and a white type with a lower optimum growth temperature $T_{opt} = 17.5°C$ (W_{cool}), are introduced in addition to the original black ($B_{original}$) and white ($W_{original}$) types, $c = 100$. (a) Temperature. (b) Populations.

environment and thus extending the range of regulation.

On Earth, temperature limits on adaptation are narrower for more recent, more structurally complex life forms. This suggests that if the system is self-regulating, the climate is kept within narrower bounds now than it was in the past. In the future, the ability of the biota to adapt to warming and low carbon dioxide levels should be an important factor in determining how long life survives on Earth. The more structurally complex life forms are likely to perish first and the system may eventually revert to a prokaryote world with greater climate variability, in which adaptation has greater scope to prolong the survival of life.

7. Conclusion

Our results confirm that the Daisyworld model is a remarkably robust self-regulating system. Biological processes that have been argued to undermine regulation, including increased inter-specific competition (Cohen and Rich, 2000) and adaptation to prevailing conditions (Saunders, 1994; Robertson and Robinson, 1998), are less disruptive than previous studies suggest, and they can have beneficial effects on system regulation. Previous results indicating that albedo mutation can generate (Lenton, 1998) and extend the range (Stöcker, 1995; Von Bloh et al., 1997) of environmental regulation are supported, as is the suggestion that density-dependent ecological interactions can contribute to environmental regulation (Hambler, 1997). The growth response of organisms and the degree of variation in environment-altering traits are also found to have significant effects on the range of regulation and the strength of environmental feedback.

We have highlighted the potential relevance of our results to the Earth system, but we remind readers that Daisyworld is a parable. Daisyworld is to Earth system modelling what Lotka and Volterra's rabbit and fox model is to ecological modelling – an inspiring first attempt. Daisyworld pioneered modelling of feedback between the biota and the environment, and has proved a valuable stimulus in other areas of science, for example, physiology (Koeslag et al., 1997). The hypothetical nature of Daisyworld does not detract from these useful contributions. The capacity to model the

real world has increased greatly since Daisyworld was formulated. Attempts to include biotic effects in models of the Earth system offer the potential to explore whether the general lessons we have drawn from Daisyworld are relevant to the real world.

8. Acknowledgements

We are grateful to Andrew Watson for many valuable discussions of the functioning of Daisyworld and its relevance (or not) to the Earth. We thank Peter Saunders and an anonymous reviewer for their helpful comments on the manuscript.

9. Appendix

Sensitivity analysis for the albedo mutation model

At the high mutation probability ($p = 0.5$) used in the presentation of the model with albedo mutation (Subsection 5.3), it very rarely fails to evolve all of the daisy types that are more reflective than the ancestral type. However, at low mutation probabilities the system can collapse without evolving some or all of the more reflective types. For example, Fig. 9 shows the temperature trajectories for 10 runs with $p = 0.05$ ($A_{max} = 0.75$ and $c = 100$ as in Fig. 5), together with the mean temperature trajectory. The randomness of mutation in the model is now apparent and translates into randomness in the length of persistence of life on the model planet. In one run, all the more reflective types evolve and temperature regulation occurs up to $L \sim 1.5$. However, in two cases no new types ever achieve a significant population, and the ancestral type perishes at $L \sim 1.1$. The mean temperature trajectory only shows slight temperature regulation. The large variance amongst the runs at low mutation probability should be borne in mind, as mean temperature trajectories are now used to illustrate the parameter sensitivity of the model.

Fig. 10a shows the effect of varying the mutation probability, p, on the mean temperature trajectory, which is the mean of 10 runs in each case (for fixed $c = 100$). The system is particularly sensitive for $p < 0.2$. At $p = 0.2$ and above the system evolves all the allowable, more reflective daisy types, in
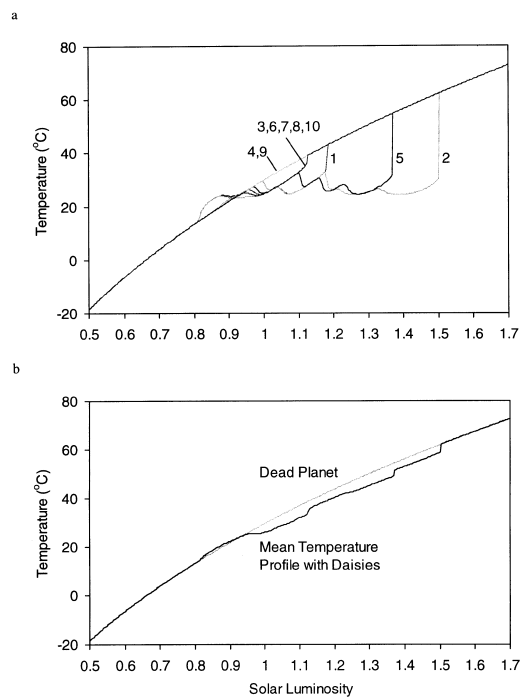
Fig. 9. Randomness of mutation affecting the persistence of life on Daisyworld: (a) Temperature trajectories for 10 separate (labelled) runs with a low probability of mutation, $p = 0.05$. Shows randomness in the length of persistence of life (and temperature regulation) on Daisyworld due to randomness in the mutation. (b) Mean temperature trajectory for the ten runs shown in (a), contrasted with the temperature of the planet without life. Shows only minor temperature regulation due to averaging.

Fig. 10. Sensitivity analysis of the mutating albedo model: (a) Dependence of temperature regulation on probability of mutation, p. Each temperature trajectory is the mean of 10 runs at the indicated value of p. (b) For $p = 0.15$, which gives high sensitivity, the dependence of temperature regulation on the proximity of the populations to equilibrium, determined by c (the number of population cycles at each luminosity step). Each temperature trajectory is the mean of 20 runs at the indicated value of c.

almost all the runs. We don't find any evidence for an optimal mutation rate above which regulation begins to be impaired, but this has been reported in models with continuous (not discrete) mutation of albedo (Stöcker, 1995; Von Bloh et al., 1997).

At low mutation probabilities with a wide variance in outcomes, temperature regulation is sensitive to the number of population cycles at each luminosity step, c. This parameter determines how close the system gets to equilibrium before the
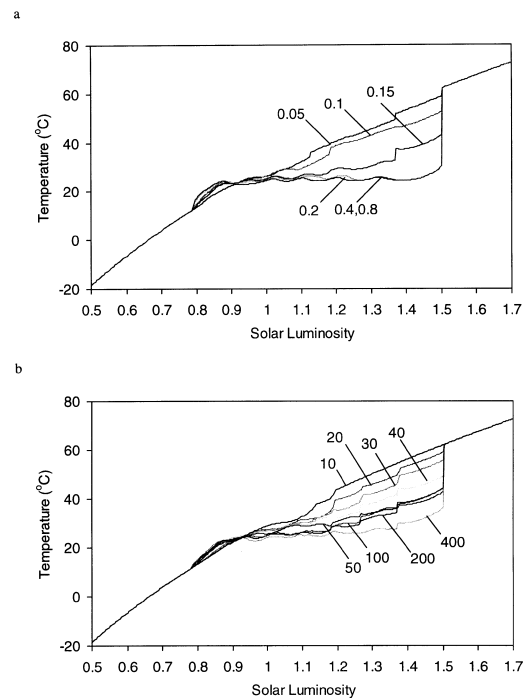
minor perturbation of stepping up the luminosity. Fig. 10b shows the effect of c on the mean temperature trajectory for $p = 0.15$ (the mean of 20 runs for each c). At larger values of c, the mean temperature regulation is improved, because with more cycles of the population equations after each mutation event, the daisy type with albedo best suited to that luminosity is more likely to attain dominance. At higher mutation probabilities the results are much less sensitive to c.

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