The importance of timescales for the emergence of environmental self-regulation

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HIGHLIGHTS

► We identify competing timescales in a reduced version of the original Daisyworld model.
► It is found that the reduced model retains much of the expected behaviour.
► Homeostasis may only occur beyond a critical ratio of albedo and forcing timescales.
► Closed form expressions are found for damping of shocks, and oscillation onset.
► Spatially embedded Daisyworlds are found to exhibit identical fixed points.

ARTICLE INFO

ABSTRACT

Models which explore the possibilities of emergent self-regulation in the Earth system often assume the timescales associated with changes in various sub-systems to be predetermined. Given their importance in guiding the fixed point dynamics of such models, relatively little formalism has been established. We analyse a classic model of environmental self-regulation, Daisyworld, and interpret the original equations for model temperature, changes in insolation, and self-organisation of the biota as an important separation of timescales. This allows a simple analytical solution where the model is reduced to two states while retaining important characteristics of the original model. We explore the consequences of relaxing some key assumptions. We show that increasing the rate of change of insolation relative to adaptation of the biota shows a sharp transition between regulating, and lifeless states. Additionally, in slowing the rate of model temperature change relative to the adapting biota we derive expressions for the damping rate of fluctuations, along with a threshold beyond which damped oscillations occur. We relax the assumption that seeding occurs globally by extending this analysis to solve a two-dimensional cellular automata Daisyworld. We conclude by reviewing a number of previous Daisyworld models and make explicit their respective timescales, and how their behaviour can be understood in light of our analysis.

1. Introduction

To what extent the emergence and evolution of life on Earth has resulted in a planetary system that is in some respects homeostatic or self-regulating was the focus of the original Gaia Hypothesis (Lovelock and Margulis, 1974). The antecedents of this argument can be traced to the work of Vernadsky who popularised the term *biosphere* and argued that one cannot understand the surface conditions of the Earth without factoring in life's effects (Vernadsky, 1926). Lovelock's initial insight was to realise that any widespread biosphere should, in principle, be detectable from space as the effects of life would be to produce atmospheres far from equilibrium (Lovelock, 1965). A terrestrial example is the presence of both non-negligible amounts of oxygen and methane in the atmosphere. Is it the continual biogenic production of methane that replaces the methane that would be rapidly lost as it reacts with oxygen (Cicerone, 1988). Life, via unavoidable metabolic by-products, affects the movement and cycling of chemical species within the Earth system and in doing so has affected not only the Earth's atmosphere but also its oceans, crust and cryosphere. Lovelock speculated that the evolution of life and its interaction with different elements of the Earth system gave rise to a system in which the surface conditions of Earth had been regulated to within the bounds that would be required *for* widespread surface life, i.e. maintaining surface liquid water over appreciable fractions of the globe (Lovelock, 1979). The teleological

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implications of this were not lost on contemporary thinkers and the original hypothesis was controversial and subject to pointed critique (Dawkins, 1983; Doolittle, 1981). As more recent reviews show, the Gaia Hypothesis has matured over time and rather than being fundamentally incompatible with neo-Darwinism, geology or climatology is now seen as being relevant to a range of subjects that investigate the Earth system (Lenton, 1998; Free and Barton, 2007). For example, the abiotic process of chemical weathering of silicate rocks has produced a negative feedback loop that has to a certain extent offset the increased luminosity of the sun over geological timescales (Walker et al., 1981; Berner, 1991). It has been proposed that land plants have an overall increasing effect on this process and so have altered the fixed points of atmospheric CO_2 (Schwartman and Volk, 1989). Evidence for the biological amplification of chemical weathering by land plants has been traced back to the Ordovician (Lenton et al., 2012).

In terms of quantitative models and simulations, much of the investigation into the plausibility of Gaian self-regulation has been progressed via developments and extension of the Daisyworld model (Watson and Lovelock, 1983). Daisyworld was originally intended as a mathematical proof of concept for planetary homeostasis that emerged from the interactions between simple life forms and their environment. Daisyworld is a grey, Earth sized planet that orbits a sun-like star. Much like our own sun, this star has increased in luminosity over geological timescales. On a lifeless planet, this increase in luminosity would produce a proportional increase in global temperature. However, Daisyworld is seeded with black and white daisies which prove to be important components in a planetary self-regulating system that leads to global temperature not increasing but remaining within comparatively narrow bands for a wide range of luminosity. It is assumed that there are sufficient nutrients and water for daisies to grow and the only environmental factor that determines their growth is the local temperature. As well as being affected by temperature, the changing coverage of black and white daisies affects the albedo of the planet and so the amount of energy from the star that is reflected back out into space and consequently global temperature. As luminosity increases, it is the proportional coverage of black and white daisies that changes while the global temperature remains relatively stable. The original model has since been significantly extended, developed and applied to new domains (see Wood et al., 2008 for a review).

An initial and ongoing criticism of Daisyworld was that the model is too simple and too contrived to give us any useful information and insights into the actual Earth (Kirchner, 2002). While some of these criticisms were addressed at the time by Lenton and Wilkinson (2003) there has been relatively little concentration on the respective timescales of the different processes operating in Daisyworld before or since. In particular, while the luminosity of the star, which increases over geological timescales, can be approximated as remaining constant while daisy coverage changes, many perturbations of the Earth system occur over much faster timescales. The response of organisms and ecosystems to an impact of a sizeable meteorite into the Earth would not be adaptation but obliteration and less dramatic perturbations will occur over short timescales relative to biological organisms and ecosystems. Some of these may be related to geological processes such as earthquakes and vulcanism (Zielinski et al., 1994). With regards to anthropogenic climate change, it is not simply the total amount of CO_2 that humans have emitted into the Earth's atmosphere but rather the *rate* at which this has happened and consequently the speed of the change in radiative forcing (Solomon et al., 2007). Other anthropogenic perturbations can occur over even faster timescales and affect different elements of the Earth system. For example humans' impacts on the nitrogen cycle have, post industrialisation, led to dramatic changes in the global nitrogen cycle (Vitousek et al., 1997) and such effects need to be considered alongside other processes such as land use change and deforestation. Models of self-regulating mechanisms need to be able to incorporate these processes or alternatively tell us when regulation will fail. They also need to consider how the different timescales operating within the Earth system interact to function as a coherent self-regulating mechanism and what are the bounds and limits for such interacting processes. As well as being subjected to different timescales of perturbation, the Earth system is composed of a multitude of interacting sub-systems that operate over a wide range of temporal and spatial scales. The Earth's oceans have profound effects on climate and given that liquid water has approximately four times the mass heat capacity of air, interactions between oceans and atmosphere will feature lags, delays and other behaviour associated with the interactions of processes interacting over different timescales. This represents a fundamental challenge in understanding processes such as the El Niño/La Niña-Southern Oscillation (Battisti and Hirst, 1989).

It is appreciated that the biota will not only respond to changed climate, but that such changes could attenuate or amplify initial forcing. The development of a new generation of coupled general circulation and dynamic vegetation models predict land ecosystems and oceans act as net sinks for increased CO_2 until critical thresholds are reached at which point they will start to behave as net sources (Cox et al., 2000). Consequently, rather than environmental conditions remaining fixed while life adapts to a perturbation, the relaxation to a steady state is instead a moving target with biotic effects continually moving environmental conditions. Depending on the particular elements of the Earth system of interest, the oscillations and progress towards the steady-state values may be more important than the steady-state values themselves.

Time dependencies have been examined in Daisyworld previously (Zeng et al., 1990; De Gregorio et al., 1992; Wood et al., 2006). However these have all proceeded on the basis that the timescales of certain processes have already been determined. In particular the increase in luminosity occurs over the very longest timescales. Other timescales such as the rates of daisy removal and establishment and the response of environmental variables (such as temperature) to changes insolation and albedo can remain implicit.

In this study we make explicit these timescales and explore the self-regulating mechanism as they are relaxed. Our motivation in doing so is to assess the robustness of self-regulation and consequently how it may be applied to the analysis of elements of the Earth system. To begin, we reintroduce Watson and Lovelock's (1983) Daisyworld model in Section 2, and identify the model timescales in Section 2.1. Here we show that by making the relevant timescales explicit and make comparisons with timescales of similar processes on Earth. We are able to eliminate the time dependance of global temperature and daisy coverage by instead solving for their steady-state values. Following Hankin and Mitchell (2011), we eliminate the need to explicitly include bare habitable ground. However, rather than parametrising infiltration between daisy species, we further separate the timescales associated with changes in daisy coverage and begin analysis when the daisy growth process occurs on much shorter timescales than daisy removal. Solutions to this model in Section 2.2 highlight some aspects of the original Daisyworld model such as the decrease in temperature with increased solar forcing and hysteresis loops. These solutions represent limiting cases, and are exploited in Section 2.3 to relax the previous assumption of separated timescales and produce illuminating analysis of the model response to increased rates of external forcing and instantaneous shocks. The onset of temperature oscillations due to increased heat capacity and the impact of seed diffusion rates, and effects of local seeding are also explored.

2. Daisyworld

The original equations governing Daisyworld allow sites to be bare with albedo A_e or to have one of two occupied states; b or w denoting the presence of a black or white daisy with albedo A_b and A_w, respectively. Using α as the fractional coverage of black and white daisies, and x for bare ground, we can write the normalisation condition

$$\alpha_b + \alpha_w + x = 1. \tag{1}$$

Daisies proliferate by seeding sites in state x at a temperature dependant rate $\beta(T)$, and sites revert to being empty at a rate γ, the constant death rate. We first consider a *zero-dimensional* model in which spatial distributions and non-uniformities are not explicitly resolved; seeding therefore occurs globally. The change over time in the coverage of the daisies is written as a pair of differential equations

$$\frac{d\alpha_b}{dt} = \alpha_b(x\beta(T_b) - \gamma), \tag{2a}$$

$$\frac{d\alpha_w}{dt} = \alpha_w(x\beta(T_w) - \gamma), \tag{2b}$$

where T_b and T_w are the local temperatures of the black and white daisies, respectively, the importance of which is discussed shortly. Next, we describe the time evolution of the mean global temperature, T, as that of a black body with heat capacity C, heated by insolation L

$$C\frac{dT}{dt} = L(1-A) - \sigma T^4, \tag{3}$$

where A is the mean albedo $\alpha_b A_b + \alpha_w A_w + x A_e$. The heat capacity term is of interest in investigating the co-evolution of environment and biota in time, which may lead to oscillations (Nevison et al., 1999; Fernando and Poveda, 2009). The exact form of this heating is commonly found to be unimportant to the fixed point dynamics of the model (Wood et al., 2006). As such, this expression is commonly replaced by the linearised Stefan–Boltzmann equation to assist analysis

$$C\frac{dT}{dt} = L(1-A) - \sigma T_{eq}^3 T, \tag{4}$$

where T_{eq} is the steady-state temperature of a bare planet ($x=1$). For simplicity, we replace T, C and L with their dimensionless counterparts, normalised by the factor σT_{eq}^3.

Finally, the minimal ingredient for self-regulation to emerge from this model is that the black and white daisies must be differentiated by their local temperatures. For finite diffusion rates, this property will emerge due to gradients in the absorption of heat between black and white daisies. Watson and Lovelock (1983) assume that all daisies in the black or white populations experience the same local temperature, given by

$$T_i = T + q(A - A_i), \tag{5}$$

which ensures the mean global temperature $T = \alpha_b T_b + \alpha_w T_w + x T_e$, where q parametrises the departure of local temperatures from the global mean. Given finite rates of diffusion of heat, the black daisies are slightly hotter and the white daisies are slightly colder than the global temperature. As q increases, the amount of insulation between the daisy fields increases and so the temperature difference between black and white daisy populations increases. Negative values for q, as well as being thermodynamically implausible, destroy homeostasis as we will show later.

2.1. Separation of timescales

Thus far this description of the Daisyworld model has not yet made any assumptions about the timescales over which these competing processes take place. In terms of the parameters introduced so far, we have four distinct timescales;

$$\tau_\gamma = \frac{1}{\gamma} \qquad \qquad \text{Daisy removal}$$

$$\tau_\beta = \frac{1}{\beta(T)} \qquad \qquad \text{Daisy establishment}$$

$$\tau_H = C \qquad \qquad \text{Mean temperature change}$$

$$\tau_L = \left(\frac{dL}{dt}\right)^{-1} \qquad \text{Insolation change}$$

Watson and Lovelock (1983) assume zero heat capacity in Daisyworld. For a fixed luminosity, any change in the albedo of the planet produced an instantaneous change in temperature. For greater clarity, we refer to this convention as being in the limit $\tau_H \ll \tau_{\gamma,L}$. Changes in global temperature happen faster than any other element. Consequently, changes in the albedo due to γ and changes in insolation L occur sufficiently slowly that the model is always in a state of radiative equilibrium, and the global mean temperature, T, can be defined as the steady-state temperature

$$T = L(1-A), \tag{6}$$

where we have substituted our dimensionless T and L. At the other end of the spectrum, Watson and Lovelock assumed that changes to insolation occur so slowly that it may remain fixed while all other variables are numerically integrated to steady state. Therefore, $\tau_L \gg \tau_{\gamma,H}$. Now as well as reaching radiative equilibrium, the daisy turnover processes are also able to achieve a steady state between adjustments in L. In this section we determine the nature of the steady state with these assumptions.

On Earth, the separation between abiotic forcing timescale τ_L and abiotic relaxation τ_H is reasonable. While there are a number of processes which may contribute to this abiotic relaxation, operating over a range of timescales, they are rapid compared to changes in external forcing. Due to it's mass, ocean temperature lags behind changes in external forcing by $\sim 10^3$ years (Battisti and Hirst, 1989), while the response of the cryosphere range from decadal variance in glacier extent to millennial changes in ice sheets (Goodison et al., 1999). In contrast, abiotic forcing processes which influence the surface temperature can be shown to occur on the very longest timescales; fluctuations in the luminosity of the sun are sufficiently small to be neglected except over $\sim 10^9$ years, and the effects of secular cooling of the Earth is only felt over comparable timescales (Anderson, 1989).

On the other hand, the timescales associated with changes in the biota are less clear, and the extent to which the separation of timescales described here can be justified is a limitation of the Daisyworld model. The response of the biosphere to changes in its abiotic environment range over ecological time, from tens to hundreds of years for different stages of ecological succession to evolutionary processes that can occur over geological timescales. As well as the distribution and abundance of species changing in response to environmental change, the frequency of alleles in biological population can also change and so evolution can be an important process. The original Daisyworld featured life forms with fixed traits and no capacity for evolution. Subsequent studies relaxed this assumption and explored evolutionary dynamics with the conclusion that the behaviour of the model and its homeostatic behaviour is largely preserved (Lovelock, 1992; Lenton, 1998). Our analysis is limited to the original DW and so we do not include adaptation in our model.

In the following sections we examine the effects of relaxing these assumptions.

2.2. Fixed points and regulation

The following is a brief derivation of the model fixed points, following a similar approach to (Saunders, 1994; Wood et al., 2008). Inspecting Eqs. (2a) and (2b) reveals the condition for a fixed point to be where both differential equations return zero

$$\alpha_b(x\beta(T_b)-\gamma)=0, \tag{7a}$$

$$\alpha_w(x\beta(T_w)-\gamma)=0, \tag{7b}$$

which leads to a number of trivial fixed points such as both species b and w extinct, $\alpha_b=\alpha_w=0$ or a single extinction such as $\alpha_b=0$ and $\alpha_w=1-\gamma/\beta(T)$. Initially, we are interested in solutions with $\alpha_b>0$ and $\alpha_w>0$ which clearly only occur together for $\beta(T_b)=\beta(T_w)$. Here, our exact choice of β becomes relevant, although we may make some generalisations. If β is chosen to be a symmetric function with a single maximum at $T=T_{opt}$, or q is sufficiently small that it can be approximated parabolic in the vicinity of T_{opt}, we can write this condition as

$$T_{opt}-T_w=T_b-T_{opt}. \tag{8}$$

At this point, we replace the albedos A_b, A_e and A_w by their commonly chosen values of $1/4, 1/2$ and $3/4$, and specify $T_{opt}=1/2$. Substituting expressions for the local temperatures gives the black daisy population at this fixed point to be

$$\alpha_b = \frac{1}{2} - \frac{L-1}{L-q} - \frac{\gamma}{\beta(T_{b,w})}. \tag{9}$$

This fixed point is of great interest as it corresponds to a temperature $T\approx T_{opt}$. As we will show, this model shares the essential features of previous Daisyworld models in which this is an attractive fixed point. Consequently the model will self-regulate in that the temperature is maintained approximately constant over a range of insolation L.

Watson and Lovelock employ a fixed death rate which produces a steady turnover of daisies. We further simplify the model by assuming this turnover to occur on sufficiently long timescales compared to growth such that no significant fraction of bare ground exists at any time. This corresponds to the limit of rapid daisy colonisation compared to removal, $\tau_\beta \ll \tau_\gamma$ or $\gamma/\beta(T_b)\rightarrow 0$ and ensures $x\rightarrow 0$. The model is then reduced to a two-state model in which the surface of the planet is covered by a mixture of only black and white daisies with no bare ground. This limit is only sensible providing $\beta(T_{b,w})>0$ (which is surely the case where $T\approx T_{opt}$). It is important to note that in doing so, we constrain our analysis away from some population effects which hinge on the relationship between establishment and removal. However, this reduction will be found to facilitate very simple, yet highly general analysis of a number of other effects. We have now identified and separated all four relevant timescales according to

$$\overset{\tau_{H,\beta}\;\cdots\;\tau_\gamma\cdots\;\tau_L}{\text{fastest}\xrightarrow{\hspace{2cm}}\text{slowest}.}$$

The basin of attraction for this point must assume $0<\alpha_b<1$ which we denote with:

$$L^-\leq L\leq L^+, \tag{10}$$

$$L^-=\frac{2+q}{3}, \tag{11a}$$

$$L^+=2-q. \tag{11b}$$

In this range, the behaviour of Eq. (2a) is sketched for typical parameter values in Fig. 1. Having determined the black daisy population as a function of L in Eq. (9), this result can be substituted into the definition of T in Eq. (6) along with the normalisation condition to yield the global mean temperature

$$T = \begin{cases} \frac{3}{4}L & L\leq L^-, \\ \frac{L(1-q)}{2(L-q)} & L^-\leq L\leq L^+, \\ \frac{1}{4}L & L\geq L^+. \end{cases} \tag{12}$$

The change in global temperature for a range of luminosity is shown in Fig. 2. Note how the decrease in temperature between L^- and L^+ is parametrised by q.

The limit $\tau_\beta \ll \tau_\gamma$ is useful in providing a transparent analysis, but requires a different treatment if the function chosen for $\beta(T)$ is allowed to be zero. Indeed, the original Daisyworld model uses a parabola, cut off at the axis to ensure $\beta\geq 0$. For greater generality, let $\beta(T)$ be a function which is positive in the range $T^-<T<T^+$ but zero everywhere else. Following Ashby (1960) we call this the *essential range* as it is the range of environmental conditions that are essential for life. Outside this range, we have a lifeless planet with $T=A_eL$, while within the allowed temperature range, the model behaves exactly as discussed. This leads to some interesting consequences, such as hysteresis loops shown in Fig. 3.
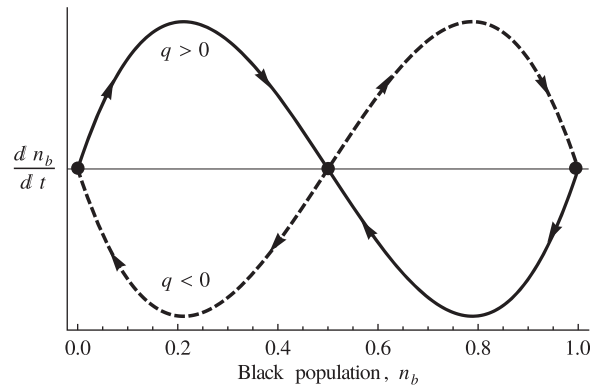

Fig. 1. For $q>0$, we can see the trivial fixed points are unstable. Initial conditions in their vicinity instead approach the attractive central fixed point leading to self-regulation. Here, we have set $L=1$ and intuition tells us this should correspond to $\alpha_b=\alpha_w=\frac{1}{2}$. For $q<0$, the picture is inverted and the only attractive fixed points are those corresponding to extinction of one species.
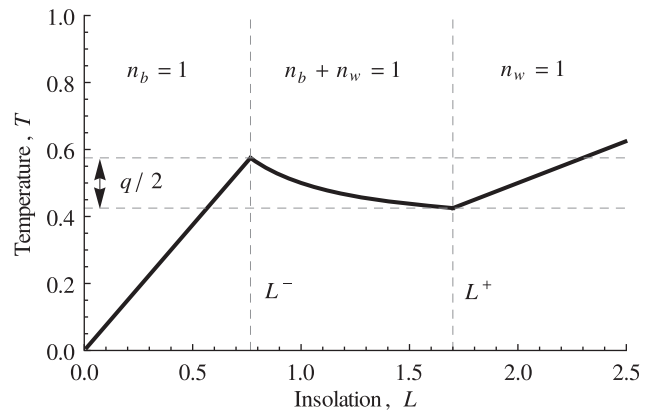

Fig. 2. The geometry of self-regulation in Daisyworld for a growth function which always satisfies $\beta(T)>0$, allowing the separation of timescales $\gamma/\beta(T)\rightarrow 0$. The onset, and width of the regulating region is determined by the limits of the effect of Daisies on the global temperature, L^- and L^+, given in Eqs. (11a) and (11b). Beyond these, no further changes can occur to planetary albedo. Outside the regulating range, $\beta(T_b)\neq\beta(T_w)$, leading only to trivial fixed points corresponding to extinction of one daisy type.
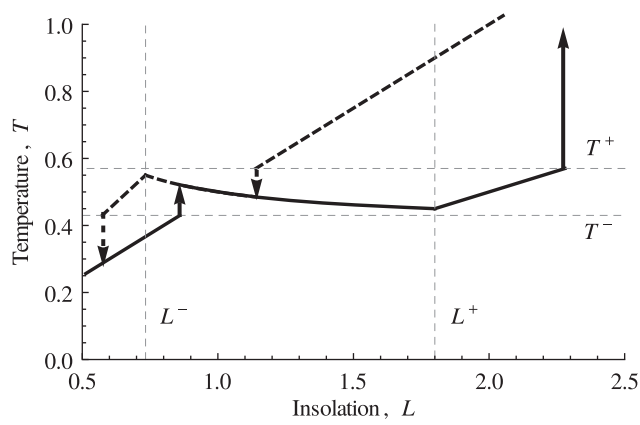
Fig. 3. Global temperature, T, with increasing (solid) and decreasing (dashed) insolation, L. In contrast with Fig. 2, the growth function $\beta(T)$ is only non-zero in the range $T^- < T < T^+$. Self-regulation can only emerge in this range, resulting in hysteresis. Once in a regulating state, the system is subject to the limits of regulation as before.

2.3. Relaxing assumptions

In this section we examine the impacts of relaxing three important assumptions. These are very slow driving (changes to luminosity occur so slowly that it remains fixed while Daisyworld relaxes to a steady state), zero heat capacity (any change in the radiative balance of Daisyworld produces an instantaneous change in global temperature) and maximum seed diffusion (daisy seeds can establish themselves anywhere on the surface of the planet and consequently there are no spatial factors in how daisy coverage changes).

2.3.1. Slow driving
So far we have assumed that changes to insolation occur over the very longest timescale in the system. i.e. τ_L is so large that insolation is fixed while daisy coverage and temperature change towards their stead states values. This is the same assumption as in Watson and Lovelock's original model and many subsequent studies. In this section we relax this assumption, represented schematically below.

$$\underset{\text{fastest}}{\overset{\tau_{H,\beta} \quad \cdots \quad \tau_\gamma \leftrightarrow \tau_L}{\xrightarrow{\hspace{3cm}}}}\text{slowest.}$$
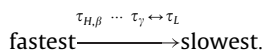
$\tau_{H,\beta}$ are the timescales for rates of heating and daisy establishment, respectively. It is assumed that these occur so fast as to be instantaneous processes when compared to τ_γ, the rate of change of daisy removal and τ_L, the rate of change of insolation. While previously τ_γ and τ_L were taken to be separated, we explore the model's behaviour as the external driving on the system increases. We do this by keeping τ_H and τ_β fixed as the fastest timescales (they are sufficiently small that the model exists in a state of constant radiative equilibrium, and colonisation of bare ground is rapid) and evaluate the model's stability as the separation between τ_γ and τ_L decreases. We have already introduced changes in insolation and secular cooling as examples of driving forces, and observed that they occur only on the very longest timescales. However, it is simple to imagine planets where this is not the case, for example where the orbital period is sufficiently long and elliptical.

The first step in reducing the problem is to assume that the time evolution of the daisy coverage can be represented by a linear relaxation (or equivalently a Newtonian relaxation) towards the insolation dependant fixed point value, $\alpha^*_{b,w}(L)$, found with Eq. (9). This allows us to avoid making assumptions about the form of β and in particular sidestep issues arising from

non-linearity in the daisies' response to temperature. We then introduce the daisy removal timescale, τ_γ, in order to examine how the evolution towards the fixed point changes as τ_γ increases and so daisy removal becomes *slower* with respect to the change in insolation

$$\frac{d\alpha_b}{dt} = \frac{1}{\tau_\gamma}[\alpha^*_b(L) - \alpha_b], \tag{13a}$$

$$\frac{d\alpha_w}{dt} = -\frac{d\alpha_b}{dt}. \tag{13b}$$

As shown in Fig. 4, the behaviour of this linearised system is barely distinguishable from the solutions given in Eqs. (2a) and (2b). We are only able to formalise the evolution of this system in terms of functions that are quite unwieldy, and no analytic solution exists. However, we find that the onset of homoeostasis is abrupt and occurs at the critical point $\tau_\gamma/\tau_L = R_{crit}$, where R_{crit} is some function of q, and the essential range. This threshold confines the system to either extinction, or self-regulation. With a fixed and very fast establishment rate, increasing τ_γ slows down the daisies' responses to changing insolation. This is equivalent to insolation continuing to increase while the daisies are moving towards a fixed point. The rate of change of insolation can be so great as for the system to be driven out of the essential range. The system is most sensitive to changes in τ_L ($R_{crit} \to 0$) at the limits of regulation where fixed point temperatures are close to the maximum of the growth function. As white daisy coverage approaches the maximum, there is less 'head room' to accommodate faster changes in insolation and so any increase away from the very longest of timescales for τ_L results in the collapse of homeostasis and extinction.

Adjustment of the timescales of certain processes, and its effects on the Daisyworld self-regulating mechanism, has been considered implicitly in a number of previous studies. Luminosity timescales were relaxed in Dyke et al. (2007) and McDonald-Gibson et al. (2008) who developed zero-dimensional agent based versions of Daisyworld in which the population of daisies change during changes to external perturbations. self-regulation was observed under such conditions. Our analysis has shown that while it is not necessary for luminosity to remain fixed as the system evolves to a steady state, relaxing this assumption will inevitably reduce the region of luminosity over which the system will be stable. As De Gregorio et al. (1992) and Wood et al. (2006) previously noted, the size of the basin of attractor will change as luminosity changes. Such sensitivity is most pronounced at the
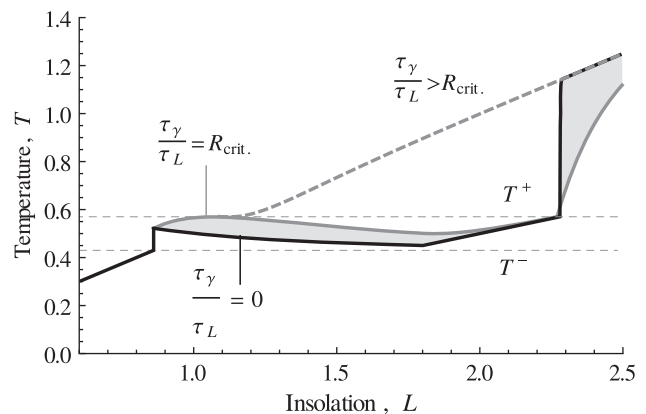

Fig. 4. The onset of regulation is abrupt, and occurs at a critical value of τ_γ/τ_L. Above this limit, no regulation may occur while below this limit, regulating solutions are found in the shaded region, down to the limit where τ_γ and τ_L are fully separated. Dashed lines indicate the region where $\beta(T) > 0$, outside which only fixed points corresponding to extinction exist.

limits of self-regulation, regions that are characterised by large hysteresis loops.

2.3.2. Zero heat capacity

In the previous section, we explored the effects of relaxing the assumption that changes to insolation were very slow and consequently how robust the self-regulation in the model was to greater rates of external driving. In this section we examine how the model responds to sudden perturbations or *shocks*. A shock can be thought of as a fluctuation, driving a system away from its current state on timescales much shorter than any dissipation can occur. Such fluctuations may originate within, or outside the system under consideration, and are not necessarily small. Planet Earth has been subjected to numerous such events of wildly differing magnitudes; events such as comet impacts, or changes in atmospheric composition by volcanic out-gassing or anthropogenic emission of greenhouse gasses occur on dramatically shorter timescales than any dissipation, resulting in an *instantaneous* perturbation to abiotic factors (Solomon et al., 2007). Similarly, life may be subject to similar perturbations, whereby the composition of the biota undergoes rapid change; forest fires and anthropogenic land use change for example occur on shorter timescales than reorganisation of the biosphere may otherwise occur.

In this section, we examine the role of timescales τ_H and τ_γ in dissipating such shocks, while assuming τ_L is sufficiently large that L may be held constant, and τ_β is small such that colonisation is rapid, as before. This can be represented schematically by evaluating the model's behaviour as the separation between τ_H and τ_γ changes

$$\underset{\text{fastest}\xrightarrow{\hspace{3cm}}\text{slowest.}}{\tau_\beta \ \cdots \ \tau_H \leftrightarrow \tau_\gamma \ \cdots \ \tau_L}$$

As in the previous section, we approximate the time evolution of $\alpha_{b,w}$ by a linear approach to the respective temperature-dependant fixed point values, but now we perturb the model temperature by a temperature fluctuation of size ΔT away from it's steady-state value. By further approximating the parameter q to be small, and departures of T from it's fixed point value, T^* given by Eq. (12) to be small, we find the time evolution of α and T can be found in closed form, although the exact result is somewhat unwieldy. Fortunately we can gain useful insights into the behaviour of the model simply by studying the leading exponential

$$T(t) \approx T^* + \Delta T e^{-t/\tau_{\text{damp}}}. \tag{14}$$

where τ_{damp} is the characteristic decay time of fluctuations in T, given by

$$\tau_{\text{damp}} = \frac{2\tau_H}{1 + \sqrt{1 - 2L\frac{\tau_H}{\tau_\gamma}}}, \tag{15}$$

which may also be extracted very easily by way of linear-stability analysis about the known fixed points. Eq. (14) results in an asymptotic approach to the fixed point in T. This expression gives us two important insights; first, we have the exponent for exponential decay of fluctuations in T. The rate of decay of fluctuations is maximised by our original separation of timescales, where heating occurs on the shortest timescales, and $\tau_\gamma \gg \tau_H$. In this case, we have $\tau_{\text{damp}} = \tau_H$ and the system relaxes back to the steady-state value as quickly as possible. In the opposite limiting case of slow heating, the decay rate is minimised, and $\tau_{\text{damp}} = 2\tau_H$. These results are illustrated in Fig. 5. Our second observation is that the sum of terms under the square root may be negative, resulting in a complex exponent and therefore oscillations. We can determine the limit of timescales which
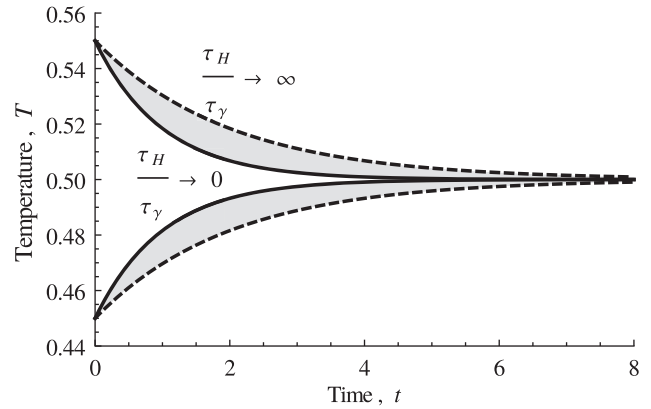

Fig. 5. The decay of fluctuations in T over time is shown for the limiting cases of very large, and very small τ_γ. For $\tau_\gamma \gg \tau_H$, the decay time is minimised $\tau_{\text{damp}} = \tau_H$, while in the other extreme, it is maximum at $\tau_{\text{damp}} = 2\tau_H$. All intermediate timescales lie in the shaded region.
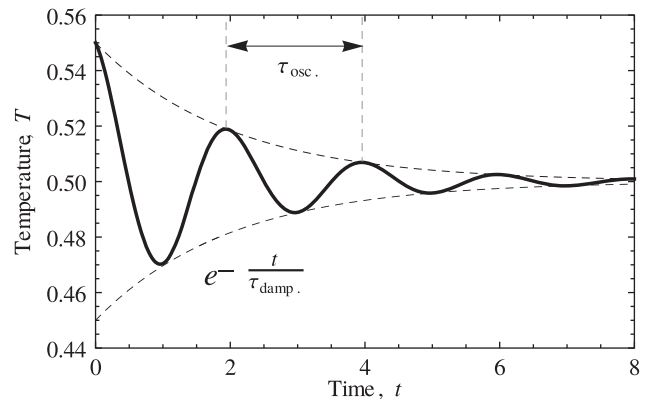

Fig. 6. For sufficiently small τ_γ / τ_H, oscillations occur along with the exponential damping. Here they are shown for $\tau_H = 1$, $\tau_\gamma = 0.1$ for the case of $L = 1$.

marks the onset of oscillations in T to be

$$\frac{\tau_\gamma}{\tau_H} < 2L. \tag{16}$$

Beyond this, damped oscillations occur with period τ_{osc}

$$\tau_{\text{osc}} = \frac{4\pi\tau_H}{\sqrt{2L\frac{\tau_H}{\tau_\gamma} - 1}}. \tag{17}$$

This is illustrated by Fig. 6, along with oscillations in daisy fractions in Fig. 7. This formulation of oscillations is consistent with Nevison et al.'s (1999) observation that oscillation period increases roughly linearly with the heating timescale, or equivalently the model heat capacity. Such oscillations have been examined numerically before (De Gregorio et al., 1992; Wood et al., 2006). Oscillations and chaotic behaviour in Daisyworld were reported by Zeng et al. (1990), a study that has since been shown to be fundamentally flawed (Jascourt and Raymond, 1992). Oscillations in environmental variables was reported in (McDonald-Gibson et al., 2008). These emerged from population dynamics whereby selective sweeps moved through the population as environmental conditions changes. This is equivalent to increasing the timescale associated with daisy establishment and so slowing down the speed of response of the biological component in the control system.
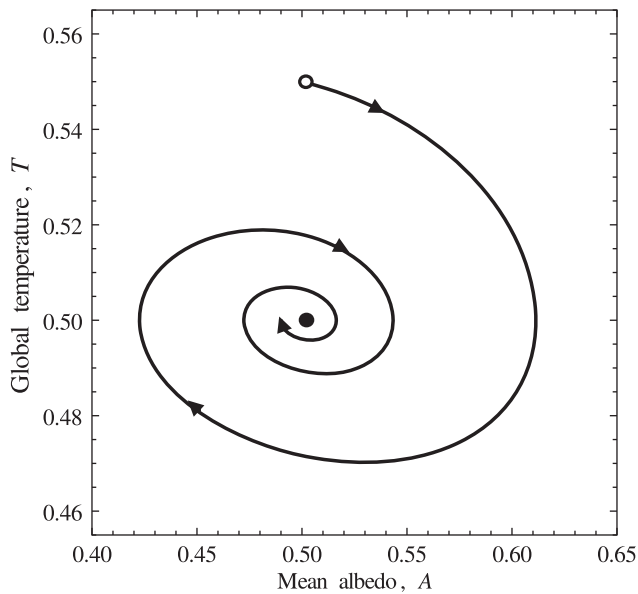
Fig. 7. Oscillations occur not only in temperature, but also in the daisy coverage, and therefore mean albedo. Oscillations are shown here in T and A, with arrows indicating the advancement of time. The white dot indicates the initial conditions, while the solid dot shows the long time fixed point solution. Relative timescales used are $\tau_H / \tau_\gamma = 10$ for the case of $L = 2$, identical to values used in Fig. 6.

2.3.3. Maximum seed diffusion

Zero-dimensional Daisyworld assumes that diffusion of seeds is sufficiently rapid that the species are well mixed and only the abundance of a daisy type limits its rate of growth. However, the biosphere is not well mixed, and local seeding clearly plays a significant role in the distribution of the biota. Ecological succession of newly habitable, or recently vacated ground occurs across a broad range of timescales, from r-selected pioneering grasses over decades, to K-selected plants and trees (MacArthur and Wilson, 1967). Introducing spatial factors such that daisies can only reproduce by seeding into neighbouring empty bare areas seeding begins to relax this assumption. The first spatially explicit Daisyworld was formulated by von Bloh et al. (1997) in which the original zero-dimensional model was translated onto a two-dimensional lattice in which each square or cell could be in an empty, black daisy or white daisy state. The update rules for each cell in this cellular automaton are probabilistic; an occupied cell will turn into an empty cell, with probability $\gamma \Delta t$, while occupied cells may seed empty cells in their seeding neighbourhood with probability $\beta(T) \Delta t$. In this cellular automata Daisyworld the diffusion of seeds from daisies to bare ground for establishment was limited to local interactions; a bare cell would be seeded by one of its occupied immediate neighbours.

Heat diffusion was modelled explicitly with the relevant transport equations, allowing the non-uniform temperature field to emerge, parametrised by the diffusion coefficient rather than the choice of q. von Bloh et al. (1997) make some progress in reconciling this model with the original Daisyworld model; a Taylor expansion is used to illustrate that the discretised Daisyworld shares key behaviour with the zero-dimensional model under the homogeneous (or *mean field*) approximation. Similarly, the behaviour of our simplified model can be recovered from a two-state cellular automata iteration of the model, where cells occupy either state b or w having albedo A_b or A_w, respectively. An updating rule which can be used to recover Eq. (9) under the mean field approximation is to randomly select, and update site i according to

$$P(b)_i = \frac{n_{b,i}\beta(T_b)}{n_{b,i}\beta(T_b) + n_{w,i}\beta(T_w)}, \tag{18a}$$

$$P(w)_i = 1 - P(b)_i, \tag{18b}$$

where $P(b)_i$ and $P(w)_i$ are the local probabilities of a site being replaced by a black or white daisy, respectively, and $n_{b,i}$ and $n_{w,i}$ are the numbers of black and white daisies in the neighbourhood of i, typically chosen to comprise only the four nearest adjacent cells. The separation of τ_γ and τ_β is satisfied as removal occurs sufficiently slowly that only one site is ever removed in an iteration, and is always occupied before the next removal.

It is simple to see that regulation emerges from this cellular automaton under the mean field approximation. Here, we approximate the neighbourhood of individual sites to be that of the global average; rather than local effects, sites are influenced only be a mean field (the classic example of an application of mean field theory is to the Ising model. For an example see Bar-Yam, 2003). In this instance we set the local populations, n, to the global mean populations, α, multiplied by the number of neighbouring lattice sites, z. Steady states then exist where we have no net change in the populations of black and white daisies, a condition which is expressed by

$$P(b)z\alpha_w = P(w)z\alpha_b. \tag{19}$$

Substituting in the normalisation condition gives

$$\alpha_b(1-\alpha_b)\beta(T_b) = \alpha_b(1-\alpha_b)\beta(T_w), \tag{20}$$

which only has non-trivial roots for $\beta(T_b) = \beta(T_w)$, a familiar observation made earlier in Eqs. (7a) and (7b), and can be solved under the same assumptions as previously. Lenton and Van Oijen (2002) implement such a cellular automaton with highly non-linear versions of Eqs. (18a) and (18b). This alternative formulation does not yield regulating steady states of this nature, highlighting the importance of our choice of updating rules. A comparison of the mean field solution with the numerical result is shown in Fig. 8.

Relaxing the assumption of maximum seed diffusion introduced spatial variations into our model. Applying mean field theory we were able to produce very accurate approximations of numerical results. The mean field approximation becomes exact in the limit of very high-dimensional, or highly connected systems. In these cases, each site genuinely does experience the mean field of all other sites. However, the approach enjoys much success in even two-dimensional and three-dimensional systems. It correctly predicts the geometry of regulation shown in Fig. 8. The precise agreement is surprising. Mean fields commonly extract the *gist* from spatially embedded systems, though fail in the details. The implication of this result is that either the long-range correlations reported by Wood et al. (2006) which would break the mean-field assumptions do not exist, or that
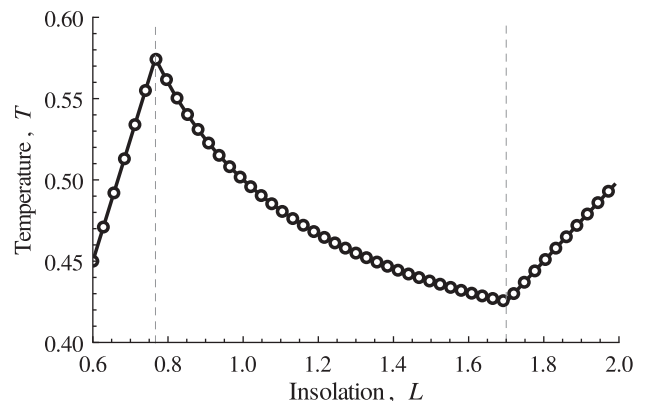

Fig. 8. Comparison of numerical simulation of the simplified two-dimensional CA with the corresponding mean-field prediction finds near-perfect agreement for all q, shown here for $q = 0.3$. Errors are no greater than the size of plot points.
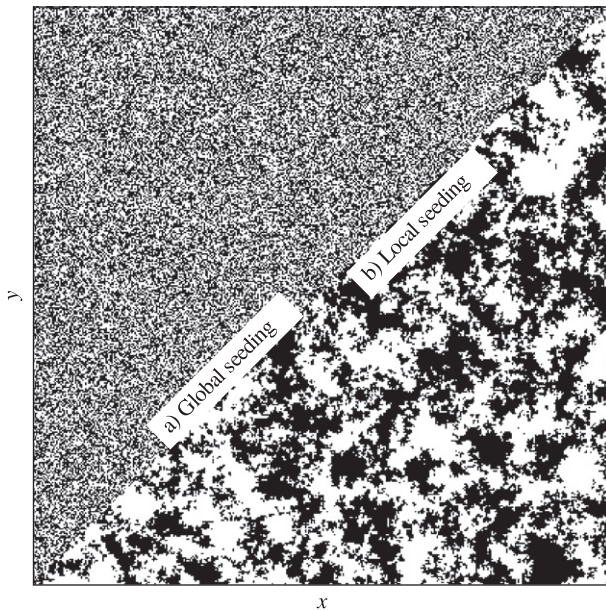
Fig. 9. Comparison of the mean field picture where spatial correlations are minimised (a), and a simulated local seeding where strong spatial correlations are evident (b). Black and white daisies are regions representing the two daisy types and x and y are spatial dimensions. While Fig. 8 illustrates exact agreement between the mean field approximation and simulation of homeostasis, it would fail in predicting spatial correlations.

while long-ranged correlations exist, they are irrelevant to the ability of the model to exhibit homeostasis. As Fig. 9 shows our mean field approximations do not capture the spatial correlations, which may be important for observing some strong spatial effects, such as desert formation, where the local temperature departs the essential range (Ackland et al., 2003). This point may only be addressed by the development of an exact solution to the spatially embedded Daisyworld, incorporating the possibility of spatial correlations. Doing so may shed light on the role of local seeding and the resulting correlations in dissipative systems, such as the latent heat exchange field investigated by Baldocchi et al. (2005).

3. Conclusion

Our analysis of a simplified version of the original Daisyworld model has demonstrated that some of the original assumptions relating to timescales can be relaxed and self-regulation is still observed. From Watson and Lovelock's (1983) original mathematical formulation of the zero-dimensional Daisyworld model, we have identified the four competing timescales. They are associated with changes in external forcing or insolation, equilibration of global temperature, and daisy turnover that includes establishment and removal. By making explicit a separation of timescales between external forcing, and internal processes, and further assuming establishment to occur much more rapidly than removal, the long time behaviour of the model can be expressed very simply. In this reduced model, it is simple to see that self-regulation may emerge, as well as to identify the limits over which self-regulation can occur. Indeed, the essence of the original model remains entirely intact. Of course, in applying this significant reduction, we constrain ourselves from investigating a number of population effects which may be introduced by slower rates of population establishment. However, this simplified model gave us keen insights as we depart from other simplifying assumptions. First, we relaxed the assumption of a separation

between the external forcing and daisy turnover timescales. This is equivalent to increasing the rate of change of luminosity. Regulation is found to occur providing these timescales are related by a critical ratio, beyond which the self-organisation of daisy coverage is slow, and the population is driven to extinction before significant regulation occurs.

Next, the assumption that the global temperature equilibrates on much shorter timescales than daisy turnover was relaxed. This is equivalent to introducing heat capacity such that global temperatures evolve towards a steady state in response to changes in radiative forcing. Despite this generalisation, we found a closed form expression for the time evolution of global temperature when perturbed from its steady-state value. As expected, the perturbation decays exponentially, though surprisingly, a more rapid response by the daisy population enables fluctuations to persist for significantly longer. At the threshold where decay time is exactly doubled, we find the onset of temperature oscillations.

Finally, we addressed Watson and Lovelock's (1983) assumption that there are no spatial effects in the daisy seeding process by introducing local seeding in a cellular automata version of the model. Through appropriate choice of probabilistic updating rules, we can recover the exact same fixed points as in the previous case through a mean field approximation. While local seeding clearly results in very strong correlations which are not accounted for in a mean field approach, near perfect agreement with simulation indicates such correlations have no impact on the regulatory fixed points. Given that mean field approximations typically perform better with increasing dimensions, these results along with the rest of our analysis of timescales are promising in that they suggest how important dimensions of interaction of the very complex Earth system can be captured in relatively simple models that will be mathematically reducible and so able to provide important insights into the real world.

Acknowledgments

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