One-dimensional daisyworld: spatial interactions and pattern formation

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Abstract

The zero-dimensional daisyworld model of Watson and Lovelock (1983) demonstrates that life can unconsciously regulate a global environment. Here that model is extended to one dimension, incorporating a distribution of incoming solar radiation and diffusion of heat consistent with a spherical planet. Global regulatory properties of the original model are retained. The daisy populations are initially restricted to hospitable regions of the surface but exert both global and local feedback to increase this habitable area, eventually colonizing the whole surface. The introduction of heat diffusion destabilizes the coexistence equilibrium of the two daisy types. In response, a striped pattern consisting of blocks of all black or all white daisies emerges. There are two mechanisms behind this pattern formation. Both are connected to the stability of the system and an overview of the mathematics involved is presented. Numerical experiments show that this pattern is globally determined. Perturbations in one region have an impact over the whole surface but the regulatory properties of the system are not compromised by transient perturbations. The relevance of these results to the Earth and the wider climate modelling field is discussed.
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1. Introduction

The global climate and terrestrial biosphere form a complex coupled system of which there is an increasingly urgent need to deepen our understanding. Sophisticated simulation models (for instance Gordon et al., 2000) are a powerful tool for predicting the behaviour of this system. However, that same sophistication can obscure the mechanisms responsible for the predicted behaviour. In contrast, simple, transparent 'tutorial' models can be used to analyse potential mechanisms and help to identify them in more sophisticated models or the real world.

Daisyworld (Watson and Lovelock, 1983) is such a tutorial model. It was conceived to demonstrate the feasibility of the Gaia hypothesis which states that, *without foresight or planning*, life can regulate the global environment (see for instance Lovelock, 1988). Daisyworld consists simply of an Earth-like planet populated by just two types of plant, black daisies and white daisies, and an environment described by a single variable, namely global temperature. The planet is warmed by radiation from its sun. There is no atmospheric greenhouse and the global temperature is determined solely by the incoming radiation and the surface albedo. The growth rates of the daisies are temperature dependent and the two types are differentiated only by the contrasting absorption of solar energy by black and white surfaces. As the radiation from the sun increases, the relative area of black and white daisies adjusts, changing the surface albedo and hence the temperature. The global temperature is maintained close to the optimum for daisy survival for a significantly greater luminosity range than when no daisies are present.

The original daisyworld is a zero dimensional, or point, model (Watson and Lovelock, 1983) with no explicit representation of space. Solar radiation is assumed to be distributed evenly over the planet. The two daisy populations receive the same solar radiation but, because of their contrasting albedos, they generate local microclimates with different temperatures. There

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have been many subsequent studies and extensions of the daisyworld model (for instance De Gregorio et al., 1992; Saunders, 1994; Harding and Lovelock, 1996; Nevison et al., 1999; Lenton and Lovelock, 2000; Weber, 2001; Lenton and Lovelock 2001), but few have considered spatial effects. Those that do extend daisyworld as a two-dimensional stochastic cellular automaton model with an infinite number of possible daisy albedos. Von Bloh et al. (1997, 1999) use a planar formulation to study the impact of different patterns of habitat fragmentation and diversity. Ackland et al. (2003) use a similar model but include some curvature (equivalent to the surface of a torus) to investigate the role of feedback in desert formation.

In this paper we present a partial differential equation based formulation of a one-dimensional daisyworld projected from the surface of a sphere. This is the zero-dimensional daisyworld simply extended to include the basic properties of a spherical planet. It allows a latitudinal gradient of solar radiation and heat transfer, as well as some spatial variation in the daisy populations. We find that the albedo feedback mechanism continues to regulate global temperature over a wide range of solar forcing, but the latitudinal variation in solar forcing has a marked local effect. As soon as life becomes possible at one point on the surface there is an explosion of the daisy population and within one timestep it expands to cover a wide equatorial band, only the poles remaining cold and lifeless. As the solar forcing increases, daisies expand toward the poles until the whole surface is covered. Eventually, the daisy population crashes as rapidly as it established and the daisies disappear leaving only small clusters at the poles.

In the zero-dimensional model the stable solution for a wide range of luminosities involves the coexistence of the two daisy types. Interestingly, the inclusion of a spatial dimension destabilizes this solution. At temperatures for which coexistence is expected from the zero-dimensional model only one type of daisy can exist at any point in space, to the exclusion of the other type. Consequently, a striped pattern of black and white daisy colonies emerges. Mathematical analysis reveals that there are two separate mechanisms behind this. A Turing-like mechanism (see Murray, 1993) is responsible for the initial emergence of the pattern. Then, as the solar forcing increases, the pattern adjusts to ensure a stable steady state under the new conditions. Furthermore, numerical experiments indicate that the patterning is a global phenomenon, with localized disturbances having an impact on the whole population. Like the original daisyworld model, this extension is intended as a parable. However, it suggests an intriguing potential link between Gaian feedback processes and spatial patterning.

The paper is arranged as follows: Section 2 contains a description of the one-dimensional model and its relationship to the Watson and Lovelock (1983) model.

In Section 3 numerical solutions of the model are presented, covering both the global and local dynamics. Section 4 has a more detailed account of the striped patterning and an intuitive explanation of the mathematics behind it using a slightly simpler set of equations. In Section 5 the effects of local perturbations on the patterning are considered. Finally, Section 6 contains a discussion of the results and their relevance to climate science.

2. The model

By allowing variation with latitude (θ), but not longitude, Watson and Lovelock's (1983) daisyworld can be extended to a one-dimensional projection of the surface of a sphere. For simplicity, daisyworld is assumed to rotate on an axis perpendicular to the plane of its solar orbit, thus obviating seasonal differences of the northern and southern hemispheres. Incoming solar radiation is thus symmetrically distributed, with a maximum at the equator and minima at the poles. Considering the relative change of surface area and cross-sectional area with latitude, the distribution of solar radiation is given by $R(\theta) = 4S\cos(\theta)/\pi$, where $S = 917L$ is the solar radiation and L the solar luminosity in the Watson and Lovelock (1983) model. Latitudinal heat transport is represented by the familiar Laplacian operator expressed in spherical coordinates: $(D/\cos(\theta))\,(\partial/\partial\theta)[\cos(\theta)\frac{\partial T(\theta)}{\partial\theta}]$ with a diffusion rate D. Thus the temperature at time t and latitude θ, $T(\theta,t)$ is the solution of

$$\frac{\partial T(\theta,t)}{\partial t} = (1 - A(\theta,t))R(\theta) - \sigma T^4(\theta,t)$$
$$+ \frac{D}{\cos(\theta)}\frac{\partial}{\partial\theta}\left[\cos(\theta)\frac{\partial T(\theta,t)}{\partial\theta}\right]. \quad (1)$$

Here σ is the Stefan–Boltzmann constant, $A(\theta,t)$ is the albedo at latitude θ and time t, given by $A(\theta,t) = A_g(1 - \alpha_w(\theta,t) - \alpha_b(\theta,t)) + A_w\alpha_w(\theta,t) + A_b\alpha_b(\theta,t)$ where A_g, A_w and A_b are the albedos of bare ground, white daisies and black daisies respectively and $\alpha_w(\theta,t)$, $\alpha_b(\theta,t)$ are the proportional areas of white and black daisies at θ and t. At equilibrium, Eq. (1) reduces to Arrhenius's equation equating absorbed and emitted radiation of a black body.

Given the temperature and solar radiation at θ, the local temperatures, growth rates and hence areas of each daisy type at that point are determined by applying Watson and Lovelock's (1983) original equations at each point in space. The local temperatures of white and black daisies are given by

$$T_w(\theta,t) = q(A(\theta,t) - A_w) + T(\theta,t), \quad (2)$$

$$T_b(\theta,t) = q(A(\theta,t) - A_b) + T(\theta,t), \quad (3)$$

where q is a measure of implicit heat diffusion (in the longitudinal direction) between the three surface types (bare ground, white daisies and black daisies). This is assumed to occur on a very localized level and is therefore considered independent of the regional-scale diffusion operating on the main grid. The daisies have parabolic temperature-dependent growth rates given by

$$\beta_w(\theta, t) = 1 - \delta(C - T_w(\theta, t))^2, \tag{4}$$

$$\beta_b(\theta, t) = 1 - \delta(C - T_b(\theta, t))^2, \tag{5}$$

where δ and C are constants. Then the changes in daisy area are expressed by an area competition model (Carter and Prince, 1981):

$$\frac{\partial \alpha_w(\theta, t)}{\partial t} = \alpha_w(\theta, t)((1 - \alpha_w(\theta, t) - \alpha_b(\theta, t))\beta_w(\theta, t) - \gamma), \tag{6}$$

$$\frac{\partial \alpha_b(\theta, t)}{\partial t} = \alpha_b(\theta, t)((1 - \alpha_w(\theta, t) - \alpha_b(\theta, t))\beta_b(\theta, t) - \gamma), \tag{7}$$

where γ is a constant death rate.

For mathematical convenience these equations can be combined and written as three partial differential equations:

$$\frac{\partial T}{\partial t} = (1 - A_g + (A_w + A_g)\alpha_w + (A_b + A_g)\alpha_b)R(\theta)$$
$$- \sigma T^4 + \frac{D}{\cos(\theta)}\frac{\partial}{\partial \theta}\left[\cos(\theta)\frac{\partial T}{\partial \theta}\right], \tag{8}$$

$$\frac{\partial \alpha_w}{\partial t} = \alpha_w((1 - \alpha_w - \alpha_b)(1 - \delta(C - q(A_g - A_w$$
$$+ (A_w - A_g)\alpha_w + (A_b - A_g)\alpha_b) - T)^2) - \gamma), \tag{9}$$

$$\frac{\partial \alpha_b}{\partial t} = \alpha_b((1 - \alpha_w - \alpha_b)(1 - \delta(C - q(A_g - A_b$$
$$+ (A_w - A_g)\alpha_w + (A_b - A_g)\alpha_b) - T)^2) - \gamma) \tag{10}$$

for $-90 < \theta < 90$ with no flux boundary conditions. As before T, α_w and α_b are functions of θ and t.

This system of equations is numerically solved to equilibrium for a given luminosity L. The luminosity is then increased by an increment ΔL to represent the warming of the sun, and the previous solution taken as the initial condition for the following iteration. Unless stated otherwise in the text, parameter values used throughout this paper are as given in Table 1.

Table 1
Parameter values used in numerical simulations (unless stated otherwise in the text)

q	A_g	A_w	A_b	C	δ	γ	σ	ΔL
20	0.5	0.75	0.25	295.5	0.003265	0.3	5.67×10^{-8}	0.005

3. General dynamics

3.1. Global dynamics

The global temperature is found by calculating an area weighted average over the whole surface. For the system discretised with n grid points (as is necessary for the numerical solution) this is given by

$$T_G = \frac{1}{2}\sum_{i=1}^{n} T(\theta_i)\left|\sin\left(-\frac{\pi}{n} + \frac{i\pi}{n}\right)\right.$$
$$\left. -\sin\left(-\frac{\pi}{n} + \frac{(i-1)\pi}{n}\right)\right|, \tag{11}$$

where $\theta_i = -\pi/2 + (i - \frac{1}{2})\pi/n$ for $i = 1, \ldots, n$.

The global dynamics of the system under three different rates of heat diffusion can be seen in Fig. 1. Global temperature is regulated in all of these cases. When the diffusion rate is high ($D = 10$), the one-dimensional model is close to the zero-dimensional model as heat transport is so rapid that the temperature is almost evenly distributed over the surface. As the diffusion rate is reduced the two models diverge. When $D = 1$, there is still significant temperature regulation by the daisies. This begins at a lower luminosity than in the zero-dimensional model but also ceases at a lower luminosity. Overall the period of regulation is reduced and there is a constant upward trend in the temperature (compared with a small downward trend in the zero-dimensional model). When $D = 0.1$ both of these factors are more pronounced. The increased temperature gradient over the surface is behind these differences. Although the average temperature in the latitudinal model agrees with the zero-dimensional model, the equatorial region is hotter and the poles cooler than the
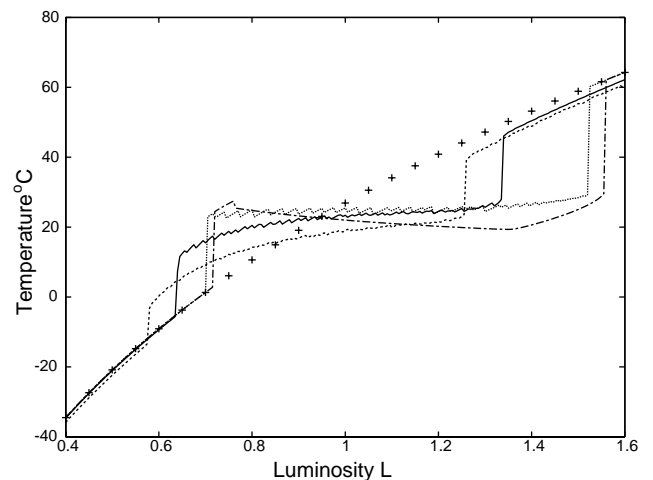

Fig. 1. Global temperature of one-dimensional daisyworld under different rates of heat diffusion: $--$, $D = 0.1$; $—$, $D = 1$; $\ldots$, $D = 10$; $- \cdot -$, zero-dimensional model; $+ + +$, zero-dimensional model with no daisies.

average. Thus the equatorial region becomes habitable, and regulation begins, at a lower luminosity. Similarly the same region becomes inhospitable, and regulation ceases, at a lower luminosity. Furthermore, the total habitable area at any time is limited. With fewer daisies present, the capacity for temperature regulation is compromised. This is described more clearly in the following section.

3.2. Local dynamics

Without daisies the temperature profile has a distribution corresponding to the cosine variation in solar radiation, modified by heat transport. When the heat diffusion rate $D = 1$, there is a population explosion when $L = 0.7$ and black daisies establish over a wide equatorial region. The rapidity of this extensive colonization is the result of local positive feedback. Black daisies initially appear at the equator, increasing the albedo, and hence surface temperature, in that region. This heat quickly diffuses and warms neighbouring regions, enabling more black daisies to establish, increasing the surface temperature and continuing the feedback process. The final extent of the initial colonization is determined by the rate of heat diffusion. For $D = 1$ this is insufficient to make the polar regions habitable and they remain devoid of life (Fig. 2). As solar luminosity increases, the black daisy population migrates towards the poles and a white colony takes

their place around the equator and begins to spread outwards, moderating the rate of increase of both local and global temperatures. The whole surface is populated when $L = 1$ and remains so until $L = 1.4$. At this point there is a sudden collapse of the population as the loss of a small section of the equatorial white daisy population triggers positive feedback. If white daisies are replaced by bare ground the decrease in albedo leads to rapid warming in that area. As this heat diffuses, adjacent areas become inhospitable, the daisies die and the situation is exacerbated. Within a single luminosity increment the daisy population crashes and only small pockets of life remain, restricted to the polar regions.

The general trends of the population dynamics on the surface as described above are largely as expected. However, there is a more remarkable phenomenon operating at the local level. Reviewing Fig. 2, it can be seen that both the black and white daisy populations are almost always either close to carrying capacity (approximately 0.7) or 0. There is never any coexistence of the two types. Note that the one-dimensional model can be thought of as a family of zero-dimensional Watson and Lovelock (1983) models distributed over latitudinal space and linked by heat diffusion. Therefore, by 'coexistence' we mean that both populations are non-zero at the same latitude, even though the implicit assumption that the two populations grow in patches in longitudinal space is retained in order to preserve the generation of local microclimates. In the
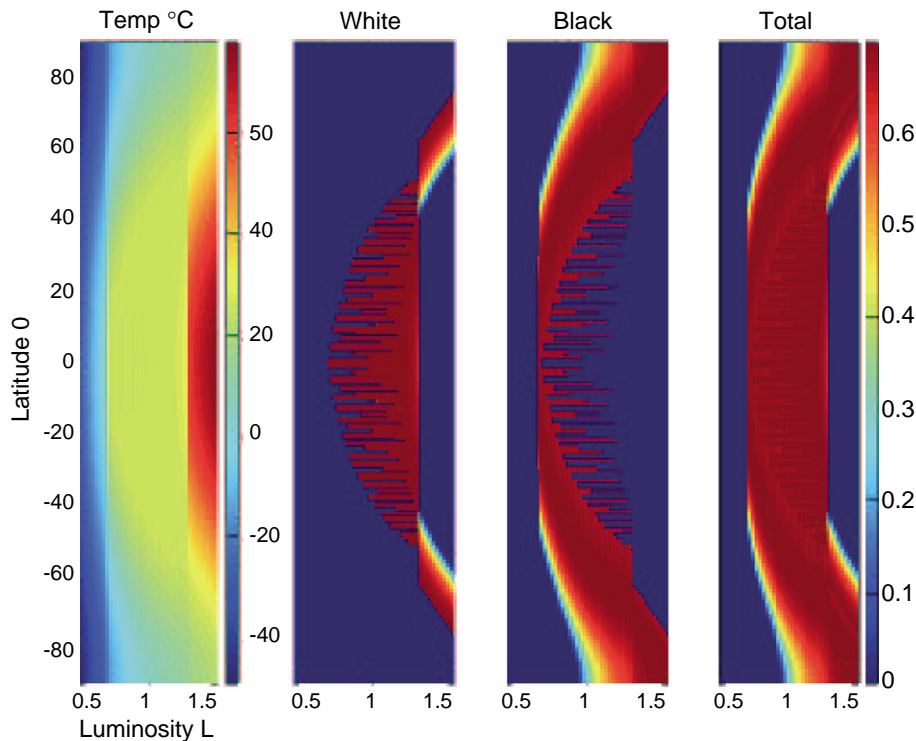

Fig. 2. Local dynamics of temperature and daisy density under increasing solar luminosity L. Here $D = 1$.

one-dimensional model we find that in regions where the temperature is such that coexistence might be expected to occur (for instance in the interval $-54 < \theta < 54$ when $L = 1$), a striped pattern of distinct black and white colonies emerges instead. This is not a numerical artefact but a product of the delicate equilibria of daisyworld and is discussed in detail in the next section.

4. Stripes

Numerical results show that, in the one-dimensional daisyworld presented here, black and white daisies never coexist at the same latitude. One type always excludes the other, producing a spatially striped pattern of single-species colonies close to carrying capacity. According to Saunders (1994), in the absence of diffusion, stable coexistence should occur when the received solar radiation R is in the range $688 < R < 1265$. In the one-dimensional model, when $L = 1$, $R(\theta)$ is in this range for $-54 < \theta < 54$. Fig. 3 shows the actual equilibrium solution for $L = 1$. Clearly there is no coexistence at any point in space and, in the range $-54 < \theta < 54$ the solution consists of well defined blocks, or stripes, of each daisy type. An intuitive account of the mathematics is presented here. For a more detailed exposition, see Adams and Carr (2003).

In order to understand the mechanisms behind this patterning, it is helpful to study a slightly simpler form of Eqs. (8)–(10):

$$\frac{\partial T}{\partial t} = \frac{(2 - \alpha_w + \alpha_b)R}{4} - \sigma T^4 + D\frac{\partial^2 T}{\partial \theta^2}, \tag{12}$$

$$\frac{\partial \alpha_w}{\partial t} = \alpha_w \left[\left(1 - \delta\left(C - \frac{q}{4}(\alpha_w - \alpha_b - 1) - T \right)^2 \right) \right.$$
$$\left. \times (1 - \alpha_w - \alpha_b) - \gamma \right], \tag{13}$$

$$\frac{\partial \alpha_b}{\partial t} = \alpha_b \left[\left(1 - \delta\left(C - \frac{q}{4}(\alpha_w - \alpha_b + 1) - T \right)^2 \right) \right.$$
$$\left. \times (1 - \alpha_w - \alpha_b) - \gamma \right] \tag{14}$$

where T, α_w and α_b are functions of θ and t.

Eqs. (12)–(14) represent a one-dimensional daisy-world projected from a plane, rather than the surface of a sphere, with the given parameter values for A_g, A_w, and A_b substituted directly and uniform $R = 4SL/\pi$. Again no flux boundary conditions are applied.

For fixed θ (i.e. no space) there are four equilibrium solutions to Eqs. (12)–(14). These correspond to no daisies, only black daisies, only white daisies, and coexistence. For the parameter values given in Table 1, $D = 1$ and luminosity in the range $0.72 < L < 1.22$, there is a unique stable equilibrium determined by the
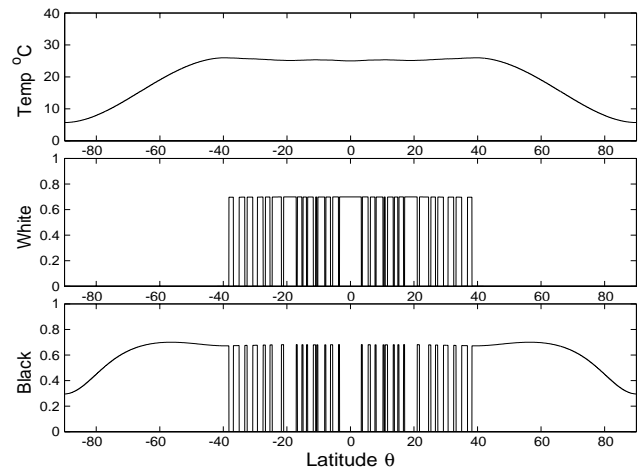

Fig. 3. Snapshot of the equilibrium solutions when $L = 1$. Here $D = 1$.

temperature component T_E. The no daisy solution is always unstable. The black only solution is stable for $T_E < 298.87$ and unstable for $T_E \geqslant 298.87$, the white only solution is stable for $T_E > 292.13$ and unstable for $T_E \leqslant 292.13$ and the coexistence solution is stable for $292.13 < T_E < 298.87$ and unstable otherwise.

In the zero-dimensional system for $0.72 < L < 1.22$, $T_E \geqslant 298.87$ if only black daisies are present and $292.13 \leqslant T_E$ if only white daisies are present. But there is also a coexistence solution such that $292.10 < T_E < 298.87$ and this is the unique stable equilibrium. However, it can be shown that this coexistence equilibrium has a very small negative eigenvalue and is thus very delicately balanced. The reintroduction of space into the equations can cause this eigenvalue to become positive, and the coexistence equilibrium unstable, if the system is perturbed. There is some interplay between the value of D and the mode of the perturbation required to destabilize the system. For very small D the system is only unstable for very high mode perturbations. For $D = 1$, perturbations of mode 6 or greater will destabilize it. Note that if $D = 0$ there is no spatial coupling at all and coexistence always remains stable.

If the coexistence equilibrium is destabilized, the solution has no spatially homogeneous stable solution since all four equilibria are unstable. Therefore a Turing-like mechanism (see Murray, 1993) comes into operation. The coexistence equilibrium is always unstable, but the white only equilibrium will be stable at the point θ if $T_E(\theta) > 292.13$. Similarly, the black only equilibrium will be stable at θ if $T_E(\theta) < 298.87$. Note that the equilibrium temperatures are now locally defined. The juxtaposition of blocks of black or white daisies, and the resultant heat exchange between them, can have the effect that locally the temperature is within the stability limits for the all black or all white equilibrium. Thus a pattern of black and white stripes over the whole interval can result in a temperature

profile $T(\theta)$ such that $T(\theta) > 292.13$ for all θ such that $\alpha_w(\theta) > 0$ and $T(\theta) < 298.87$ for all θ such that $\alpha_b(\theta) > 0$. This solution is then stable. There are an infinite number of such stable equilibrium solutions.

Numerical experiments indicate that the particular equilibrium pattern that the solution converges to depends primarily on the value of D, the initial perturbation and, critically, the solar radiation. In general, lower solar radiation levels lead to black stripes being broader than white, higher values of D result in a coarser pattern and increasing the number of oscillations in the initial perturbation leads to a finer pattern.

Fig. 4 shows the development of the white solution towards such an equilibrium and indicates the time scales involved in the pattern formation. A small temperature perturbation was applied to an initial condition of the (unstable) constant black only equilibrium ($\alpha_w = 0.0001$, $\alpha_b = 0.377$, $T = 304.98$). By $t = 50$ the solution is at the coexistence equilibrium and appears to be stable. However, by $t = 200$ the effects of the perturbation are apparent. Even so, by $t = 300$, the right-hand side of the interval is still unaffected and it is not until $t = 800$ that the solution settles to its final equilibrium state. In the zero-dimensional model the final stable equilibrium is always achieved by $t = 50$.

Initially, a pattern forms in order to attain a stable solution after the coexistence equilibrium has been destabilized by a perturbation. Once it is in place a second mechanism operates to alter it. Again this is a response to the temperature passing the critical stability

thresholds of 292.13 and 298.87. Even in the planar model described by Eqs. (12)–(14) the striped pattern generally causes an undulating temperature distribution with peaks and troughs corresponding to black and white regions respectively. As outlined above, in a stable pattern the maximum temperature must be less than 298.87 in all regions where black daisies are present and the minimum temperature greater than 292.13 in all regions where white daisies are present. The longer a stripe is the higher (if black) or lower (if white) the temperature extremum is. Now, suppose that the luminosity is increased. In regions where the black equilibrium holds this may cause part of the temperature profile to exceed 298.87, resulting in an instability. In response the solution at those points immediately tends towards the white equilibrium solution, which is still stable. As the local albedo changes the temperature may subsequently fall below 298.87 again but by this time the solution has escaped the basin of attraction of the black only solution and does not return. Thus a small white region subdivides the black and a new pattern is created. In a similar way, if the minimum temperature in a white region falls below 292.13 then a black stripe will be formed to stabilize the solution. This process continues until a stable equilibrium is achieved at all points.

The diffusion rate plays a crucial role in this. A very high value of D smooths the temperature distribution, reducing the magnitude of both peaks and troughs. This results in wider stripes and a coarser pattern. A very low value of D tends to emphasize the peaks and troughs and results in a much finer pattern. Numerical results indicate that the value of q has little affect on the patterning. The exception is when $q = 0$. In this case the daisy populations no longer generate their own microclimates and so there is no difference between them. This results in apparent coexistence, although this is a misnomer as there is effectively only one type of daisy present.

Numerical results from a two-dimensional analogue to Eqs. (12)–(14) also produce patterning when the solution is perturbed. The nature of these patterns depends on the perturbation. Perturbing individual points results in rings emanating from those points while perturbing a particular y-coordinate uniformly over the whole domain results in stripes parallel to the x-axis.

We conjecture that the same two mechanisms operate in the system defined by Eqs. (8)–(10). The curved distribution of the solar radiation acts as an inherent perturbation which permanently destabilizes the coexistence equilibrium. This causes large blocks of daisies to appear and more refined patterns occur through the splitting mechanism described above. It is important to note that the observed patterns can be taken only as qualitative results. Each time the solar radiation is increased, sections of the temperature profile may
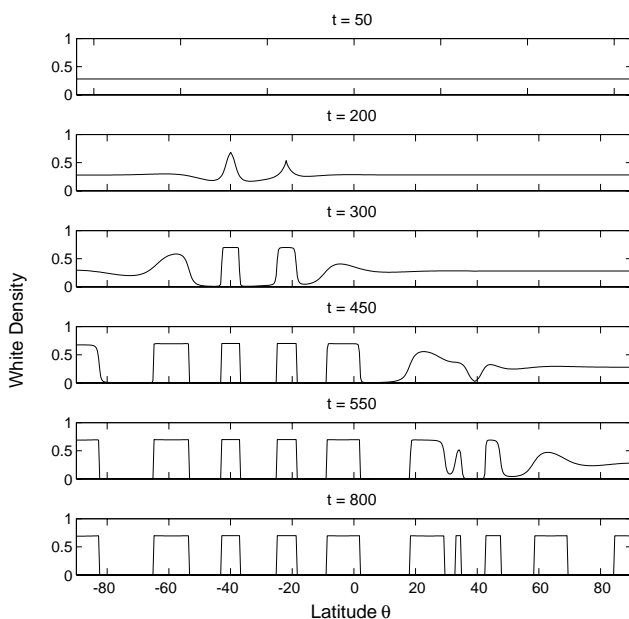

Fig. 4. Development of numerical solution to Eqs. (12)–(14) after a perturbation to the temperature profile. Initially $\alpha_w(\theta) = 0.0001$, $\alpha_b(\theta) = 0.377$ for all $-90 < \theta < 90$ and $T(\theta) = 304.98$ for all θ except for a perturbation of $T(-85.4) = 305.48$, $T(-21.8) = 305.18$, $T(39.2) = 304.88$. Here $L = 0.75$, $D = 1$.

exceed the critical threshold and new stripes will be formed. Once a stripe has been created it stabilizes directly adjacent areas. In response to further luminosity increases this stripe will not increase in width but new stripes will be created elsewhere. Therefore the number of luminosity steps (or the size of ΔL) determines the number of stripes in the pattern. Fewer steps will lead to fewer stripes. Although two simulations with different luminosity increments will not produce precisely the same patterning, this does not have a significant impact on the feedback mechanisms of the model or the global and generalized local dynamics described in Sections 3.1 and 3.2.

5. Connectivity and perturbations

The observed striped patterns are a global phenomenon. Since heat is constantly diffusing the temperature of a particular region depends on the size of the adjoining regions and the regions adjoining them and so on. Thus, a black region surrounded by two small white regions may be unstable since the white regions do

not have a sufficient cooling effect on the neighbourhood to prevent the maximum temperature exceeding 298.87. However, the same black region surrounded by two larger white regions may be stable under their increased cooling potential (see Figs. 5a and b). The same reasoning applies to more complex patterns over the whole interval. In particular, an asymmetric stripe formation will lead to the extrema occurring away from the centre of the stripe as more heat is lost or gained on one side than the other (Fig. 5c). This is further complicated by the non-uniform solar radiation distribution and diffusion rates in Eqs. (8)–(10).

To investigate the extent of the connectivity over a pattern we conducted some numerical experiments. In the first, Eqs. (8)–(10) were solved as in previous simulations until $L = 1$. Then a perturbation was introduced by instantaneously removing all of the daisies from a section of the surface before continuing the simulation. Fig. 6 shows the equilibrium solutions at three subsequent luminosity values for an unperturbed simulation and a simulation in which all of the daisies were removed in the region $25.0 < \theta < 35.8$ when $L = 1$ and subsequently allowed to regrow. As expected, the
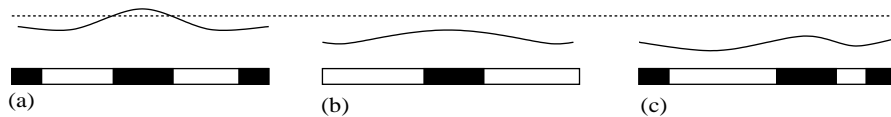

Fig. 5. Schematic diagrams showing the effect of neighbouring regions on the temperature profile of a black region: (a) small surrounding white regions are insufficient to keep the temperature below 292.13, (b) larger white regions have a greater cooling effect, (c) an asymmetric pattern causes the temperature extrema to occur away from the centre of the stripes.
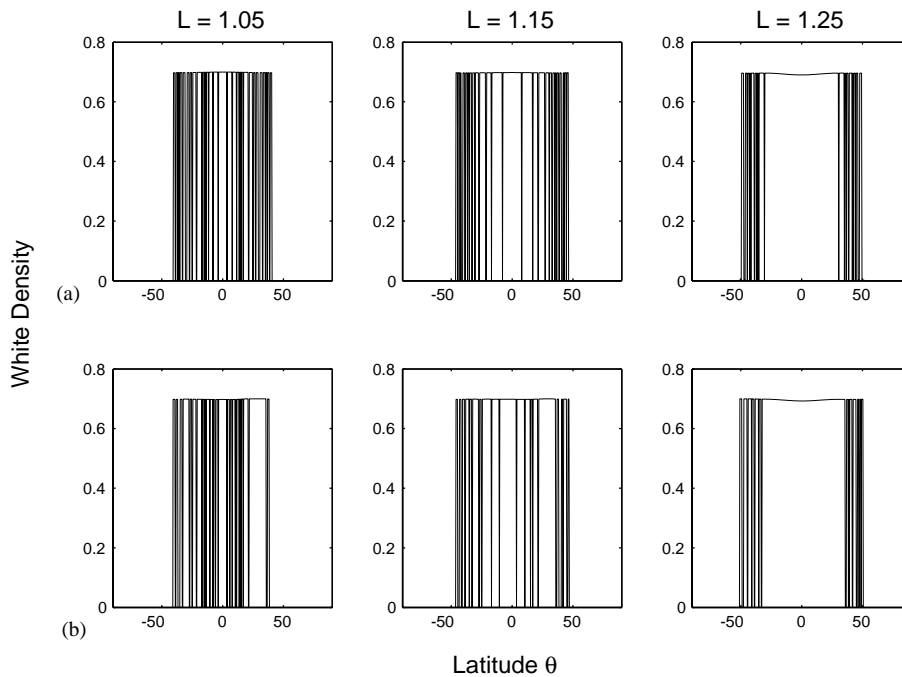

Fig. 6. Equilibrium solutions for white daisy populations in Eqs. (8)–(10): (a) no perturbation, (b) all daisies in the region $25.0 < \theta < 35.8$ removed when $L = 1$ and allowed to regrow.
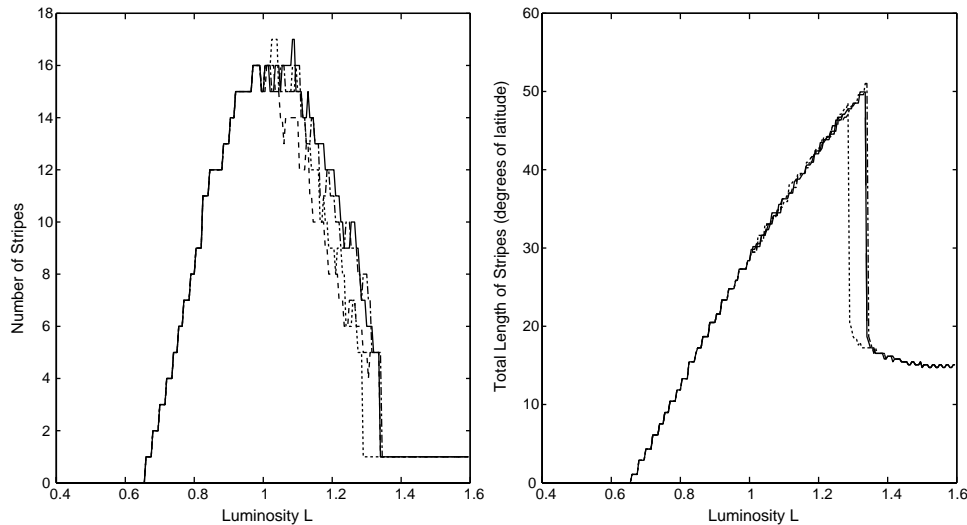
Fig. 7. (a) Total number of white stripes and (b) total length of white regions occurring in the region $-90 < \theta < 0$ after different perturbations to the region $0 < \theta < 90$: —, no perturbation; $- \cdot -$, $\theta = 30.4$ removed, regrowth allowed; $--$, $25.0 < \theta < 35.8$ removed, regrowth allowed; …, $25.0 < \theta < 35.8$ removed, no regrowth.

pattern in the vicinity of the perturbation is significantly altered as white daisies fill the perturbed area. However, the pattern is also different over the whole of the region $-50 < \theta < 0$. This can still be seen when $L = 1.25$. To demonstrate the contrast between the two patterns more clearly Fig. 7a shows the number of white stripes occurring at each luminosity value in the region $-90 < \theta < 0$ after different perturbations in the region $0 < \theta < 90$ (the opposite hemisphere). It is clear that the number of stripes changes in all cases, including the removal of a single point at $\theta = 30.4$. It is also noteworthy that, although the number of stripes in the pattern changes in response to a perturbation, the total area of white daisies in the region $-90 < \theta < 0$ (Fig. 7b) is unaffected.

In the second experiment the same perturbation was applied but regrowth was not permitted in the perturbed area. Initially, the impact on the wider patterning is similar (Fig. 7b) but the entire population subsequently crashes when $L = 1.29$, compared with $L = 1.34$ when regrowth is permitted. This is because the area of bare ground becomes very hot compared to an area of white daisies and the runaway positive feedback previously arising from the loss of white daisies in the equatorial region is triggered prematurely. This is related to the results of Von Bloh et al. (1999) which indicate that, in two dimensions, there is a critical area, and pattern, of bare ground that the system can support before runaway positive feedback is initiated.

6. Discussion

Extending daisyworld to one dimension of the surface of a sphere does not compromise biotic environmental regulation. Furthermore, the one-dimensional model shows how regulation can operate spatially. Initially, black daisies in the equatorial region warm the mid-latitude areas and allow life to establish there. At higher luminosities white daisies in the equatorial region help to cool the mid-latitude areas. The sudden collapse of the daisy population at high luminosity is the result of runaway positive feedback initiated by a localized decline in the equatorial daisy population. This indicates that the daisy population as a whole is self-sustaining and underlines the importance of the equatorial regions in moderating the global environment. When the biota is restricted to small polar refugia it cannot achieve global regulation.

For a range of solar forcing, our one-dimensional daisyworld displays multiple stable states as a consequence of strong feedback between vegetation and climate. Qualitatively, the same phenomenon is thought to occur in regions of the real world. Models suggest that under the present solar forcing the South-west Sahara could be vegetated rather than desert (Brovkin et al., 1998) and that the boreal forest has a regional warming effect which allows it to persist in large areas that would otherwise support only tundra vegetation (Bonan et al., 1992). Studies also indicate that the Great Plains of North America can support either grassland or woodland under essentially the same global forcing (Woodcock, 1992) and the Amazon rainforest increases water cycling such that without it arid pasture would persist (Shukla et al., 1990). A coupled climate model study (Betts, 1999) predicts that desert, boreal forest and tropical forest are all self-sustaining systems and it seems that in many cases the initial conditions determine the observed vegetation.

While the stripes in our one-dimensional daisyworld are a mathematical phenomenon, resulting from the delicately balanced equilibria of the model, it is possible that one factor influencing the distribution of vegetation over the Earth's surface is the requirement for a pattern capable of climate regulation. The interactions and relationships are significantly more complex, but there may be a number of different possible vegetation patterns on the Earth that are capable of producing such an effect. These will be the only stable states. It should be noted that, although there are an infinite number of stable patterns in this one-dimensional daisyworld, not all patterns are stable and unstable patterns introduced into the system are modified. Determining the temperature profile corresponding to a given pattern is a global problem and assessing the stability beforehand, or off-line, is not always straight-forward.

The results of the perturbation experiments indicate that, even in a model as simple as daisyworld, a local disturbance can have a global effect as the system adjusts to a new stable state. More realistic models show similar spatial responses to climate change. It has been predicted that removing the boreal forest north of $45°$N would result in air temperatures at $10°$N being $1°$ cooler (Bonan et al., 1992) and that the decline in the Amazon rainforest over the coming century will be accompanied by an increase in the boreal forest (R.A. Betts, P.M. Cox, pers.comm.).

To conclude, our study shows that the regulatory mechanism of daisyworld, though not itself a spatial process, is a controller of spatial phenomena.

References

Ackland, G.J., Clark, M., Lenton, T.M., 2003. Catastrophic desert formation in daisyworld. J. Theor. Biol. 223, 39–44.

Adams, B., Carr, J., 2003. Spatial pattern formation in a model of vegetation-climate feedback. Nonlinearity 16, 1–19.

Betts, R.A., 1999. Self-beneficial effects of vegetation on climate in an ocean-atmosphere general circulation model. Geophys. Res. Lett. 26, 1457–1460.

Bonan, G.B., Pollard, D., Thompson, S.L., 1992. Effects of boreal forest vegetation on global climate. Nature 359, 716–718.

Brovkin, V., Claussen, M., Petoukhov, V., Ganoplski, A., 1998. On the stability of the atmosphere-vegetation system in the Sahara/Sahel region. J. Geophys. Res.—Atmos. 103 D24, 31613–31624.

Carter, R.N., Prince, S.D., 1981. Epidemic models used to explain biogeographical distribution limits. Nature 293, 644–645.

De Gregorio, S., Pielke, A., Dalu, G.A., 1992. Feedback between a simple biosystem and the temperature of the Earth. J. Nonlinear Sci. 2, 263–292.

Gordon, C., Cooper, C., Senior, C., Banks, H., Gregory, J., Johns, T., Mitchell, J., Wood, R., 2000. The simulation of SST, sea-ice extents and ocean heat transport in a version of the Hadley centre coupled model without flux adjustments. Clim. Dynam. 16, 147–168.

Harding, S.P., Lovelock, J.E., 1996. Exploiter-mediated coexistence and frequency dependent selection in a numerical model of biodiversity. J. Theor. Biol. 182, 109–116.

Lenton, T.M., Lovelock, J.E., 2000. Daisyworld is Darwinian: constraints on adaptation are important for planetary self-regulation. J. Theor. Biol. 206, 109–114.

Lenton, T.M., Lovelock, J.E., 2001. Daisyworld revisited: quantifying biological effects on planetary self-regulation. Tellus 53B, 288–305.

Lovelock, J.E., 1988. The Ages of Gaia. A Biography of our Living Earth. Oxford University Press, Oxford.

Murray, J.D., 1993. Mathematical Biology, 2nd Edition. Springer, Berlin.

Nevison, C., Gupta, V., Klinger, L., 1999. Self-sustained temperature oscillations on daisyworld. Tellus 51B, 806–814.

Saunders, P.T., 1994. Evolution without natural selection: further implications of the daisyworld parable. J. Theor. Biol. 166, 365–373.

Shukla, J., Noble, C., Sellers, P., 1990. Amazon deforestation and climate change. Science 247, 1322–1325.

Von Bloh, W., Block, A., Schellnhuber, H.J., 1997. Self-stabilization of the biosphere under global change: a tutorial geophysical approach. Tellus 49B, 249–262.

Von Bloh, W., Block, A., Parade, M., Schellnhuber, H.J., 1999. Tutorial modelling of geosphere-biosphere interactions: the effect of percolation type habitat fragmentation. Physica A 266 (1–4), 186–196.

Watson, A., Lovelock, J.E., 1983. Biological homeostasis of the global environment: the parable of daisyworld. Tellus 35B, 284–289.

Weber, S.L., 2001. On homeostasis in daisyworld. Clim. Change 48 (2–3), 465–485.

Woodcock, D.W., 1992. The rain on the plain: Are there vegetation-climate feedbacks? Global Planet. Change 97 (3), 191–201.