DAISYWORLD: A REVIEW

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[1]   Daisyworld is a simple planetary model designed to show the long-term effects of coupling between life and its environment. Its original form was introduced by James Lovelock as a defense against criticism that his Gaia theory of the Earth as a self-regulating homeostatic system requires teleological control rather than being an emergent property. The central premise, that living organisms can have major effects on the climate system, is no longer controversial. The Daisyworld model has attracted considerable interest from the scientific community and has now established itself as a model independent of, but still related to, the Gaia theory. Used widely as both a teaching tool and as a basis for more complex studies of feedback systems, it has also become an important paradigm for the understanding of the role of biotic components when modeling the Earth system. This paper collects the accumulated knowledge from the study of Daisyworld and provides the reader with a concise account of its important properties. We emphasize the increasing amount of exact analytic work on Daisyworld and are able to bring together and summarize these results from different systems for the first time. We conclude by suggesting what a more general model of life-environment interaction should be based on.

1. INTRODUCTION

[2]   The Daisyworld model [*Lovelock*, 1983a, 1983b] was invented to demonstrate that planetary self-regulation can emerge automatically from physically realistic feedback between life and its environment, without any need for foresight or planning on the part of the organisms, an early criticism [*Doolittle*, 1981; *Dawkins*, 1983] of Lovelock's Gaia hypothesis [*Lovelock*, 1972; *Lovelock and Margulis*, 1974]. As it was impossible to fully represent how the biota and its environment are coupled on Earth, *Lovelock* [1983a, 1983b] offered a simple parable: Daisyworld is an imaginary grey world orbiting, at a similar distance to the Earth, a star like our Sun that gets brighter with time. The environment of Daisyworld is reduced to one variable, temperature, and the biota consist of two types of life, black and white daisies, which share the same optimum temperature for growth and limits to growth. The soil of Daisyworld is sufficiently well watered and laden with nutrients for temperature alone to determine the growth rate of the daisies. The planet has a negligible atmospheric greenhouse, so its surface temperature is simply determined by solar luminosity and its overall albedo, which is, in turn, influenced by the coverage of the two daisy types. This produces a nonlinear system with interesting self-regulating properties. The governing equations were first given and analyzed by *Watson and Lovelock* [1983].

[3]   Despite its abstract nature, in the nearly 25 years since its invention, Daisyworld has become an iconic model, which has inspired many variants and extensions and some unexpected applications. Much of the literature centers on the use of variants of the model to make points for or against the Gaia theory that the Earth system self-regulates in a habitable state, in which life, on average, contributes to planetary self-regulation [*Lovelock*, 1988; *Lenton*, 1998]. A key point about Daisyworld is that the daisies alter the same environmental variable (temperature) in the same direction at the local level and the global level. Hence what is selected for at the individual level is directly linked to its global effects. This makes the original model a special case (and it is one that is not particularly prevalent in the real world). Evolutionary biologists often criticize the original model for this reason. Consequently, some of the variants of Daisyworld have considered other special cases and shown that it is possible to engineer Daisyworlds in which life disrupts or destroys regulation, although their reasonableness can also be questioned. Conversely, a number of other special cases have been created in which robust planetary self-regulation occurs; much of the theoretical interest in the

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model centers on establishing the conditions in which regulation does, and does not, emerge.

[4] The field has now matured to the extent that the viability of the Gaia theory is no longer directly tied to the validity of the Daisyworld model, as was sometimes the case in the early years after its inception. Hence we treat Daisyworld as an interesting mathematical model in its own right. It may inform the debate on Gaia, but they are not inextricably tied. There have been many offshoots to other areas of science, including nonlinear dynamics, ecosystem and food web theory, evolutionary theory, physiology, maximum entropy production, and artificial life. Thanks to its relatively simple mathematical formulation, Daisyworld is also widely used in the teaching of Earth system science [e.g., *Kump et al.*, 1999; *McGuffie and Henderson-Sellers*, 1997; *Ford*, 1999].

[5] It is timely to review the body of work on Daisyworlds for the following reasons: (1) While recent years have seen a burgeoning of papers, the main results that can be obtained from variants of the model are now out there in the literature, and in some cases they are being repeated by authors unaware of previous work. (2) An elegant analytical treatment of the original model is now available as is a more complete understanding of the control theory behind Daisyworld. (3) Many of those who have been inspired by Daisyworld agree that it is now time to move on to develop new conceptual models to address questions regarding planetary self-regulation and the coupling of life and the environment. Hence we aim in this paper to provide a comprehensive, critical review and clarification of existing work on Daisyworlds and to point the way forward. Further interesting results are sure to emerge from Daisyworlds in the future, but we expect these to be mostly in new applications of the model and its spatially and/or ecologically extended variants.

[6] The paper is organized as follows. Section 2 introduces the equations and formalism of Daisyworld and provides a review of previous analytical solutions alongside a new simplified solution that aids understanding. We also discuss the basis of the control system through a further simplified model and the appearance or otherwise of chaos in the model. Section 3 examines the effects of extending the original zero-dimensional model to higher dimensions from one-dimensional (1-D) strips to three-dimensional curved surfaces. Section 4 considers Daisyworld in an evolutionary context and reviews studies that examine the effects of evolution on Daisyworld. Section 5 considers ecological extensions of Daisyworld. Section 6 discusses applications of Daisyworld, including its use as a test arena for the maximum entropy production hypothesis and alternative models that it has inspired.

2. ORIGINAL MODEL

[7] Mathematically, Daisyworld is simply a coupled set of nonlinear differential equations that may be analyzed using standard techniques from applied mathematics. The original model is termed zero-dimensional because it excludes spatial structure (although the heat transfer law may be considered an approximation to it). Here we present the original equations, review analytic progress, and then include a simplified analytic solution. We then detail aspects of control theory, especially the concept of rein control, before reviewing the claimed appearance of chaos in the Daisyworld model.

2.1. Original Equations

[8] Daisyworld [*Watson and Lovelock*, 1983] (hereinafter referred to as WL) consists of two different types of "daisy," which may be considered distinct species (because there is no possibility of mixed replication of the types) or, alternatively, as distinct phenotypes of the same species. The two types are identified as either black or white according to their reflectivity or albedo.

[9] The model starts with the equations of population growth that are used to describe the daisy fields. These equations are standard replicator equations from population genetics, with the particular form inspired by the work of *Carter and Prince* [1981]

$$\frac{\partial \alpha}{\partial t} = \alpha(p - \alpha)\beta(x) - \alpha\gamma(x), \tag{1}$$

which, in general, describe logistic growth and constant death within a limited resource system over time t. Here α is a fractional coverage of the ground by a species, p is the proportion of habitable bare ground in the system, and β and γ are the birth and death rates, respectively, having some dependence on an unspecified environmental parameter x.

[10] For Daisyworld a coupled set of equations describe the growth of each of the daisy types:

$$\begin{aligned} \frac{\partial \alpha_w}{\partial t} &= \alpha_w \big[\alpha_g \beta(T_w) - \gamma\big] \\ \frac{\partial \alpha_b}{\partial t} &= \alpha_b \big[\alpha_g \beta(T_b) - \gamma\big], \end{aligned} \tag{2}$$

where the notation parallels that defined above. Here $\alpha_g \equiv p - \alpha_b - \alpha_w$ describes the amount of available bare ground. Note that p, the proportion of fertile ground in the system, is a scaling parameter that is set to unity for the remainder of this review. The environmental parameter above is identified as the local temperature felt by each daisy type, T_w and T_b, respectively. The death rate γ is now kept fixed, and the functional form for β is chosen conventionally as

$$\beta(T) = \begin{cases} 1 - k(T - T_{\text{opt}})^2 & |T - T_{\text{opt}}| < k^{-\frac{1}{2}} \\ 0 & \text{otherwise,} \end{cases} \tag{3}$$

representing a symmetric single-peaked function. Other choices are possible, a Gaussian, for example, but this is the accepted choice in the literature and in the original work with the optimal temperature $T_{\text{opt}} = 295.5$ K ($22.5°$C). The parabolic width k is chosen so that the growth is bracketed between $5°$C and $40°$C, i.e., $k = 17.5^{-2}$.

[11] As noted above, the daisies have a single defining characteristic: their color or albedo. Albedo, or reflectiveness, defines the proportion of incident light, or energy, reflected back. Therefore, in this simplified case a pure white daisy would have albedo 1 and reflect all incident light back. A totally black daisy would have albedo 0 and perfectly absorb all incident light. Fixed albedos are prescribed for the white daisies a_w, for the black daisies a_b, and for the bare ground a_g. Therefore the mean planetary albedo A is given by

$$A = \alpha_w a_w + \alpha_b a_b + \alpha_g a_g; \tag{4}$$

$a_g = \frac{1}{2}$ by convention, and $a_b < a_g < a_w$ to keep the definitions of colors sensible.

[12] The local temperatures T_w and T_b and the bare ground temperature T_g are defined by making a simplifying assumption about the heat transfer: a linearization of a diffusion term [Budyko, 1969; North et al., 1981]. This gives a degree of connectedness to the daisy patches or stands without introducing space explicitly. A parameter q is defined as the heat transfer coefficient, thereby defining the local temperatures as

$$T_w^4 = q(A - a_w) + T^4, \tag{5}$$

$$T_b^4 = q(A - a_b) + T^4, \tag{6}$$

$$T_g^4 = q(A - a_g) + T^4, \tag{7}$$

where T is the planetary temperature related to the constituent temperature by the total reradiation. This process is modeled by the quartic Stefan-Boltzmann law for black body radiation, well known to be accurate for planets because of their thermal isolation. The final equation is that the planet as a whole stays in thermal balance at all times; therefore the absorbed incident energy is equal to the energy reradiated given by the Stefan-Boltzmann law

$$SL(1 - A) = \sigma T^4, \tag{8}$$

where SL is the average solar energy incident on the planet's surface and L is an adjustable (normalized) parameter representing the luminosity of the star. $S = 917$ W m^{-2} is used, which is much higher than the average solar flux incident on the Earth today, because the Earth has a relatively low planetary albedo and a significant greenhouse effect (($4\times$)$S = 1368$ W m^{-2} is the true value, which would give a much lower figure (around 234 K) for the average planetary temperature). The parameter σ is the Stefan-Boltzmann constant, which has a numerical value of 5.67×10^{-8} W m^{-2} K^{-4} (in SI units). For the model to have physical behavior, $q < SL/\sigma$ (1.62×10^{10} K^4 when $L = 1$). WL took the value $q = 2.06 \times 10^9$ K^4, which is comfortably below this.

2.2. Analytical Solutions

[13] WL demonstrated some features relating to the steady state behavior of these equations and then proceeded to provide simulated solutions of the full model. This method of simulated solution for the zero-dimensional model has now been largely superseded by the development of exact solutions. Here we concentrate on the available analytic solutions. Two (to all essential purposes independent) primary sources are appropriate here: a detailed study of the dynamical system by DeGregorio et al. [1992a] and an exact solution by Saunders [1994].

[14] Both Saunders [1994] and DeGregorio et al. [1992a] start by examining the fixed point solutions of the replicator equations (2). The stability and full nonlinear analysis of these fixed points is presented by DeGregorio et al. [1992a]. There are four possible fixed point solutions for the equations, which correspond to possible permutations of the daisies existence, black and white daisies being either alive or dead. The stability of these points is determined by the planetary temperature and therefore the luminosity L. The most interesting of these points is, unsurprisingly, the "both alive" fixed point, which is stable for a wide range of values. DeGregorio et al. [1992a] prove, in some considerable detail, that this fixed point is unique and that the two associated stability eigenvalues are both negative. Later analysis [Weber, 2001] looks at the response of this fixed point to perturbations in population, and again it is stable, with negative eigenvalues.

[15] The key observation, made by Saunders [1994], that yields the exact mathematical solution is that at this fixed point, providing the death rate is a constant, we can equate the two growth rates and thereby find a symmetry between the two temperatures. That is

$$\alpha_g \beta(T_w) = \gamma$$
$$= \alpha_g \beta(T_b) \tag{9}$$
$$\Rightarrow (T_{opt} - T_w) = \pm(T_{opt} - T_b).$$

[16] The positive solution leads to a solution of the model that cannot sustain a heat transfer; therefore the interesting behavior of the model is governed by the solution for which the local temperatures of the two daisy stands symmetrically straddle the optimal temperature (note that the equation governing the temperature of the bare ground is ancillary to the model behavior). This simple observation may then be exploited by using it to replace one of the temperatures in the heat transfer equations and eliminating the planetary temperature to find

$$T_b^4 - (2T_{opt} - T_b)^4 = q(a_w - a_b), \tag{10}$$

a cubic equation for one of the daisy stand temperatures (black in this case). This then determines all other variables in the model.

[17] Using the parameter values from WL, Saunders [1994] shows that in the coexistence region ($0.75 < L <$
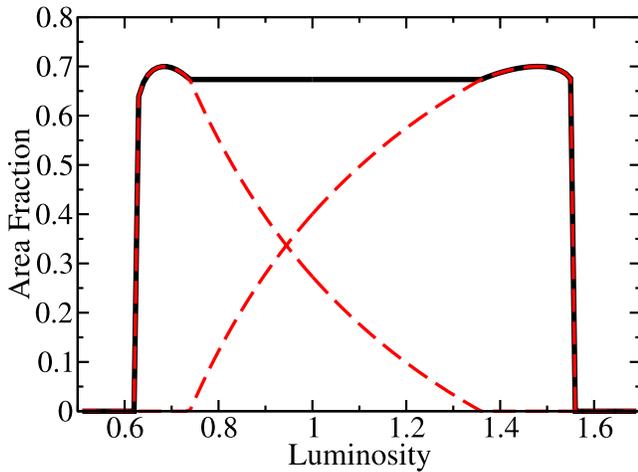
Figure 1. Plot showing the occupancy of the two different daisies types against increasing luminosity, simulated using the methodology and parameters used by *Watson and Lovelock* [1983]. The single-daisy occupancies are shown by the dashed red lines, and the solid black line shows the sum of the two-daisy types. The total amount of life is conserved in the coexistence regime in this system with a quadratic growth law.

1.38) the planetary temperature varies weakly with insolation as

$$T_T = 299\left(\frac{12.2}{14.7L - 1.9} + 0.005\right)^{\frac{1}{4}} L^{\frac{1}{4}}; \qquad (11)$$

furthermore, the regulation leads to constant growth rates $\beta(T_w) = \beta(T_b) = 0.918$ and total daisy coverage $\alpha_b + \alpha_w = 1 - \gamma/\beta = 0.673$, which we shall elucidate more fully in section 2.3. The behavior of this model is shown in Figures 1 and 2 in two plots obtained through computer simulation.

2.3. Simplification

[18] It has long been noted [*Watson and Lovelock*, 1983; *Saunders*, 1994; *DeGregorio et al.*, 1992a; *Weber*, 2001; *Wood et al.*, 2006] that linearizing the Stefan-Boltzmann law makes little difference to the results, because the chosen optimal temperature (295.5 K) is sufficiently far away from the repeated root of the quartic, σT^4, i.e., zero, that a linear approximation is accurate. It is also possible to introduce different energy budgets at this stage [*Weber*, 2001], which are more familiar in climate modeling.

$$SL(1 - A) = \sigma^{[\ell]}T, \qquad (12)$$

$$T_w = q^{[\ell]}(A - a_w) + T, \qquad (13)$$

$$T_b = q^{[\ell]}(A - a_b) + T. \qquad (14)$$

[19] We make a further simplification and assume that the albedos of the black and white daisies are symmetrically arranged by a value B around that of the bare ground and

therefore can be written as $a_b = 0.5 - B$ and $a_w = 0.5 + B$. This, and more importantly the linearization, permits considerable simplification of the results above, as now the equation determining the daisy stand temperatures (10) is linear rather than cubic, and so an explicit solution may be found for the temperatures:
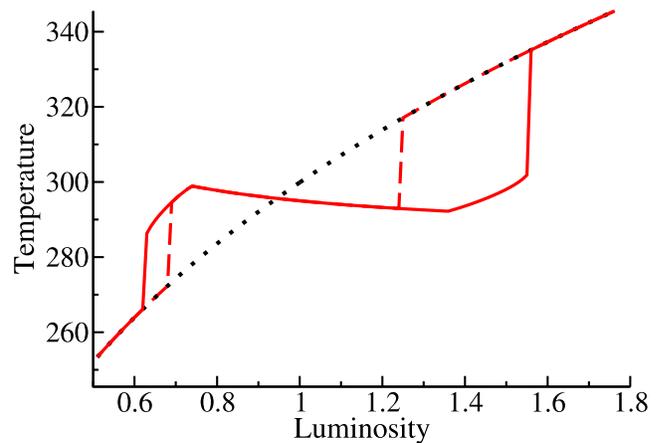
$$T_b = (\alpha_w - \alpha_b)\left[q^{[\ell]} - 2T_I\right]B + q^{[\ell]}B + T_I \qquad (15)$$

$$T_w = (\alpha_w - \alpha_b)\left[q^{[\ell]} - 2T_I\right]B - q^{[\ell]}B + T_I. \qquad (16)$$

We have introduced an additional variable T_I, an imposed temperature, which is the temperature the planet would be if there were no daisies (using (12)). Here $q^{[\ell]}$ is now a rescaled version of the WL parameter q chosen so that $T_{\text{opt}}^3 q^{[\ell]} = q$ and has a numerical value of ≈ 80. This parameter is equivalent to (4×) q' as given by WL. The relation between the daisy populations can now be written down explicitly giving

$$\alpha_w = \frac{1}{2} + \frac{T_{\text{opt}} - T_I}{2B(q^{[\ell]} - 2T_I)} - \frac{\gamma}{2\left[1 - k(q^{[\ell]})^2 B^2\right]} \qquad (17)$$

$$\alpha_b = \frac{1}{2} - \frac{T_{\text{opt}} - T_I}{2B(q^{[\ell]} - 2T_I)} - \frac{\gamma}{2\left[1 - k(q^{[\ell]})^2 B^2\right]}, \qquad (18)$$

Figure 2. Plot showing the average planetary temperature as a function of the luminosity using the techniques of *Watson and Lovelock* [1983]. Note the negative gradient of the temperature in the two-daisy regime. This effect is because the temperatures of the different daisy stands are fixed, but the relative proportion varies as the luminosity increases: The average planetary temperature is not held constant. The loops at the end of the regulating regions indicate the hysteresis effect in the model, the solid lines indicating the system path when the luminosity is steadily increased or decreased from unity and the dashed lines indicating when the system is started from infinitesimal daisy populations at each luminosity.
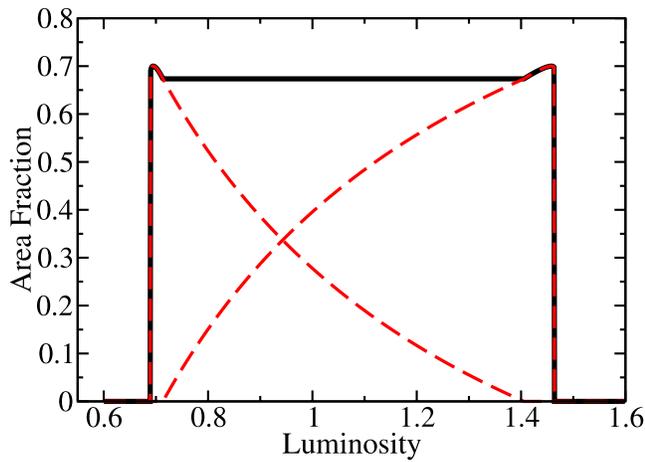
Figure 3. Plot showing daisy occupations within the linear approximation. The plot is qualitatively the same as Figure 1, but the single-daisy regions are considerably suppressed under this approximation.

which implies

$$\alpha_w + \alpha_b = 1 - \alpha_g = 1 - \frac{\gamma}{1 - k(q^{[\ell]})^2 B^2}, \qquad (19)$$

and furthermore, an exact relation for planetary temperature may then be found,

$$T = T_I \left[\frac{T_{\text{opt}} - q^{[\ell]}/2}{T_I - q^{[\ell]}/2} \right], \qquad (20)$$

which (curiously) has not been previously presented in the literature. A binomial expansion, noting the approximate order of magnitude difference between the temperatures and $q^{[\ell]}/2$, gives $T \approx T_{\text{opt}}$: homeostasis. The manner in which the temperature decreases at this fixed point steady state in response to rising luminosity can then be shown exactly by differentiation,

$$\frac{\partial T}{\partial T_I} < 0, \qquad (21)$$

confirming the early observation of WL. This form of the solution is similar to that of *Weber* [2001], and the results are very similar to those obtained by *Saunders* [1994], indicating the accuracy of the linearization. *DeGregorio et al.* [1992a] also present the linearization, and our results agree with the forms presented by them. The solutions for the single-species stability at either end of the range may also be computed exactly up to a cubic with or without the linearization. These solutions and their stability range are responsible for hysteresis in the model. Figures 3 and 4 show the occupational plots and stabilities of these solutions.

[20] The existence of a full analytic solution has provided a solid foundation for Daisyworld; the model attracted much criticism in its early life for issues that turned out to be implementation details rather than substantive critiques.

However, like all analytic approaches, there are limitations, and therefore the solution should be seen as illustrative.
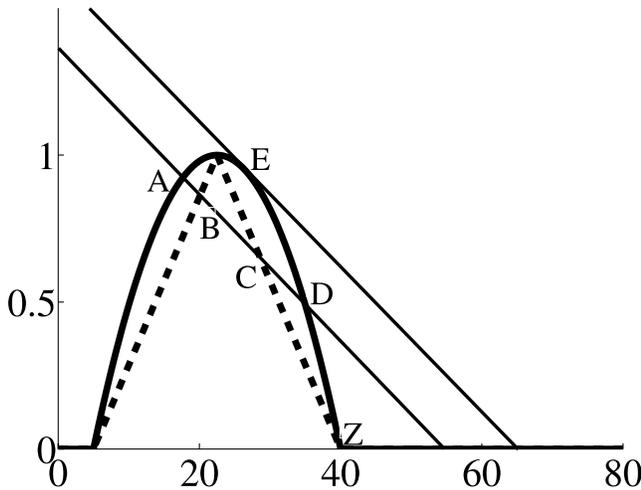
2.4. Nature of the Control System

[21] Building on previous work, *Saunders* [1994], *Saunders et al.* [1998], and *Harvey* [2004] argue that Daisyworld can be understood as an example of a rein control system. Rein control was introduced in a physiological context by *Clynes* [1969] where it is hypothesized that certain variables (e.g., core body temperature in mammals) are maintained within a range of values by separate control "reins" that oppose forces that seek to perturb the variable. The rein metaphor is apt in that reins can only pull not push. It is possible for a single rein to regulate a variable against perturbations that move the variable one way. For example, a heater will be able to maintain a room temperature of 22.5° if it is always colder outside (assuming that the heater is able to provide sufficient heat). If the variable is subject to two opposing perturbations, two opposing control reins are required.

[22] The rein control concept was further developed by *Saunders et al.* [1998] as integral rein control within an analysis of the regulation of blood glucose in humans (see section 6.3). This type of control system differs, as the opposing reins not only control a central variable but also interfere with the action of the opposing rein. We prefer the term "antagonistic rein control" for this reason. This control mechanism can lead to a situation with zero steady state error, an effect also realized by some other control systems such as a proportional integral controller. We can now identify WL Daisyworld as a system of this type where the interference is due to the growth rate of each daisy being a function of shared bare ground and, consequently, a competition for bare
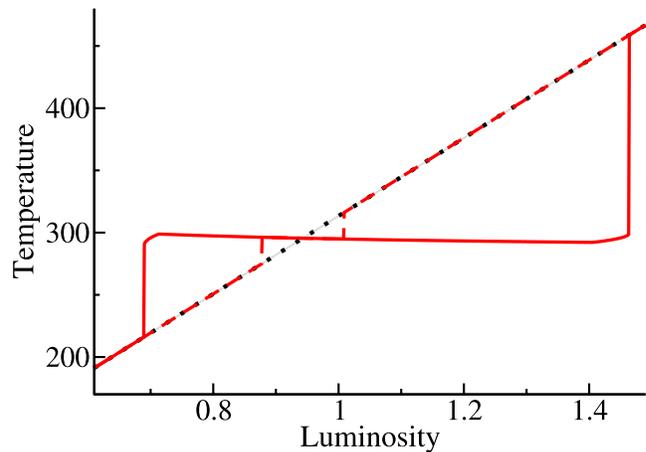
Figure 4. Plot showing the temperature response of Daisyworld within the linear approximation (12). The plot is qualitatively the same as Figure 2, with the single-daisy regions once more suppressed (Figure 3). The visual difference is because the linear approximation becomes increasing less valid away from the optimal temperature. This, in effect, creates a rescaling of L and greatly increases the temperature range at which the daisies can survive. This rescaling is also responsible for the enhanced hysteresis regions.

how closely the two daisy bed temperatures are to each other.

$$T_b = SL(1 - A_b) - D(T_b - T_w)$$

$$T_w = SL(1 - A_w) + D(T_b - T_w).$$

(22)

[24] Additionally, the parabolic birth rate function of (3) is replaced with a peaked piecewise linear function (see Figure 5), or "hat function $(H(T))$," that specifies the steady state population size for a daisy bed as a function of its temperature:

$$\frac{\partial \alpha_i}{\partial t} = H(T_i) - \alpha_i,$$

(23)

where

$$H(T) = \begin{cases} 1 - \frac{2(|T - T_{\text{opt}}|)}{k} & |T - T_{\text{opt}}| \frac{k}{2} \\ 0 & \text{otherwise.} \end{cases}$$

(24)

[25] The function defined by (24) determines the steady state coverage of the daisies rather than the rate at which the daisies grow and replaces the replicator equations (2). Steady states of the system as a whole were found for each incremental level of luminosity by numerical integration using the Euler method.

[26] The model has three key differences from the original Daisyworld. First, the population is assigned in separate beds according to the growth function rather than allowed to replicate. This removes the abilities of daisy populations to overshoot or compete: It is a rein system rather than an antagonistic rein system. Second, the use of the simplified heat transport has the effect of making the q parameter used by WL a linear function of the applied temperature. Finally, the witches hat function, though creating some mathematical inconveniences, linearizes the response of the system to changes in insolation. The proportion of respective daisy beds may be found analytically as

$$\alpha_b = \frac{k}{k + \frac{4T_I B}{(1+2D)}} - \frac{2(T_I - T_{\text{opt}})}{k + 4T_I B}$$

(25)

$$\alpha_w = \frac{k}{k + \frac{4T_I B}{(1+2D)}} + \frac{2(T_I - T_{\text{opt}})}{k + 4T_I B},$$

(26)

where B and T_I are identical to those defined in section 2.3. A similar principle of the total occupation is observed, as the only dependence on the applied temperature is through the explicit dependence of the heat transfer parameter (effectively q). Regulation in the coexistence region is once more observed

$$T = T_I \left[\frac{|T_{\text{opt}} + k/4B|}{T_I + k/4B} \right],$$

(27)

a similar form to that in section 2.3 but which now yields a positive gradient in the coexistence regime as opposed to (21).

Figure 5. Two growth rate functions plotted: original WL in thick solid line and linear "witches hat" from *Harvey* [2004] in dashed line. Temperature increases from left to right on the horizontal axis. Growth rates increase from zero on the horizontal axis. The thin sloping lines represent the negative feedback that white daisies exert on temperature. Steady state growth rates are found where the thin lines bisect the growth functions. Points C and D are steady state growth rates to the right of the optimal growth temperature of 22.5°C that prove to be unstable. Any decrease in daisy coverage would result in the population decreasing to zero at point Z. Any increase in daisy coverage would result in the growth increasing and the daisy temperatures passing the optimum and coming to rest at point A or B depending on which growth function is used. As luminosity varies, the sloping line slides along the horizontal axis. Point E shows the greatest luminosity that can still support a white daisy population with an original WL growth function. The slope of the thin line is determined by the albedo of the white daisies. The higher the albedo, the more obtuse the angle it makes with the horizontal axis. The line of feedback representing black daisies would be less than 90°C, with darker daisies making a more acute angle with the horizontal axis.

space to grow into. Consequently, during daisy coexistence, $\alpha_b + \alpha_w = $ const. In equations (11) and (20) we see that the planetary temperature depends on the imposed insolation L, while $\alpha_b + \alpha_a$ does not. Antagonistic rein control in WL Daisyworld will cease when there are only black or only white daisies at the limits of regulation or in models such as those of *Staley* [2002] and *Harvey* [2004] where a rein control rather than antagonistic rein control paradigm is more appropriate.

[23] To illustrate the rein control concept, *Harvey* [2004] created a "cut-down" Daisyworld in which he simplified the physics of the original model and assumed that each daisy type will inhabit a separate grey daisy bed. The two beds are coupled via the transference of heat, which can be considered analogous to heat diffusion modeled in climate energy balance models [*North et al.*, 1981] (see section 6.1). The amount of diffusion D between the two beds determines

[27] Hysteresis is observed in both the original and the cut-down models, but this latter model is more convenient to study the details. *Dyke and Harvey* [2005] show in the cut-down system that this hysteresis is largely dependent on the value for the viability range k^{-1} that is used in the growth function (24); this parameter does not effect the limits of regulation; the system still regulates even in the extreme case of $k \to \infty$. *Dyke and Harvey* [2006] show further that extending the viability range of the daisies can counterintuitively decrease the range of luminosity over which global temperature is regulated. At the limits of daisy coverage, allowing the daisies to grow over a wider range of temperatures can result in a higher proportion of daisies that interfere with the regulating daisy type.

2.5. Chaos in Daisyworld?

[28] The emergence of chaotic and oscillatory solutions from the basic equations proposed by WL has greater significance in the development and critique of the Daisyworld system than might be expected because one of the earliest mathematical developments of the model empha- sized the creation of chaotic solutions [*Zeng et al.*, 1990 (hereinafter referred to as ZPE), *Zeng et al.*, 1992]. ZPE argue that Daisyworld was more likely to display chaotic rather than regulatory behavior. Many of their conclusions were robustly dismissed by *Jascourt and Raymond* [1992] in a succinct response. This helped to clarify details about implementation of the model, in particular the use of continuous or discrete models, and the manner in which the environment is coupled to the growth equations. A more careful analysis of the problem was presented independently by *Maddock* [1991] addressing all of the issues raised, which regrettably received far less attention in the literature. The debate has now become a tutorial analysis of potential modeling pitfalls [*Ford*, 1999].

[29] ZPE used a version of equation (2) implemented as a difference equation

$$\alpha_w(t+1) = \alpha_w(t) + \alpha_w(t)[1 - \alpha_w(t) - \alpha_b(t)]c\beta - \gamma\alpha_w(t) \quad (28)$$

and used a similar equation for the black daisies.

[30] ZPE introduce a new parameter c, so that the equations more closely resemble the logistic map intro- duced by *May* [1974] in his classic analysis of chaos in population dynamics

$$\alpha(t+1) = r\alpha(t)[1 - \alpha(t)], \quad (29)$$

where the similarity arises from the linear increase and quadratic reduction in population. In the logistic map, chaos appears for $r > 2.5$, the origin of which is the discrete generation time (the time evolution of the population is a series governed by a difference equation rather than function governed by a differential equation). In the logistic map the series represents discrete, nonoverlapping genera- tions, and the time step is a generation time: This makes sense when applied to the daisies, but ZPE (implicitly) use the same time step in the equilibration of the temperature. The notion of discrete generations of temperature is peculiar

since heat flow is a continuous process; it can be rationalized by assuming the temperature equilibrates with each generation before reproduction can occur and the large intergenerational swings of temperature have no effect on the biota. The chaotic instability explicitly requires both discretization and the fourfold increase in birth rate from the WL equations and implicitly requires the entire planet to oscillate in phase, i.e., seeds to be dispersed equally across the planet.

[31] ZPE's flawed analysis could be read as an attempt to discredit the basic premise of the original Daisyworld and by extension the Gaia hypothesis. However, as *Jascourt and Raymond* [1992] observe, the altered Daisyworld continues to regulate in the neighborhood of any reasonable parameter space. Even in this potentially difficult case the system still achieves a homeostatic state on average.

[32] A more complete analysis of the effect of explicit time lags was presented by *DeGregorio et al.* [1992b], who introduce three different forms of explicit time lag into the system. The first is simply a standard two-species Daisy- world model as described in section 2 but with the growth rate β [$T(t)$] replaced by β [$T(t - \tau)$], where τ is the fixed delay time that makes the growth in the present dependent on the temperatures in the past. This simple substitution leads to a complicated set of coupled equations, but a fixed point analysis can proceed as in the nondelayed case [*DeGregorio et al.*, 1992a] as the time stationary solution is unaffected by the delay. The characteristic equation for the linear perturbation analysis is found to be transcenden- tal, but in the case of ideal solar driving the black/white symmetry may be exploited to factorize the characteristic equation.

[33] As *DeGregorio et al.* [1992b] note, this analysis is equivalent to that of the linear approximation of a classical logistic equation [*Cushing*, 1977]. Three scenarios may occur; the system may be stable, oscillatory and stable, or oscillatory and unstable according to the value of τ. Here the bounded nature of the system yields oscillatory solutions even in the unstable case. The boundary between the former two solutions is $\sim[(1 - \gamma)\gamma]^{-1}$, the natural timescale in the system: essentially, the death or turnover rate.

[34] For a continuous system, however, the integrated history approach is more appropriate. The growth rate $\beta[T(t - \tau)]$ is replaced by
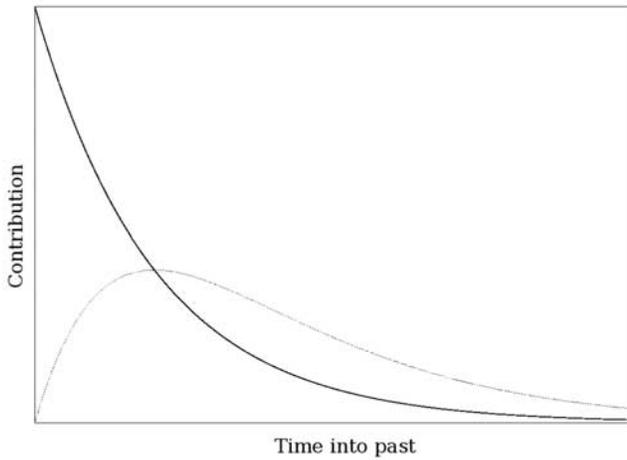
$$\beta[T(t)] = \int_{-\infty}^{t} k(t, t')\beta[T(t')]dt', \quad (30)$$

where the kernel is chosen so that $k(t, t') = k(t - t')$ and the authors permit it to take one of two forms

$$k(t) = \frac{1}{\tau}e^{\frac{-t}{\tau}}, \quad (31)$$

corresponding to so-called Weak delay, and

$$k(t) = \frac{1}{\tau^2}te^{\frac{-t}{\tau}}, \quad (32)$$

Figure 6. Systematic plot of the kernels for weak (solid line) and strong (dashed line) delay plotted as a function of relative weighting and time from the present.

corresponding to so-called Strong delay. A plot of these curves is shown in Figure 6 to illustrate the implied history dependence. The characteristic equation derived is polynomial in each case, cubic for weak delay and quartic for strong delay. Factorization is possible for the case of perfect solar driving, i.e., $T_{\text{opt}} = T_I$. For the weak delay the system remains asymptotically stable for even very large values of the τ parameter (long history dependence), but for the strong case the system undergoes a Hopf bifurcation to a purely periodic solution for a particular value of τ that is once more $\sim[(1 - \gamma)\gamma]^{-1}$.

[35] Thus *DeGregorio et al.* [1992b] demonstrate how an oscillation occurs in the time series response when some form of delay is introduced into the model. For more complicated implementations of the model that explicitly take into account the thermal relaxation time, this is likely to lead to pure oscillatory solutions. The history kernel method is particularly effective because of its generality: Any spatial models will lead implicitly to a kernel of this general type because of their degree of spatial inhomogeneity.

[36] *Nevison et al.* [1999], who regrettably seem unaware of the work of *DeGregorio et al.* [1992b], generate such oscillations by introducing a heat capacity C (and hence thermal relaxation) to the simple zero-dimensional model with two distinct daisy species present:

$$C\frac{\partial T(t)}{\partial t} = SL[1 - A(t)] - \sigma T(t)^4. \qquad (33)$$

This is sufficient to trigger sustained oscillations. However, the nonlinear evolution of the albedo field means it is not a simple matter to extract the exact form of the integral kernel for this system.

[37] It is interesting to note that oscillations were not seen in the two-dimensional (2-D) model of *von Bloh et al.* [1997] (discussed in section 3) that includes a heat capacity. The presence of thermal capacity in the simplified model with two distinct daisy types leads to a strong decay kernel,

yet in a fully spatial case the thermal capacity alone does not create a sufficient lag to trigger the Hopf bifurcation. To date, there has not been a more detailed simulation that has produced a chaotic solution to the Daisyworld system.

3. SPATIAL EXTENSIONS

[38] WL's q parameter governs the difference between the temperatures experienced by the black and white daisies. It represents a level of structure between the individual daisies and the total planet. The limiting cases are $q = 0$ representing perfect heat conduction, with all regions of the planet at the same temperature, and $q = SL/\sigma$ representing zero heat flow. The existence of this intermediate level structure is crucial to Daisyworld: With either limiting case choice for q, coexistence regulation collapses. The formulation of energy balance using q assumes that even a vanishingly small population of daisies can create their own microclimate and achieve perfect local homeostasis of temperature.

[39] One way to eliminate the arbitrary choice of q is to use an explicit spatial model with a heat diffusion equation:

$$\frac{dT(\mathbf{r})}{dt} = -D\nabla^2 T + SL[1 - \alpha(\mathbf{r})] - \sigma T(\mathbf{r})^4, \qquad (34)$$

where T and α vary with spatial location $\mathbf{r}$. The simplest heat flow equation with explicit spatial resolution would be a 1-D Daisyworld with q removed. Surprisingly, this model appears not to have been studied.

[40] The extension to spatial Daisyworlds also opens the possibility of inhomogeneous forcing (e.g., a curved planet with poles and equator) and the possibility of explicit seeding, mutation, and daisy patch structure. These models with explicit diffusion can exhibit rich behavior including catastrophic desert formation or population explosions.

3.1. One-Dimensional Daisyworlds

[41] *Adams* [2003], *Adams and Carr* [2003], and *Adams et al.* [2003] examine a 1-D Daisyworld with curvature based on a spherical planet. Each location can support a population of black and/or white daisies. An explicit diffusion equation is implemented, but implicit diffusion via q is retained, setting an effective minimum to the heat transfer. Because of curvature this model exhibits desert formation where, depending on insolation, the equatorial or polar regions are denuded of biota.

[42] Less intuitively, the distribution of daisies forms stripes of pure black and white daisies rather than a coexisting population. For finite diffusion, stripe formation increases the heat transfer between the two regions (equivalent to lowering q in (7)). Additional heat transfer cools the black and warms the white daisies, increasing the growth rate of both: Hence this separation is favored. However, as, for example, the black stripe widens, the temperature at the center increases, until the limiting value for black daisy growth occurs. A stripe of white daisy can now form in this region. This process determines the maximum width of a stripe, which is thus related to the diffusion length.
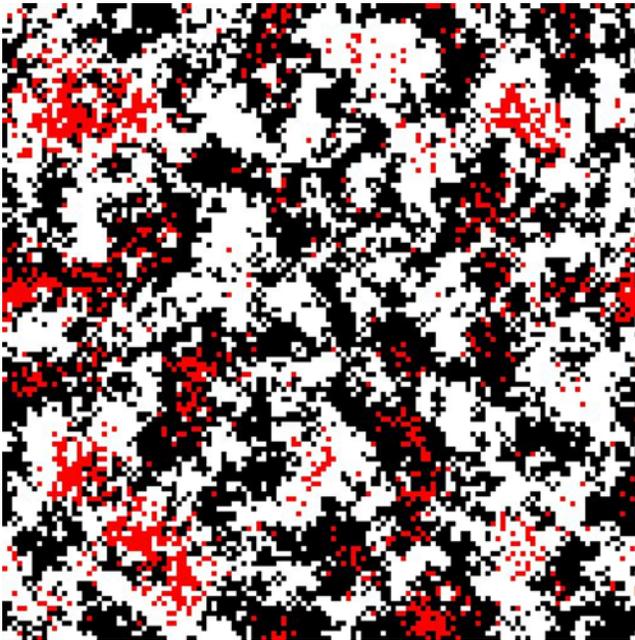
Figure 7. Snapshot showing a 2-D, two-species model consisting of only black and white daisies. Red patches are bare ground. This system has been little studied, but it does regulate the planetary temperature well, although it is more susceptible to collapse under perturbation. Interestingly, there is no characteristic size expressed by the daisy patches (A. J. Wood and G. J. Ackland, unpublished results, 2005).

[43] The spatial Daisyworld is also analyzed with respect to perturbations (removal of some daisies and watching for regrowth). This changes the stripe pattern, without affecting the ratio of black to white, suggesting that the observed stripe patterns are metastable. Alternate perturbations in which some areas are permanently unavailable for growth reduces the range over which regulation is possible, an effect similar to increasing γ. The equations of the 1-D Daisyworld are readily generalizable to two dimensions and produce regular patterns that depend on the initial seeding (B. J. Adams, unpublished results, 2003).

3.2. Two-Dimensional Daisyworlds

[44] Work on 2-D Daisyworlds has been based around replacing q with explicit diffusion and representing the surface by a cellular automaton grid. Each grid site is either occupied or unoccupied at a particular time step. An occupied cell will remain occupied at the next time step with a probability of $1 - \gamma$, where γ is the death rate of the vegetation it contains. An unoccupied cell can regrow according to the local temperature.

[45] The simplest regrowth rule in the spirit of equation (1) is to have two daisy types regrow black or white according to their relative proportions. This model has not been published, primarily because it fails to show any regulation. The minimal change needed in order to achieve regulation is that seeding is local (i.e., the new daisy is a copy of one on an adjacent site). A model of this type, with explicit closest

approach (CA) growth rules, was presented by *Lenton and van Oijen* [2002]. This introduces the crucial intermediate length scale and allows successful regions of space to expand while maintaining their black/white ratio. These local spatial interactions can lead to bifurcations and limit cycles in the single-daisy regimes [*Lenton and van Oijen*, 2002]. The spatial scales associated with clustering can also be studied in this model, but no particular length scale is selected; see Figure 7.

[46] The most studied 2-D model, introduced by *von Bloh et al.* [1997], includes multiple daisy types with a regrowth rule as follows: At a given time step, one cell is chosen at random. If the neighboring cell is empty, there is no colonization. If the neighboring cell is vegetated, then it has a chance, determined by its growth rate $\beta(T)$, of colonizing the empty cell. During successful colonization the albedo of the colonizing vegetation is allowed to mutate in a random fashion by a small amount. After many such mutations a continuous spectrum of possible albedos ($0 < a < 1$) can be realized. This is the basic model henceforth referred to as 2-D Daisyworld; see Figure 8.

[47] This Daisyworld is an almost perfect temperature regulator [*von Bloh et al.*, 1997; *Ackland et al.*, 2003]; there is no luminosity dependence in the variation from the optimal value; the only deviations are stochastic in origin. The planetary temperature is maintained very close to the optimum for daisy growth over a wide range of solar luminosity. A rapid switch occurs at the termination of temperature regulation, and solar luminosity (S') must be decreased to 1.25 before the biosphere recovers; that is, there is a large hysteresis loop. The perfect regulation is not a result of the spatial nature of the model, rather it arises from the ability of the model to have near-optimal growth temperature everywhere and simultaneously regulate temperature and maximize life [*Ackland et al.*, 2003].

[48] Despite the existence of a particular daisy albedo that optimizes temperature at any given insolation, the model actually shows a distribution of daisy types. This distribution of albedo is affected by diffusion and by mutation. In the limit of low diffusion, mutation produces a Gaussian peak around the optimum value. By contrast, for high diffusion the distribution is a bounded exponential in albedo that maximizes entropy (subject to optimizing temperature) (see section 6.1). The general case is a distribution that interpolates between these extremes.

[49] Different growth rules make a significant difference to the range of planetary temperature regulation. Using parameters from *von Bloh et al.* [1997] when colonization is determined by the temperature of the cell to be invaded (rule A), regulation breaks down at $S' \approx 1.8$. When colonization is determined by the temperature of invading vegetation, regulation persists to $S' \approx 2.3$ (rule B). There are two explanations: First, under rule B, at high solar luminosity, pale invading vegetation is significantly cooler than the ground to be invaded and is thus able to colonize it. In addition, under rule A it is no more likely for one albedo type to colonize than another. However, under rule B the daisies with an albedo better suited to the prevailing solar
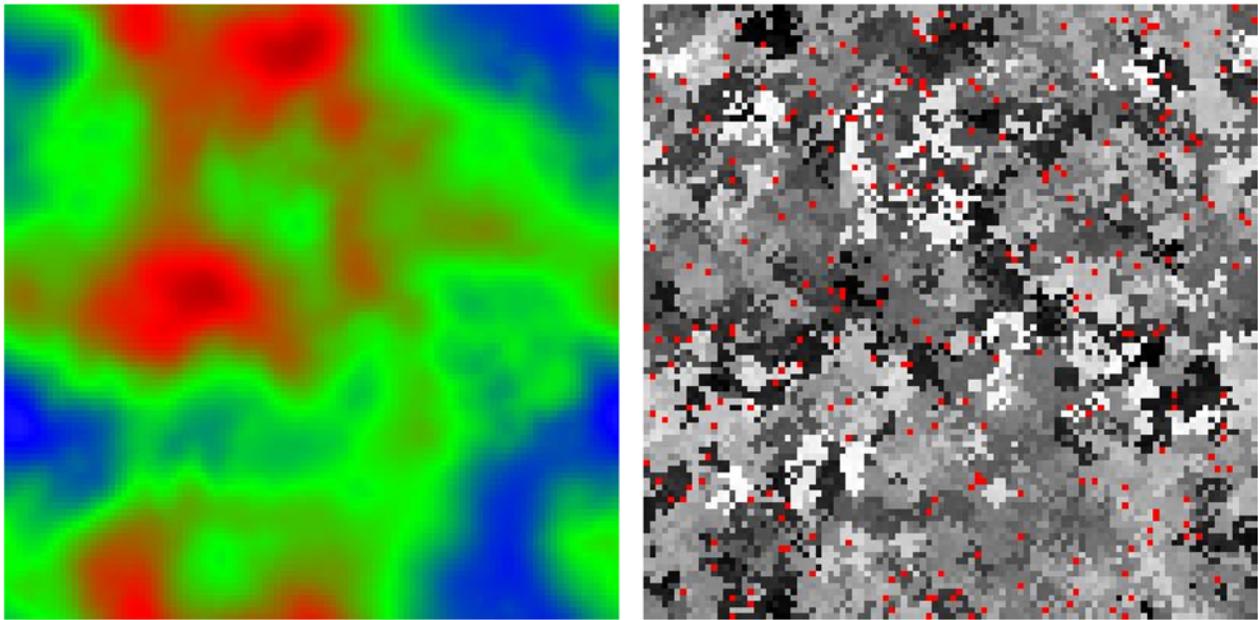
Figure 8. Plot showing a 2-D, single-species model, originally introduced by *von Bloh et al.* [1997]. (left) A large number of different albedos are present at any different time in the model, including large numbers of grey pigmented daisies. Bare ground is represented by red. (right) There are also considerable temporal as well as spatial fluctuations in the temperature field. In the false color image, white is the coldest color, then blue, then green (which is optimal). The hotter than optimal colors are red and then black.

luminosity are more likely to colonize empty areas, thus improving the regulation of the whole system.

[50] Fully spatial models allow us to explicitly consider more realistic geometries for the planet. Curvature introduces inhomogeneous insolation that leads to desert formation. In two dimensions it was found that desert formation is a nucleation and growth process: As insolation increases, the system becomes unstable to persistent desert formation. The desert is formed at the equator once regulation from daisies on all sides is insufficient and immediately spreads to a latitude where cooling by daisies on one side only can cool the area sufficiently. However, before the desert forms in a band around the equator, transient desert regions of roughly circular shape grow and shrink, until eventually one of these fluctuations reaches a critical size and engulfs the planet. A relatively small amount of planetary cooling can prevent desert formation if applied during this transient period; however, once the desert engulfs the entire planet, much greater cooling is required to eliminate it [*Ackland et al.*, 2003].

[51] Another effect is spatial segregation: Habitat fragmentation affects the biodiversity and the functioning of climate regulation [*von Bloh et al.*, 1997]. Human intervention was modeled by making randomly chosen sites unavailable for growth. When these infertile areas generate a spanning cluster that disconnects areas of vegetation, self-regulation begins to progressively break down (the "percolation threshold," where 0.408 of the cells are infertile [*Essam*, 1980]). Up to this point, temperature regulation is hardly affected because the transport of heat between the infertile areas and adjacent vegetation prevents them from becoming hot spots. As the vegetation fragments, competi-

tion between different albedo types is restricted to within the fragments (but not between them). Founder effects in the islands created and genetic drift due to weakened selection may then lead to suboptimal regions that destroy the regulation of Daisyworld. The geometry of habitat destruction is also critical. When habitat is destroyed by progressively reducing the size of disconnected square regions available for daisy growth, temperature regulation is immediately impaired. Thus regulation appears to depend on the size of the fully connected region of vegetation rather than the total amount.

4. EVOLUTION

[52] The original Daisyworld model considers two fixed species that have no capacity for genetic or phenotypic change, thus effectively prescribing the system solutions. Evolutionary biologists have criticized the model for this and a host of related reasons, suggesting that the preordained species were chosen so as to have the correct properties to regulate temperature and asking: How could such a system evolve by natural selection?

[53] *Dawkins* [1983] first argued that in a real world there would be daisy species that "cheated" by saving the energy of producing pigment, while enjoying the climate regulation offered by the other daisies. Daisyworld is often perceived as an example of altruism: where an organism, to the detriment of its own fitness, performs some function that benefits others, raising the well-known theoretical "problem" of how such altruism could evolve [*Hamilton*, 1964]. However, it is arguably inappropriate to view Daisyworld in
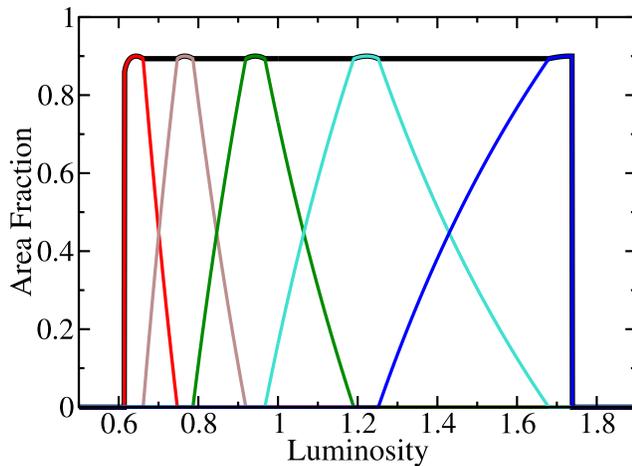
Figure 9. Plot showing the area fractions when five daisies are present on a Daisyworld. The data presented here are obtained numerically by integrating the original model of *Watson and Lovelock* [1983]. The parameters are varied slightly in order to emphasize the regions where only one daisy species is present, and so $k = 7.5°$, $\gamma = 0.1$, and q is 1.5 times the WL value. The single-daisy region is identifiable by the gap that appears on the x axis and the slightly raised area on the total occupation where the single-daisy region may raise the total population to almost $1 - \gamma$.

altruistic terms, because the successful daisy traits benefit their carriers whether or not they benefit others.

[54] Evolutionary biologists have also argued that there is an inherent conflict between the more immediate, local optimization of evolution by natural selection and the longer-term, larger-scale process of environmental regulation [*Hamilton*, 1995, 1996; *Lenton*, 1998]. To address this demands a move from "static" evolutionary models toward those mimicking the generation of new traits [*Hamilton*, 1996]. Sections 4.1–4.5 categorize variants of Daisyworld according to which of the traits are allowed to evolve and in which manner before considering variants that have attempted to alter the underlying nature of the feedback loops.

4.1. Discrete Changes in Albedo

[55] A series of studies have examined the effect of introducing daisies of differing albedo. This began with *Lovelock* [1992], who in answer to the criticism of *Dawkins* [1983] began by introducing a "cheat" in the form of a third, grey daisy type with an improved growth rate (for not producing pigment of one type or the other). This makes little difference to the temperature regulation. The grey daisies clearly flourish when temperatures are ideal, but they do not destabilize the regulation as they recede when temperatures are far from optimal. They noticeably level off the regulation (i.e., distort the result (21)) of temperature in the occupancy regime. Subsequently, *Lansing et al.* [1998] showed that the growth benefit given to the grey daisies is incidental; the same qualitative behavior arises with no benefit.

[56] Introducing one additional daisy type inspired *Lovelock* [1992] to introduce many types. When there are

multiple daisy types available, no more than two survive for any given applied temperature; see Figure 9. This significantly levels off the temperature curve in the regulating regime. This effect has been expanded upon in subsequent work [*Lenton*, 1998; *Lenton and Lovelock*, 2001; *Ackland*, 2004]. What consistently emerges is that where there are discrete species of daisy with distinct albedos, then the solution at a given imposed temperature will usually be one with two daisy types only. They will have albedos that correspond to the planetary temperatures that most closely bracket the ideal temperature. There also exists a narrow range of luminosities where only one daisy type exists. This effect occurs because the single-daisy solution can populate a larger area of planet than a two-species solution, i.e., $\alpha_g = 1 - \gamma$ as opposed to (19).

4.2. Adaptation to Prevailing Conditions

[57] There is a further way daisies could evolve in the model, namely, that a given daisy type could change its preferred growth temperature over generations. This seems eminently reasonable; for example, if the surroundings of a black daisy are slightly too hot, then any offspring that grows better in warmer conditions should be preferentially selected. In the model this should result in the black daisy population evolving its optimal temperature upward toward its local temperature. From the point of view of the white daisies this may be described as a "selfish" evolutionary step. This type of adaptation has been considered repeatedly in the Daisyworld literature and has somewhat unfortunately been termed "Darwinian" by *Robertson and Robinson* [1998]. We avoid this convention here because it could be taken to imply that altering the environment is not "Darwinian," which clearly it can be.

[58] *Keeling* [1991] first considered alternative optimum growth temperatures by introducing a species, kudzu, with the same albedo as the black daisies and a growth curve that peaks at 33°C (rather than the 22.5°C peak of the daisies) but otherwise has the same mathematical properties. The presence of the kudzu caused an environmental catastrophe at imposed temperatures where in the normal daisy solution, black daisies would be expected to dominate. The black daisies are outcompeted and wiped out by the kudzu, which does differentially better on the warmer patches. With the regulating effect of the black daisies removed, the kudzu drags the temperatures higher causing the white daisies to die out at lower than the expected values of the luminosity. With the white daisies gone, the kudzu has only limited regulatory properties, as with any single species solution, and the loss of all life results.

[59] Similar results were reported by *Saunders* [1994], who noted the decrease in the range of regulatory range for small deviations from the optimal, but it was an article by *Robertson and Robinson* [1998] (hereinafter referred to as RR) (recently elaborated by *Weber and Robinson* [2004]) that first tried to incorporate this effect into an evolving model. They allow the optimal temperature for daisy growth to shift slowly toward the current prevailing temperatures. The model shows that even small rates of adaptation tend to

destabilize the regulatory effect of Daisyworld. Considering only the case of increasing luminosity, the black daisies, once established, simply shift their optimal temperatures rather than give up space to the white daisies.

[60] RR's approach has been criticized in a number of ways [*Lenton and Lovelock*, 2000; *Sugimoto*, 2002]. On a purely practical level the authors provide limited implementation details of their model, which makes it difficult to reproduce. *Lenton and Lovelock* [2000] point out that RR's approach leads to grossly unphysical situations (for instance, life is able to flourish happily around absolute zero) and that including a simple bounding function on the growth rate (that takes into account, say, the efficiency of chemical and photochemical processes at different temperatures) restores a form of homeostasis

$$\beta(T) = \left[1 - k\left(T - T_{\text{opt}}\right)^2\right]\left[1 - k'\left(T_{\text{opt}} - T_{\text{ideal}}\right)^2\right], \qquad (35)$$

where the ideal temperature T_{ideal} is predetermined by these physical processes. *Lenton and Lovelock* [2000] show that regulation is still provided even when k' is large compared to k or when the bounding function deviates from parabolic.

[61] At a conceptual level, there is no reason to expect organisms that are capable of perfect and infinite adaptation to regulate their environment; they have no need to do so. So we should not be surprised by RR's result. A secondary critique is that the treatment of the two traits in the model (preferred temperature and color) is manifestly unequal. There is no way to determine a priori which kinds of adaptation are "Darwinian" (i.e., by RR's terminology, which traits are subject to mutation and selection), and RR's specification of growth temperature as the sole "Darwinian" adapting trait seems arbitrary. Moreover, this trait is specifically directed toward a goal and neglects random genetic drift.

[62] *Sugimoto* [2002] later claimed, with an analytic proof, that the results of RR must be incorrect. However, it is not clear this claim is valid as the nature of the fixed point was not established, which may invalidate this exact result. Later models with continuous phenotype [*Williams and Noble*, 2005; *Wood et al.*, 2006] fail to support *Sugimoto* [2002], so if true, it may be a special result for the RR model.

4.3. Continuous Phenotype Models

[63] Thus far we have only considered the case where the daisies have fixed phenotypes that express a particular albedo. As discussed in section 4.1, if a series of individuals with distinct phenotypes are permitted to exist, then the system will exclusively select no more than two of the the existing types and thereby select a homeostatic state. This contrasts with work where the albedo phenotype is generalized to a continuous range or gray scale.

[64] The use of completely continuous phenotypes has a mixed history in biology. The continuous phenotype is expressed by a fundamentally discrete object: the genetic code. These systems are often more easy to tackle mathematically, as mutation can be approximated as a diffusive process acting upon the phenotypic space in ignorance of genetic details such as diploid inheritance, recombination, and epistatic effects. A model of this type was proposed, and treated analytically, for Daisyworld by *Stöcker* [1995] and has been recently extended by *Wood and Coe* [2007]. It is also the basis for many of the spatial models that utilize a cellular automata to model the daisies described in section 3 [*von Bloh et al.*, 1997].

[65] The key point of *Stöcker* [1995] is the approximate solution of a differential equation that is a continuous analogue of the Carter-Prince equations, namely,

$$\frac{\partial \alpha(a)}{\partial t} = \alpha(a)\left\{\beta[T(a)]\alpha_g - \gamma\right\} + m\frac{\partial^2 \alpha(a)}{\partial a^2}, \qquad (36)$$

where

$$\alpha_g = 1 - \int_0^1 \alpha(a')da', \qquad (37)$$

where $\alpha(a)$ is the fraction of area taken up by daisies with albedo a within some small albedo neighborhood of a. The mutation m gives a measure of the rate of change of albedo (diffusion in the phenotypic space). The other parameters and equations are identical to those presented in section 2.2. Simulating this system leads to Gaussian distributions of albedos, which also possess a relationship to the mutation rates, namely, that the occupation of the space $(1 - \alpha_g)$ tends to $1 - \gamma$ in the limit $m \to \infty$ and that $m \sim \sigma_a^4$, where σ_a is the standard deviation of the albedo distribution.

[66] *Stöcker* [1995] proves these results analytically by extending the range of integration to the full range of a and making an ansatz for the Gaussian distribution. The former step is valid for small values of m and for driving temperatures sufficiently close to optimality. The latter step was made more precise by *Wood and Coe* [2007] by making a linearizing assumption for the Stefan-Boltzmann law, analogous to that presented in section 2. This enables Stocker's equation to be split into two separate equations, one for the total planetary occupancy and one for the probability distribution of the daisies. The former has a fixed point solution, which, when inserted into the latter, yields a differential equation

$$\frac{\partial p(a;t)}{\partial t} = \alpha_g\left\{\beta[T(a)] - \bar{G}\right\}p(a;t) + m\frac{\partial^2 p(a;t)}{\partial a^2}, \qquad (38)$$

where $\bar{G} = \int p(a;t)\beta[T(a)]da$ and α_g is the amount of bare ground in the system at the fixed point. The equation has a formal general solution for $\alpha(a)$ at steady state, namely, a parabolic cylinder function $D_\chi(x)$, which has the property that $D_0(x)$ is simply the Gaussian distribution. For this special case, which also self-consistently implies that σ_a is constant, there is an analogous result to (20)

$$T = T_I\left[\frac{T_{\text{opt}} + \frac{q\alpha_g}{2\left(1 - \alpha_g\right)}}{T_I + \frac{q\alpha_g}{2\left(1 - \alpha_g\right)}}\right], \qquad (39)$$

a statement once more of near homeostasis. The binomial expansion is more accurate for this form of the equation and also has a weak positive gradient in the regulating regime in contrast to (21). The system now does not regulate explicitly through the process of rein control; the daisies evolve to a single-peaked albedo distribution, which provides for optimal regulation at prevailing insolation rather than an ecosystem in which regulation arises from varying the proportions of distinct daisy types. Regulation occurs by adaptation of the albedo of individual daisies rather than relative populations at the ecosystem level.

[67] The analysis also allows us to make a link with quantitative genetics and the notion of fitness [*Wood and Coe*, 2007]. The self-consistent solution of (38) is a Gaussian with constant standard deviation, and this is precisely the necessary requirement on a distribution in order for the evolution process to be described by the weighted fitness approach of *Lande* [1976]. This is a key result in quantitative genetics and, with the assumptions noted above, enables the temporal evolution of the mean phenotype to be described as differential movement in fitness space. For this approach to be applicable to Daisyworld we must both identify the appropriate measure of fitness and assume that the daisies exist in discrete, nonoverlapping generations. The latter is not an unreasonable assumption for this system, and we may equate fitness $W(a)$ with lifetime reproductive success $\beta[T(a)]/\gamma$. This construction satisfyingly leads to the identical results of the exact analysis (39).

[68] A similar connection to the notion of fitness arises in the original Daisyworld. We make the natural association of fitness with $(1/\alpha)(\partial\alpha/\partial t)$ and view daisy color as two alleles of the same gene locus in the same species. Though the exact form is complicated and certainly frequency-dependent, the standard analysis [*Charlesworth and Charlesworth*, 2003] requires that at coexistence the fitnesses must be equal. This leads to

$$\alpha_g \beta(T_w) - \gamma = \alpha_g \beta(T_b) - \gamma, \qquad (40)$$

which leads to (9) and *Saunders*' [1994] solution. It has yet to be confirmed the extent to which, given the stringency of the assumptions, this kind of approach may be applied to more complex evolutionary systems such as those described in section 4.4.

4.4. Multiple-Character Adaptation

[69] There are two phenotypic daisy traits on which selection can act: albedo and growth response to temperature. Thus far we have discussed studies where one or the other of these traits is allowed to evolve. Some recent work has considered the case where both traits evolve simultaneously [*Williams and Noble*, 2005; *Wood et al.*, 2006; *Williams*, 2006].

[70] *Williams and Noble* [2005] based their model on the simplified system of *Harvey* [2004]. This model is stochastic and individual-based, dividing the available growing surface into a grid of bare earth patches that might be colonized by daisies. Each of these bare earth patches is

equivalent to a daisy bed in the Harvey cut-down model but may only be occupied by a single daisy or may be bare. Growth is once more reinstated into the model in a similar way to *von Bloh et al.* [1997] (see section 3). Local temperature of a patch T_P is given by

$$\frac{\partial T_P}{\partial t} = (1 - \alpha)(T_S - T_P) + T_P, \qquad (41)$$

where T_S is the solar temperature. Heat flow can also be added to this model [*Williams*, 2006] in a way analogous to *Harvey* [2004]. A new relationship between phenotype and reproductive success was also employed, by which the probability of a daisy species colonizing a neighboring bare patch depended inversely on the gap between the local temperature and its genetically specified preference, so that daisies with preferences closer to the current environmental state are more likely to proliferate.

[71] This model follows a similar track to the model of *Robertson and Robinson* [1998], i.e., that regulation is lost. As predicted by *Lenton and Lovelock* [2000], the introduction of the physical plausible bounding function (35) restores homeostasis. Regulation is also observed to occur in the case of restricted sets of a few possible preferred growth temperatures. For example, two well-separated growth temperatures gives rise to a situation where temperature regulation occurs first around one temperature and then the other.

[72] The comparative rate of mutation has a strong influence on whether or not temperature regulation occurs [*Williams and Noble*, 2005]. If albedo mutates at a rate much slower than that of preferred growth temperature, then it is too slow to be effective in providing the varieties of daisy albedo needed to regulate the global temperature. However, if albedo mutates at a high enough rate compared to mutation of the growth function, regulation is restored. As the mutation rate of albedo relative to that of growth temperature is increased further, then a situation arises where sequential regulatory epochs occur, with regulation about successive growth temperatures (see Figure 10).

[73] *Wood et al.* [2006] also introduce selection on both albedo and growth temperature in a 2-D cellular automata model with space included explicitly. This may be thought of as a direct extension of the *von Bloh et al.* [1997] model introduced in section 3. If the daisies in this 2-D Daisyworld are allowed to evolve both optimal temperature and albedo, within some reasonable bounds, then the system follows a strongly oscillatory trajectory: Total population, mean temperature, and mean albedo all vary in time with a period of hundreds of daisy generations. The mechanism for this appears to be that for high-population size, cheats that inhibit regulation can prosper, causing a population collapse. In the subsequent low-population state, areas that are by chance free of cheats preferentially survive. These cheat-free areas then expand, restoring regulation to the point where cheats reemerge (see Figure 11). The so-called "cheats" emerge naturally in this system: They are, for example, dark daisies who evolve high preferred tempera-
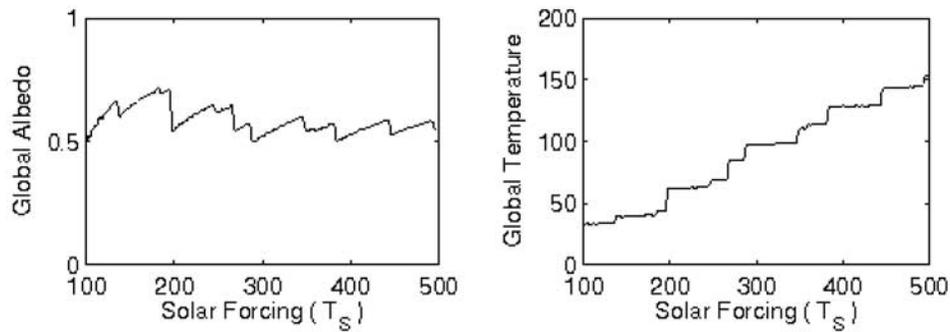
Figure 10. Plot of mean global albedo and temperature against solar forcing from model by *Williams and Noble* [2005]. When the rate of mutation of albedo is significantly greater than the rate of mutation of preferred growth temperature, sequential regulatory epochs occur during which the daisy ecology regulates temperature around a particular shared preference. Competitive exclusion prevents invasion by mutants with different preferences, until increasing luminosity eventually makes regulation impossible. At this point the ecology collapses, and new species invade, triggering the start of a new regulatory epoch based around a higher preferred growth temperature. Note that this model is fully stochastic and uses a different temperature scale than the original Daisyworld model and that in this scenario, there are no constraints on the temperatures that can potentially be adapted to. Reproduced from *Williams and Noble* [2005] with kind permission of Springer Science and Business Media.

ture. Although this degrades the environment, reducing growth rates of all daisies, the cheats obtain a relative advantage that is decisive, while growth is primarily determined by available space.

[74] Despite the internal oscillations, life persists across a range of insolation in this system. The oscillation period is determined by the heat capacity and daisy lifetime. It is speculated that the very clean oscillation arises from there being a single environment and a single species and that a more complex ecosystem/environment would lead to better regulation. The origin of this oscillation is the combination of both thermal diffusion, including a specific heat capacity, and the multiple-character adaptation. This model must therefore lead to a strong thermal decay kernel (equation (32)) sufficient to trigger the Hopf bifurcation that the spatial model alone is unable to do.

4.5. Altering the Feedbacks

[75] All the studies that we have discussed thus far have concentrated on the manner in which the daisies may adapt within the bounds of feedback loops defined in the original model. Another, less visited approach, is to alter the nature of the feedbacks in the model and see how this effects the evolution of the components of the system. This amounts to producing different special cases for the interaction (or not) between environmental effects at the individual scale and the global scale.

[76] *Watson and Lovelock* [1983] reversed the sign of interaction between daisy color and planetary temperature by assuming that convection generated over the warm spots of the black daisy clumps generates white clouds above them. In this case the black daisies are still locally warmer than the white daisies, but both daisy types now cool the planet. Hence the black daisies always have a selective advantage over their white compatriots, which they drive to extinction. Yet planetary temperature is still regulated, albeit on the cold side of the optimum for growth.

[77] *Staley* [2002] fundamentally alters the feedback loops in the system to demonstrate that environmental conditions and preferred optimal conditions are the stable solution of a Daisyworld-type system. The Daisyworld
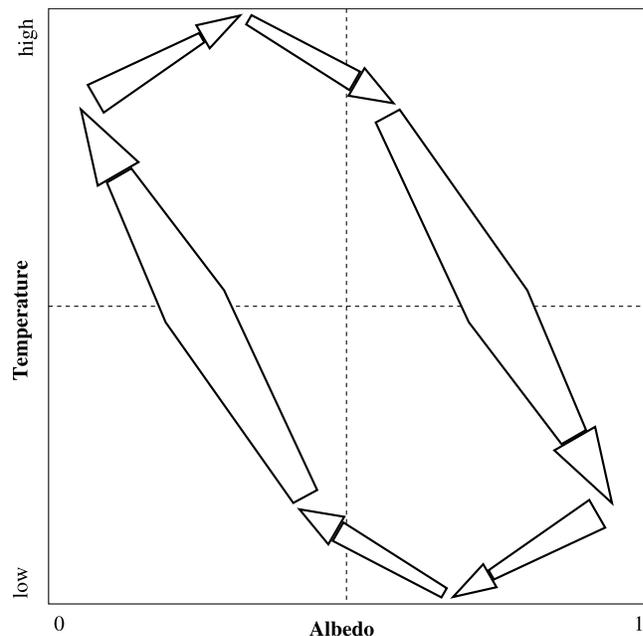
Figure 11. A schematic representation of the gene space and the "movement" around it from the model by *Wood et al.* [2006]. A given place on the plot is representative of the number of daisies with that combination of albedo and preferred temperature. The thickness of the arrows is a proxy for the amount of life on the planet at a given place in the cycle. The turning effect at the ends of oscillation is related to the decrease in life and the form of the bounded growth function. This internal cycling of the system is responsible for the surprisingly clean temperature oscillations seen in the time series of this model. Reprinted from *Wood et al.* [2006] with permission from Elsevier.

proposed by Staley has only a single daisy type, which he takes to be white (albedo $a_w = 0.75$) growing on a dark planet ($a_g = 0.25$). The planetary albedo is thus set by the proportion of the planet occupied by the daisies not by their relative populations. The limiting factor in the growth is no longer the competition for land, but it is competition for energy that is incident on the surface. The Malthusian growth rate is thus

$$\frac{\dot{x}}{x} = \kappa E(x)\left[1 - \left(\frac{T - T_0}{k}\right)^2\right] - \gamma, \qquad (42)$$

where κ and γ now give a measure of the growth and death of the planet's biota and the heritable characteristic is now purely T_0, the preferred temperature of the daisies. The energy $E(x)$ is given by the incident energy balance as before

$$E(x) = SL[1 - A(x)] = \sigma T^4. \qquad (43)$$

The fixed point solution of this model, where $T = T_0$, is proved to be a stable one. The model thus leads to a homeostatic state, provided the initial conditions are within a set of prescribed bounds and that the system is allowed to fully equilibrate.

[78] *Bardeen* [2004] uses a variable death rate, essentially an inverted copy of the birth rate function, in order to greatly strengthen the existing feedbacks in the model based on the spatial formulation of *von Bloh et al.* [1997]. This has a punitive effect when albedo mutation rates are low but actually increases the viability as the mutation rates increase. The greater selective pressure imposed by this formulation permits the system to more rapidly weed out daisies that are not adapting to the changing climate.

[79] An alternative extra feedback is through differential seeding strategies used by *Seto and Akagi* [2005]. Here the bare ground term given by WL, α_g, is replaced by a Monod function of the same quantity, $\mu(\alpha_g) = \mu_{max}\alpha_g/(\alpha_g + K)$. The Monod constants μ_{max} and K can now be used to parameterize alternative strategies of response to the amount of bare ground in the system. However, this model lacks local microclimates, i.e., has a single global temperature, and therefore the regulation reported can only be achieved in a narrow range of the seeding parameters. If heat transfer is reinstated, $q > 0$, then the effect of this feedback change is small.

5. ECOLOGY

[80] *Lotka* [1956, p. 16] proposed "that the physical laws governing evolution in all probability take on a simpler form when referred to the system (of organisms plus environment) as a whole than to any portion thereof." *Lovelock* [1986] reframed this in terms of an approach to ecological modeling, suggesting that the inclusion of environmental feedback will stabilize the whole system of environment plus populations. Subsequent work has shown that the tight coupling of plant growth to planetary temper-

ature in Daisyworld does indeed provide a stable framework upon which to build a theoretical ecology.

5.1. Nonspatial Examples

[81] Many daisy, rabbit, and fox types were first brought together by *Lovelock* [1992] to create a numerical model for biodiversity. The observation that only two daisy types can persist at equilibrium suggested that biodiversity may tend to decrease in a stable system. However, in the real world, biological systems are continually being perturbed by the cycles of day and night, the turn of the seasons, changes in the climate, and innumerable other factors. When a Daisyworld in equilibrium is perturbed by the introduction of a herbivore or a sudden change in solar input, a transient burst of different daisy types appears until the system restabilizes, with new types dominant. The greater the rate of change of the perturbation, the greater the resultant biodiversity. These results suggested that potential biodiversity is an essential resource for the response to perturbation, while expressed biodiversity is the sign of a perturbed system; hence the primary value of biodiversity may be its potential to regulate against environmental perturbations [*Lovelock*, 1992].

[82] The zero-dimensional "ecological Daisyworld" was subsequently developed to explore the implications of interorganism selection and food web structure for environmental self-regulation [*Harding and Lovelock*, 1996; *Harding*, 1999]. Initial work compared the effects of an unselective herbivore and three different types of selective herbivore that favor more abundant over less abundant daisies to varying degrees [*Harding and Lovelock*, 1996]. Frequency-dependant selection by the herbivores generates exploiter-mediated coexistence of the daisies and differing degrees of daisy biodiversity according to the precise herbivore feeding strategy. The system's temperature regulation trajectory depends subtly upon which daisies the herbivores allow to coexist. In contrast, when feedback to the environment is arbitrarily removed, regulation of both population dynamics and climate disappear [*Harding and Lovelock*, 1996].

[83] The food web was then elaborated by introducing the three types of selective herbivore together and experimenting with the introduction of a carnivore (which preys on all three herbivores) [*Harding*, 1999]. A measure of food web connectance, the number of herbivore types preying on each daisy type, was varied between only one (loosely connected) and all three (fully connected). Increasing food web connectance was found to increase system stability, contradicting the traditional result from modeling studies without feedback to the environment: that increasing complexity decreases stability [*Pimm*, 1984]. Adding a carnivore increases the stability of both population dynamics and climate regulation, and this too is the opposite result to that found in most models without feedback to the environment [*Harding*, 1999].

[84] Introducing direct interspecies competition in the original Daisyworld, by having the growth rate of a species decrease with increasing population size of the other spe-

cies, can also destabilize global temperature [*Cohen and Rich*, 2000] (extended by *Pujol et al.* [2005]). Strong direct interspecific competition tends to prevent coexistence of the black and white daisies, narrowing the range of luminosity over which there is a switch from black to white daisies and generating a corresponding sharp decline in temperature. This effect may be observed in the work of *Wood et al.* [2006] when mutation rates are low. In this case the gene pool is not well mixed, and multiple daisy phenotypes (i.e., daisies with different targets for regulation and different albedos) are able to persist in the population. Antagonistic interactions between these different and spatially separated phenotypes prevent effective regulation occurring. In the model of *Wood et al.* [2006] this effect is a transient state that may cause mortality of the entire system but may also evolve to the oscillatory steady state described in section 4.4.

5.2. Spatial Ecologies

[85] The effects of a herbivore have been studied in the two-dimensional Daisyworld by *von Bloh et al.* [1999]. These move randomly on the lattice, eating daisies and reproducing in a similar way to daisies. Species interact directly by ingestion of daisies and indirectly through temperature-dependent reproduction of herbivores. In this model, herbivores and daisies can coexist, and if the herbivores have no albedo effect, this can inhibit regulation by reducing the total daisy population. The combination of herbivores and fragmentation produces four distinct regimes, conveniently parameterized by herbivore death rate. Three are simple: For high death rates the herbivores become extinct or coexist with daisies at a low level controlled by their death rate. For low death rate, overgrazing causes ecological collapse. For a combination of intermediate death rate and fragmentation (below percolation) the herbivore population increases with increased death rate. This is because herbivore population is controlled by food supply, and in a complex environment, overgrazing impairs regulation, which produces additional negative effects by raising the ambient temperature. Thus, in the fragmenting spatial Daisyworld, herbivores tend to destabilize the system if they can persist. However, their effects on an unfragmented system are much less significant.

[86] Two identical, evolving species of daisy competing for finite space cannot coexist indefinitely. If such a system is created, the difference in population between the two follows a random walk until one population is reduced to zero. Thus coexisting multiple species must have different characteristics. M. A. Clark and G. J. Ackland (unpublished work, 2002, mentioned briefly by *Ackland et al.* [2003]) introduced a second plant species (poppies) that had the possibility of evolving the ability to feed on the daisies in return for a growth penalty. No stable two-species solution exists for this model: Either the growth penalty was too large and the poppies became extinct, or it was too small and the poppies evolved herbivory, ate all the daisies, and then evolved back to being simple plants. This showed that an evolvable ability, even if unexpressed in steady state, can reduce regulation.

[87] *Ackland* [2004] introduced a second evolving plant species (trees) in 2-D Daisyworld with a lower optimal temperature and no competition for space. This increases the range of regulation in a way analogous to the multispecies model [*Lenton and Lovelock*, 2001]. With a small difference in optimal temperatures, coexistence occurs with temperature regulated at a compromise value throughout. With a larger difference the space fragments into cool regions of trees and warm regions of daisies. *Ackland* [2004] argues that as in one dimension the stability of single species versus coexistence solutions depends on which maximizes the amount of life. The coexistence solutions have unusual albedo distributions, trees being strongly biased toward higher albedo and daisies biased to lower albedo. The overall regulation in the system arises from the balance in competition between the species rather than symbiotic cooperation.

[88] Complex dynamics also emerges when differing daisy phenotypes are induced by a growth function with multiple maxima [*Lynn*, 2005] in a two-dimensional spatial model. The system does not simply select the maxima with the largest value: Lower, broader peaks often outcompete narrower higher ones. Interfacial effects between the competing regions dominate the dynamics in the resulting model and inhibit the ability of the model to consistently find the seemingly optimal solution.

[89] In general, increasing the complexity of the ecology in Daisyworld seems to make little difference to the fundamental behavior of the model. Given the notorious instability of interacting populations in most conventional community ecology models [*Pimm*, 1991], the number of populations that can be simultaneously supported in a regulating Daisyworld is remarkable. This situation was an early illustration of how feedback loops may stabilize ecological models of increasing complexity [see, e.g., *Ackland and Gallagher*, 2004]; the Daisyworld case appears to be sufficient but not necessary for inducing ecological stability. In Daisyworlds though, the primary source of system stability remains the coupling between daisies (representing biota) and planetary temperature (representing the environment). Within a model of many interacting species the mathematical distinction between a "well-connected species" and "the environment" is moot: The necessity of stabilization by feedbacks is common to the two models.

6. APPLICATIONS

6.1. Maximum Entropy Production (MEP) and Daisyworld

[90] The method of parameterizing heat flow in the original Daisyworld model (the mechanism by which heat moves from the black daisies into the bare ground and then into the white daisies) is similar to that employed in energy balance climate models [e.g., *North et al.*, 1981]. The temperature difference between the black, white daisies, and the bare ground is determined by the difference in albedo and the diffusivity of the atmosphere. The actual mechanisms for heat transport in the climate system are

more complex as they involve turbulent eddies in the atmosphere and ocean.

[91] *Paltridge* [1975] successfully reproduced the Earth's latitudinal temperature profile in an energy balance climate model by assuming that the rate of diffusion was that which maximized the rate of entropy production via latitudinal heat transport. The maximum entropy production principle (MEPP) postulates that nonequilibrium, open dissipative systems (that exchange energy with their environment) such as the Earth's climate may be in states that maximize the rate of entropy production [*Ozawa et al.*, 2003]. If this is true, it is not necessary to understand the detailed internal dynamics of such systems in order to make accurate models and predictions.

[92] *Pujol* [2002] assumes MEPP to be valid and explores implications for Daisyworld. One of the constraints operating on the system is that the short-wave energy from the star that enters and is redistributed within Daisyworld must ultimately leave as long-wave emissions. *Pujol* [2002] formulates the energy balance equations thus:

$$\alpha_i \sigma T_i^4 = \alpha_i SL(1 - A_i) + Q_i \tag{44}$$

for $i = w$, and b, and g.

$$Q_w + Q_g + Q_g = 0. \tag{45}$$

There is an infinite set of possible heat flows Q_i that will satisfy equation (29). Pujol adopts those heat flows that will maximize the rate of nonradiative entropy production, which is the sum of heat flows divided by temperatures:

$$\mathcal{E}P = \sum_i \frac{Q_i}{T_i} \tag{46}$$

for $i = w$, b, and g. Following *Watson and Lovelock* [1983], Pujol formulates heat flow with the following:

$$Q_i = \alpha_i(\sigma q - S)(A - A_i) \tag{47}$$

for $i = w$, b. The albedo of the daisies is fixed for any value of solar forcing. As given by *Watson and Lovelock* [1983], q is regarded as a fixed parameter. Consequently, in order to maximize entropy production it is the coverage of the daisies that must adjust.

[93] In this MEPP Daisyworld the daisies are present over a wider range of solar luminosities, and hysteresis is no longer observed; there is no sudden initial population explosion of the black daisies or final population collapse of the white daisies. Instead, there is a progressive decline in the white daisy population (at the upper limit of regulation) and consequently an absence of observed hysteresis in the model. The same principle applies with low luminosity and the onset of black daisy growth. The key result is that heat flows that maximize the rate of entropy production also maximize the range of solar insolation over which the daisies grow. Furthermore, in the original Daisy-world the temperature of the planet decreases in response to increasing insolation (equation (21)) when both daisy types are present. In the MEPP Daisyworld the planetary temperature increases slightly and is regulated within a narrower range.

[94] *Toniazzo et al.* [2004] present a more general formulation that allows for an arbitrary number of daisy types. It begins with the reformulation of the equations (3) and (4) that determines the rate of change of daisy coverage with the following:

$$b_i \theta_i = \phi, \tag{48}$$

where $b_i = \beta_i/\gamma_i$ is the normalized growth and $\theta_i = T_i/T_{o,i}$, with $T_{o,i}$ being the optimum growth temperature for the ith daisy type. Here $\phi = 1/(1 - \Sigma_i \alpha_i)$ and is the inverse of the amount of bare ground. The temperature of the ith daisy type can then be found with

$$T_i = T_{o,i} b_i^{-1}(\phi). \tag{49}$$

[95] As given by *Pujol* [2002], heat flow is a function of daisy coverage, solar insolation, and albedo. The calculation for entropy production is essentially equivalent to equation (30), both approaches being effectively identical to the technique used to determine entropy production via meridional heat transport by *Lorenz et al.* [2001] and *Lorenz* [2002]. The core finding is similar to *Pujol* [2002] in that when heat flows are adjusted in order to maximize entropy production, the range of daisy growth over luminosity is increased.

[96] *Toniazzo et al.* [2004] explore the effects of the MEPP with an increased number of daisy types. It is shown that the MEPP solution only favors a maximum of two daisy types coexisting. These daisy types will have maximum daisy albedo contrast. This leads to the counterintuitive situation where the temperature of an intermediate albedo daisy that would be at the optimum and so have maximum birth rate is not present at all. The intermediate daisy would exchange little heat with its surroundings, and so lower rates of entropy production would be realized, whereas the case with darker (warmer) and lighter (cooler) daisy types operating as a piecewise two-species system is able to produce much higher rates of heat flow and so entropy production.

[97] Furthermore, the optimum growth rate for a two-daisy system can be altered so that the optimum growth temperatures for the dark and light daisy types are different. Solutions are presented in which dark-colored daisies are warm-loving and light-colored daisies are cool-loving and also where dark daisies are cool-loving and light daisies are warm-loving. It is found that greatest entropy production is achieved with a combination of dark warm-loving and light cool-loving daisies, as this represents the coupling of two positive feedback mechanisms. In a rein control context (section 2.4), MEPP selects the strongest reins that provide the greatest heat flux and greatest rates of entropy production.

[98] Rates of entropy production in a 2-D cellular automata Daisyworld were assessed by *Ackland* [2004] in which thermal entropy production, $\mathcal{EP}$ is found with

$$
\begin{aligned}
\mathcal{EP}(t) &= \sum \frac{\Delta Q}{T} \\
&= \sum_j \sum_k \frac{D_T \left[T(x_j, y_j, t) - T(x_k, y_k, t) \right]}{2T(x_j, y_j, t)}
\end{aligned}
\tag{50}
$$

for each jth cell and its eight kth neighbors. Owing to the fixed thermal diffusivity in the model, thermal entropy production is assessed by subjecting the system to an abrupt forcing in luminosity. If MEPP holds, the perturbation should lead to the thermal entropy production increasing as it seeks to find the new maximum value. This may or may not be proceeded by a relative drop immediately after the abrupt change. This effect is not seen, suggesting that the 2-D Daisyworld does not maximize the rate of thermal entropy production.

[99] The work in this area emphasizes both the generality and simplicity of the Daisyworld model and its ability to be used as a starting point for studies of different phenomena. Though rigorous analysis [*Dewar*, 2003, 2004] implies that Daisyworld, with is varying input fluxes, violates the assumptions of MEPP, the modeling in this section provided useful insights into the ongoing development of this novel hypothesis.

6.2. Alternative Maximization Principles

[100] Instead of assuming MEP, *Ackland* [2004] formulates and tests the following contrary hypotheses: (1) that Daisyworld self-organizes to maximize the rate of entropy production and (2) that Daisyworld self-organizes in order to maximize the amount of life on the planet. Two types of entropy production are defined: biodiversity and thermal entropy production. A related study by *Gaucherel* [2006] uses the exergy principle from ecology as well as the MEP hypothesis to focus attention on the spatial patterns in a cellular automata Daisyworld [*Lenton and van Oijen*, 2002].

[101] *Ackland et al.* [2003] formulates biodiversity entropy $N_A \ln N_A$ as a measure of the information entropy of the distribution of black and white daisies upon the surface of the 2-D planet, where N_A is the number of daisies with albedo A. Maximizing this gives the mean ensemble distribution

$$
\langle N_A \rangle = \frac{Ne^{\beta A}}{\int_0^1 e^{\beta A} dA},
\tag{51}
$$

with N being the total number of daisies and β found with

$$
\langle A \rangle = \int_0^1 e^{\beta A} dA = \int_0^1 A e^{\beta A} dA.
\tag{52}
$$

[102] *Ackland* [2004] extends this formulation to consider biodiversity entropy production. In order to assess whether Daisyworld self-organizes to maximize biodiversity entropy or, alternatively self-organizes to maximize the coverage of

daisies, the fixed death rate is changed to a function of daisy temperature with the temperature that gives the minimal death rate (T_d) different from the temperature that gives the maximal growth rate (T_g). The MEPP predicts that biodiversity entropy be produced at the greatest possible rate thus requiring the greatest growth rate and hence T_g, whereas the maximization of life requires the minimization of the death of the daisies and hence T_d. Ackland finds that the temperature is regulated close to T_d and hence concludes that maximum life (rather than MEPP) applies to Daisyworld.

[103] In the work of WL the coexistence region becomes unstable with respect to the single-daisy solution at exactly the point where the single-daisy solution produces more daisies than the total for the coexistence. If one adds additional (discrete) daisy colors to the WL model (*Ackland* [2004], following *Lenton and Lovelock* [2000]), the equilibrium solution alternates between single-daisy and two-daisy solutions, with the stable solution being the one that has most daisies, other solutions being vulnerable to invasion (Figure 9). A similar effect can also been seen in more complex models where species with two distinct optimal temperatures are able to coexist [*Ackland*, 2004]. Here two qualitatively different solutions were observed, coexistence at a compromise temperature or separation into single-species regions at their optimal temperature, but the stable solution was the one where the total area covered by daisies was the largest.

6.3. Daisyworld as a Control System

[104] The rein control mechanism inherent in Daisyworld has begun to find diverse applications both in understanding other self-regulating systems and in engineering new ones. *Saunders et al.* [1998], *Koeslag et al.* [1999], and *Saunders et al.* [2000] argue that the regulation of some human physiological variables are analogous to Daisyworld. To understand blood glucose regulation, the black and white daisies are replaced by the hormones insulin and glucagon, which "pull" in opposing directions the shared variable of blood glucose, which replaces planetary temperature. This analysis allows *Saunders et al.* [1998] to predict salient features of type I and type II diabetes, with these conditions representing either a single or both control reins malfunctioning. *Saunders et al.* [2000] extend this analysis into a more general model in which the same mechanism is used to model the control of ionized calcium by parathyroid hormone and calcitonin.

[105] Many engineering problems demand an effective self-regulator, and Daisyworld has been applied to such problems in both information technology and robotics. *Dyke and Harvey* [2005] embed a Daisyworld control system into a simulated robotic agent. A novel "cable car" is developed, which performs phototaxis (light-following behavior) [*Braitenberg*, 1984]. A solar panel on top of the car provided power in response to the location of a light source that moved overhead. Output from the solar panel is used to turn a winding motor that moves the car to the left. Another car is added, being identical to the first except its winding motor moves in the opposite direction and so the car moves

to the right. When the two cable cars are connected together via a spring, the reproduction of the simplified "two-bed" Daisyworld model introduced by *Harvey* [2004] is completed, and the cable cars are able to track a light source over a range of positions just as the daisies maintain global temperature to within a narrow band over a range of luminosities.

6.4. Vegetation Modeling With Hydrology

[106] *Baldocchi et al.* [2005] have created a rather different 2-D Daisyworld by introducing wet and dry "daisies" with an additional property of surface resistance and including latent and sensible heat exchange in the vertical energy balance. They exclude horizontal heat transport on the grounds that vertical heat exchange dominates in their system of interest (savannahs). The air temperature is fixed, thus altering the focus of the model from environmental regulation to the scaling up of heterogeneous landscape properties. The model uses a Gaussian growth response to temperature, makes probability of death an exponential function of temperature, and introduces density-dependent death (an occupied cell dies if all neighboring cells are occupied). The wet and dry "daisy" types have identical albedos and are distinguished by their low (wet) or high (dry) surface resistances. The wet "daisies" are analogous to trees, and the dry "daisies" are analogous to grasses. Bare soil has higher albedo and surface resistance than either plant type. *Baldocchi et al.* [2005] experiment with random seeding and regeneration of an empty grid from clusters in opposite corners (analogous to recolonization after disturbance by, e.g., fire). In the latter case the resulting system resembles a savannah in its scaling exponent for surface properties.

6.5. Beyond Daisyworld

[107] Daisyworld successfully shows how self-regulation might emerge, but the assumptions highlighted throughout this text mean that the model is not generally applicable. For those important scientific questions it cannot address, new models are required. These should vary the underlying assumptions of the Daisyworld model to a greater extent than just tweaking parameters or altering the sign of a particular feedback. However, more than 2 decades after the formulation of Daisyworld, few truly alternative models have appeared.

[108] The Guild model of *Downing and Zvirinsky* [1999] [see also *Downing*, 2003] simulates the evolutionary emergence of a bacterial community and the recycling of a suite of nutrients. The world has prescribed inputs and outputs of nutrients in arbitrary ratios and is seeded with a single bacterial genotype that specifies the phenotypic nutrient consumption pattern. New genotypes, constrained within a large genetic space, arise through mutation and crossover during bacterial reproduction, as defined by a genetic algorithm. What emerges is a system that recycles different nutrients by different amounts such that their ratio tends toward the preference of the organisms. The Guild model differs from Daisyworld in its emphasis on nutrient cycling

rather than temperature regulation and in its improved representation of evolution. However, the two models still share key underlying assumptions. Organisms still maintain a local buffer against the global environment, and individual "selfish" adaptations still always contribute to global regulation. All organisms are also assumed to have the same constant preferred nutrient ratios. When these ratios are allowed to evolve, they do so toward current conditions, thus inhibiting regulation.

[109] The GUILD model chemistry also lacks thermodynamic constraints. The subsequent metabolically abstract microorganism system model (METAMIC) addressed this by introducing an abstract chemistry with sensible thermodynamics [*Downing*, 2002, 2003]. The organism is treated as a cell in which energy-yielding and energy-demanding reactions occur and which exchanges materials with the environment by diffusion through the cell wall. Hence there is still a (realistic) distinction between the local (intracellular) and the global (surrounding) environment. The organisms' preference is defined (arbitrarily) in terms of a combination of the concentrations of the four smallest chemical compounds. Thermodynamic constraints result in a natural set of metabolic pathways. Only in 20 out of 100 cases is there a strong tendency toward global regulation, which occurs when the benefits outweigh the costs. This is not entirely surprising as the model system only has a restricted source of free energy in the form of large incoming chemical compounds that can be broken down into smaller ones. There is no large source of free energy analogous to sunlight being captured in photosynthesis. Hence there is never much free energy with which regulatory acts could be performed, and thus the model system only represents an early stage in the history of life and a minority of today's ecosystems.

7. DISCUSSION

[110] Daisyworld was originally conceived as a parable, a workable example that demonstrated that global regulation was possible because of underlying interactions of a biosphere. More specifically, Daisyworld was set up to show that regulation of the environment could in theory arise without top-down control or teleology. In this respect the model can be described as a success. Although there are many simplifications and assumptions inherent in the model, the body of published work that has since tested its limitations and explored various extensions to it has found regulation in Daisyworld to be a robust phenomenon. However, some assumptions in the model are not necessarily widely applicable in the real world.

[111] Daisyworld contains a fixed relationship between local benefit and global regulation, whereby the only phenotypic daisy traits that give reproductive success are those that also contribute to global regulation. Thus black daisies do well in cooler conditions and by doing so contribute to raising of the temperature of the planet. White daisies do well in warmer conditions and cool the planet. Where are the daisies that do well in cool conditions and

make the planet cooler or those that do well in warm conditions and make the planet warmer? This kind of positive niche construction effect is often observed in nature [*Odling-Smee et al.*, 1996]. Existing variants of the model give a limited glimpse at these other special cases as discussed in section 4.

[112] In the real world, traits of organisms that alter the global environment are often selected because they offer a local advantage unrelated to their global effect. The global effect is essentially a by-product of the local effect, as in the case of marine algae, which produce and utilize dimethyl sulphide probably for the benefit it gives them in resisting adverse osmotic pressure, irrespective of the effect it has on the global sulphur cycle [*Charlson et al.*, 1987]. In Daisyworld we might imagine local selection acting on some hidden aspect of the daisies such as leaf area or seed dispersal, rendering the environment-altering daisy trait selectively neutral (barring any epistatic gene interactions). This was studied by *Williams* [2006] where daisy albedo was made selectively neutral by using random selection between individuals to decide which daisy species colonized bare patches; unsurprisingly, no regulation of global temperature was observed, since there was no selection pressure to push mean albedo away from a neutral "grey" color, and this prevented an adaptive ecological response to different levels of solar luminosity. *Staley* [2002] also addresses the separation of local and global effects by removing any local environmental effect of the daisies, but he considers only one global environmental effect (equivalent to that of white daisies) with adaptation of optimum growth temperature, and regulation is retained. A more complete approach would consider different global environmental effects decoupled from local selection.

[113] Another key assumption of the Daisyworld model is that daisies always grow in patches large enough to create their own microclimate. This assumption is held throughout the Daisyworld literature and is taken to apply even when populations are vanishingly small (such as when the first black daisy seeds break their dormancy as the planet warms). The importance of the assumption of localized microclimates lies in the ability of different colored daisies to maintain a local temperature that deviates from the ambient abiotic level. Whatever their effect on the global climate, if a daisy species cannot create a local temperature that differs from the global temperature, they have no way of outcompeting other species. Without this competition (and the ecological balance it creates), global temperature regulation will fail.

[114] In Daisyworld the absence of a local microclimate can be represented in the WL model by setting $q = 0$, while in the work of *Ackland et al.* [2003] and *Williams* [2006] (physically unrealistic) models can be created where heat dissipation is perfect and instantaneous, that is, any local temperature gradient created by a daisy is dissipated across the whole planet before any effects on local growth rates are experienced. In this scenario the entire surface of the planet has the same temperature, although the global temperature may be altered by daisy albedo. The homogeneity of

growing conditions thus created removes the ability for selection to act on the daisy population, and the regulatory action of the daisy population is lost. Similarly, if the *von Bloh et al.* [1997] 2-D model is applied with random seed dispersal, the offspring are unlikely to have the same environment as their parents, and regulation fails. However, in a separate study [*Nordstrom et al.*, 2004] the assumption of perfect local homeostasis of temperature has been replaced with a more Earth-like formulation of energy balance, and global temperature regulation is retained.

[115] Such assumptions are examples of the general assumption of a particular kind of structure to the feedback between daisies and their environment. It appears that when this structure is perturbed as described above, the result is a loss of global temperature regulation in the Daisyworld system. However, other kinds of perturbation to the feedback structure of the model do not destroy regulation, though they may change its nature (see the discussion of *Watson and Lovelock* [1983] and *Staley* [2002] in section 4.5). The rein control analogy, antagonistic or otherwise, provides a useful visualization of the feedback structure. In systems with continuous phenotype, where the rein control analogy is less apt, the link to population genetics provides a different route to understanding and hopefully a greater acceptance of the model in mainstream theoretical biology.

[116] One way of interpreting the dynamics of the different Daisyworld models is as the interplay of processes occurring on three different timescales, i.e., the external driving (τ_D), the population dynamics (τ_P), and evolution (τ_E). In the work of WL, $\tau_D \gg \tau_P$ and $\tau_E \to \infty$. Hence the environment is regulated by changes in the populations. In subsequent criticisms of Daisyworld, finite τ_E of the inherited characteristics are considered. Typically, the direct evolution of the biota to suit the external conditions is found rather that the indirect regulation of the environment to suit the biota. Most models have a single stable state for given external driving, so short-lived spikes in the driving ($\tau_D \ll \tau_P$) that return to the initial driving cause a temporary change in populations and evolvable characteristic. If $\tau_D < \tau_P \tau_E$, then the system can never reach a stable state, and behavior is entirely dependent on initial conditions.

[117] Daisyworld is a model that is complex enough to exhibit interesting behavior yet simple enough to admit analytic work. This has positioned the model as a starting point for further studies of many different aspects of geophysics, of which we have covered the majority (to date) in this article. We hope that this trend will continue; one research area where Daisyworld may be relevant is understanding how the changing biosphere may be incorporated into more detailed models of the physical environment and ultimately into Earth system models. Changes in population, such as desertification or afforestation, can happen relatively quickly on a geological timescale. Additionally, even processes thought to be independent of the biota on long timescales, most obviously, silicate rock weathering [*Walker et al.*, 1981], are now believed to be heavily influenced and mediated by biota [*Lovelock and Watson*, 1982; *Schwartzman and Volk*, 1989].

[118] Evolutionary timescales may also be important in understanding the interaction between the biota and the physical world; after all, microbes account for around half the biomass on our planet and have short turnover times. Recent work has indicated that they contribute disproportionately to the cycling of abiotic compounds, increasing their relative environmental impact further still [*Volk*, 1998]. The control of the environment by life is now a central principle for practical work in astrobiology where Daisyworld has attracted attention; if atmospheric composition on extrasolar planets is found to be out of equilibrium, this can be taken as a surrogate measurement for the presence of life [*Lovelock*, 1965, 1975]. This suggests that remote atmospheric analysis is (the only?) a practical method for detecting extraterrestrial life.

[119] In this article we have reviewed and described Daisyworld and the numerous extensions and critiques that have been leveled at it in the 20 or more years since its inception. The existence of detailed analytic solutions backed by comprehensive modeling work has now led to a concrete body of scientific research that may now be viewed as a topic in its own right. There are still a few details of the regulatory effects and feedback structures of the Daisyworld model that warrant ongoing attention, but the primary facets of the model are now well understood. Yet to truly examine the plausibility of global regulation by the biota, which was the greater question that inspired the creation of the original Daisyworld model, we need models and theoretical results that show the occurrence (or not) of biologically mediated environmental regulation in a variety of scenarios with a variety of feedback structures. The creation of new models that challenge the fundamental assumptions of Daisyworld is surely a pressing and potentially revealing direction for future research.

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