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Biological homeostasis of the global environment: the parable of Daisyworld

By ANDREW J. WATSON, *Marine Biological Association, The Laboratory, Citadel Hill, Plymouth PL1 2PB, England and* JAMES E. LOVELOCK, *Coombe Mill, St. Giles on the Heath, Launceston, Cornwall PL15 9RY, England*

ABSTRACT

The biota have effected profound changes on the environment of the surface of the earth. At the same time, that environment has imposed constraints on the biota, so that life and the environment may be considered as two parts of a coupled system. Unfortunately, the system is too complex and too little known for us to model it adequately. To investigate the properties which this close-coupling might confer on the system, we chose to develop a model of an imaginary planet having a very simple biosphere. It consisted of just two species of daisy of different colours and was first described by Lovelock (1982). The growth rate of the daisies depends on only one environmental variable, temperature, which the daisies in turn modify because they absorb different amounts of radiation. Regardless of the details of the interaction, the effect of the daisies is to stabilize the temperature. The result arises because of the peaked shape of the growth-temperature curve and is independent of the mechanics by which the biota are assumed to modify the temperature. We sketch out the elements of a biological feedback system which might help regulate the temperature of the earth.

1. Introduction

On earth, modification of the environment by living things is apparent on any scale that one cares to look at, up to and including the global scale. In turn, geophysical and geochemical constraints have shaped the evolution of life and continue to dictate what type of life, and how much of it, can colonize the available space. One can think of the biota and their environment as two elements of a closely-coupled system: perturbations of one will affect the other and this may in turn feed back on the original change. The feedback may tend either to enhance or to diminish the initial perturbation, depending on whether its sign is positive or negative.

If we wish to explore the properties which this close-coupling may confer on the system, we at once come upon a substantial problem: the earth's biota and environment are vastly complex and there is hardly a single aspect of their interaction which can as yet be described with any confidence by a mathematical equation. For this reason we

have chosen to study an artificial world, having a very simple biota which is specifically designed to display the characteristic in which we are interested—namely, close-coupling of the biota and the global environment. By simplifying our biosphere enormously we can describe it in terms of a few equations borrowed directly from population ecology theory. But let the reader be warned in advance: we are not trying to model the Earth, but rather a fictional world which displays clearly a property which we believe is important for the Earth.

2. The equations for Daisyworld

Daisyworld is a cloudless planet with a negligible atmospheric greenhouse on which the only plants are two species of daisy of different colours. One species is dark—ground covered by it reflects less light then bare ground—while the other is light and reflects more than the bare ground. To emphasize

the contrast we will refer to them as "black" and "white" though the black daisies need not be perfectly black, nor the white ones perfectly white.

The comparative growth of the daisies is governed by (see Carter and Prince, 1981)

$$da_w/dt = \alpha_w(x\beta - \gamma) \tag{1}$$
$$da_b/dt = \alpha_b(x\beta - \gamma),$$

where α_b, α_w are the areas covered by "black" and "white" daisies respectively and x is the area of fertile ground not covered by either species, all measured as fractions of the total planetary area. The growth rate of the daisies is β per unit of time and area, and the death rate is γ per unit of time. The area of fertile ground which is uncolonized by daisies is

$$x = p - \alpha_b - \alpha_w, \tag{2}$$

where P is the proportion of the planet's area which is fertile ground.

The growth rate of the daisies is assumed to be a parabolic function of local temperature, T_1:

$$\beta_1 = 1 - 0.003265 (22.5 - T_1)^2 \tag{3}$$

which is zero when the local temperature T_1 is 5 °C and 40 °C and has a maximum value of one when T_1 equals 22.5 °C. The effective temperature at which the planet radiates, T_e °C, is found by equating absorbed and emitted radiation:

$$\sigma(T_e + 273)^4 = SL (1 - A). \tag{4}$$

Here σ is Stefan's constant, S is a constant having units of flux, L is a dimensionless measure of the luminosity of daisyworld's sun and A is the albedo of the planet. For simplicity we shall ignore spherical geometry and treat the planet as if it were flat, or at best cylindrical. Then the albedo A is simply determined by

$$A = \alpha_g A_g + \alpha_b A_b + \alpha_w A_w = \sum_1 A_1, \tag{5}$$

where α_g ($= 1 - \alpha_w - \alpha_b$) is the area, and A_g the albedo, of bare ground. A_b and A_w are the albedos of ground covered by "black" and "white" daisies, and we will assume that $A_w > A_g > A_b$ with values typically 0.75, 0.5 and 0.25. $\sum_1$ in eq. (5) signifies a summation over bare ground, black daisies and white daisies.

Finally, we wish to fix the local temperature of the daisies in terms of variables which have already been defined. Since black daisies absorb more

radiation than white; we assume they will be warmer. If we use the expression

$$(T_1 + 273)^4 = q(A - A_1) + (T_e + 273)^4, \tag{6}$$

where q is a positive constant, to calculate local temperatures as functions of local albedo, we find that $T_b > T_g > T_w$ as we would expect. This expression also preserves the energy balance of the planet, for F, the total radiation lost to space, must be the sum of that arising from each area:

$$F = \sum_1 \alpha_1 \sigma(T_1 + 273)^4$$

$$= \sigma q A \sum_1 \alpha_1 - \sigma q \sum_1 (\alpha_1 A_1) + \sigma(T_e + 273)^4 \sum_1 \alpha_1,$$

but since $\sum_1 \alpha_1 = 1$ and $\sum_1 \alpha_1 A_1 = A$,

$$F = \sigma(T_e + 273)^4,$$

as it must do for consistency with eq. (4). Since the local temperatures of black and white daisies always lie within a range 22.5 ± 17.5 °C which is small by comparison to the absolute temperature, we may if we prefer use a linear approximation to eq. (6):

$$T_{b,w} = q'(A - A_{b,w}) + T_e \tag{7}$$

where $q' = q/4 (273 + 22.5)^3$. The error introduced by this approximation is normally less than 2 °C for the temperatures of interest.

In eq. (6), the parameter q expresses the degree to which solar energy, after having been absorbed by the planet, is redistributed amongst the three types of surface. Its effect is most clearly seen if A is eliminated between eq. (4) and (6):

$$(T_1 + 273)^4 = q(1 - A_1) + (T_e + 173)^4 \times (1 - q\sigma/SL). \tag{8}$$

Now if $q = 0$, the local temperatures all become equal to the mean temperature. This situation corresponds to perfect "conduction" of energy from higher to lower temperatures. If on the other hand we set $q = SL/\sigma$, we obtain:

$$(T_1 + 273)^4 = \frac{SL}{\sigma} (1 - A_1) \tag{9}$$

In this case temperatures are set by the steady state between local absorption and local radiation to space, with perfect "insulation" between high and low temperature regions on the surface. A value of

q greater than SL/σ would be physically very suspect since it would imply a transfer of heat against the temperature gradient. In this study we used values of q less than $0.2\ SL/\sigma$.

3. Steady state behaviour of the system

The daisyworld equations form a system of non-linear, multiple feedback loops. The analysis of such systems is not a trivial problem, even for the highly simplified situation on daisyworld. Some information on the steady state behaviour of the equations can, however, be obtained without a disproportionate amount of mathematical effort.

Consider the non-zero, steady state solutions of eq. (1). When $d\alpha/dt$ is zero but α is finite,

$$x^* \beta^* = \gamma, \tag{10}$$

where the asterisks denote the steady state.

The growth parameters for both black and white daisies must satisfy this equation: it follows that

$$\beta_w^* = \beta_b^*. \tag{11}$$

Now, bearing in mind that $T_b > T_w$, it can be seen by inspection of eq. (3) that for this to be true,

$$T_b^* - 22.5 = 22.5 - T_w^*. \tag{12}$$

Furthermore, subtracting eq. (7) for T_b from that for T_w

$$T_b^* - T_w^* = q'(A_w - A_b). \tag{13}$$

Hence

$$T_b^* = 22.5 + \tfrac{1}{2}q'(A_w - A_b) \tag{14}$$

$$T_w^* = 22.5 - \tfrac{1}{2}q'(A_w - A_b),$$

so, assuming that a stable steady state with $\alpha_w > 0$, $\alpha_b > 0$ exists, T_b^* and T_w^* will be constant regardless of the initial conditions. Therefore, given sufficient time to return to the steady state, the daisies will respond to a perturbation by restoring their local temperatures to prefixed values, despite the fact that no physically real reference temperature exists within the system.

It is possible to prove by further analysis that this steady state exists and is stable for a wide range of parameter values. Here we will content ourselves with using a computer to integrate the equations to steady state for a few specific cases.

However, before abandoning the formal analysis entirely, there is one further, rather surprising feature of the steady state which can easily be proved: we can show that the steady state planetary temperature T_e^* will actually *decrease* in response to an *increase* in solar luminosity, as follows. Differentiation of eq. (8) with respect to L when T_1 is constant gives

$$4(T_e^* + 273)^3 \frac{dT_e^*}{dL}\left(1 - \frac{q\sigma}{SL}\right)$$

$$+ (T_e^* + 273)^4 \frac{q\sigma}{SL^2} = 0$$

or

$$dT_e^*/dL = \frac{-q\sigma(T_e^* + 273)}{4SL^2(1 - q\sigma/SL)},$$

which must be negative provided $q < SL/\sigma$.

Figs. 1a, b, c, d show steady state values of planetary temperature, T_e and areas of black and white daisies α_b and α_w, as the luminosity L is increased. For comparison, the dotted curves show the temperature of the planet without life. The values of the parameters adopted are given in the figure legends. The procedure used to generate the curves was as follows: for a fixed value of L, initial values of α_b, α_w were set at the previous steady state values, or 0.01 if these were zero; the equations were integrated forward in time until a steady state was reached; the value of L was incremented and the procedure was repeated. Thus the curves show the effect of increasing the luminosity slowly, so that the system has time to reach steady state at each value of L. The effect of decreasing the luminosity is not necessarily identical to that of increasing it, for the system may exhibit hysteresis. Fig. 1c shows an example.

Fig. 1a shows the response for one species of daisy only, where the daisy albedo is the same as the ground. This represents the "no feedback" case where the presence or absence of daisies makes no difference to the temperature. In Fig. 1b, black daisies only are allowed to grow. It is apparent that even for this one-species case, the homeostasis of the planetary temperature may be considerable. Fig. 1c shows the response with white daisies only, for both increasing and decreasing luminosity. Fig. 1d illustrates the behaviour of the complete model. This exhibits the expected stable region where the
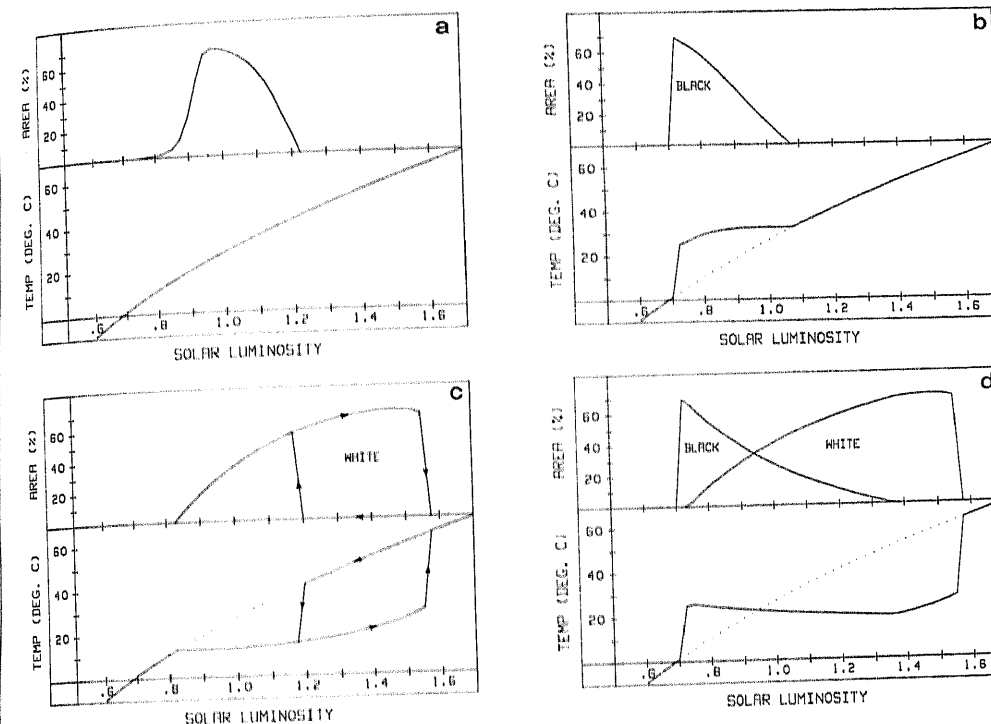
Fig. 1. Steady state responses of daisyworld. Areas of black and white daisies and effective temperature are plotted against increasing values of the luminosity parameter L. Dotted lines indicate the temperature of the planet without life. Fixed parameters used in generating these curves were: γ in eq. (1), 0.3; P in eq. (2), 1.0; S in eq. (4), 9.17×10^5 ergs cm^{-2} s^{-1}; albedo of bare ground, 0.5; q' in eq. (7), 20. (a) For a population of "neutral" daisies, albedo 0.5 (dotted and solid temperature curves are coincident). (b) For a population only of black daisies, albedo 0.25. (c) For a population only of white daisies, albedo = 0.75. This figure also shows that the effect of decreasing luminosity. Note that the system exhibits hysteresis. (d) For a population of both black and white daisies, albedos 0.75, 0.25.

two species of daisy co-exist and verifies our prediction of a decrease in effective temperature with increasing luminosity.

Before leaving this version of daisyworld it is worth mentioning the effect of taking more explicit account of spherical geometry. On a real planet, the effective value of the solar constant decreases with increasing latitude, so that T_e for a spherical planet could be calculated by some suitably weighted running mean of the displayed curves (i.e. convolution with a weighting function). The effect would be to increase the range of luminosity over which life could persist on the planet (because, for example, at luminosities where, over most of the planet, it was too hot even for white daisies, they might still survive at high latitudes). Sharp discontinuities would be less evident and the homeostasis of mean temperature rather less striking.

4. Removing the negative feedback

The "environmental feedback" in the model as described so far is strongly limiting on both species of daisy. Black daisies are warmer than white, and tend therefore to be favoured by cooler mean temperatures, yet an increase in the numbers of black daisies tends to warm the planet. The same goes in reverse for the white daisies. Under these circumstances it is perhaps not surprising that the system exhibits a stable point around which daisies can successfully homeostat the temperature over a wide range of luminosities. Not every interaction between the biota and the environment can be expected to operate in such a civilized fashion. Accordingly, we now follow what happens when we deliberately and radically alter the negative feedbacks which stabilize daisyworld.
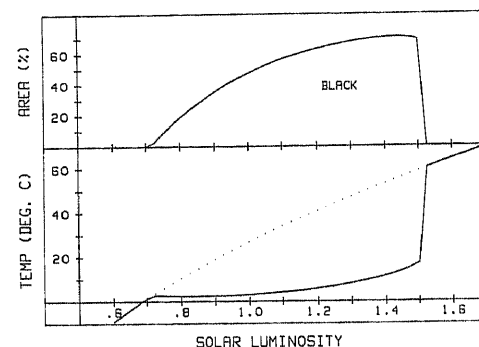
Fig. 2. Steady state response for conditions as in Fig. 1d, but with a cloud of albedo 0.8 assumed to obscure the black daisies.

Specifically, while retaining the condition that black daisies are warmer than white, we contrive to make the black daisies *cool* the planet.

Owing to a subtle change of climate, clouds appear on daisyworld. The clouds are light in colour. We will assume that the clouds form only over stands of black daisies because of the rising air generated over these warm spots. Now, therefore, black daisies no longer tend to increase the temperature. Instead, more black daisies mean more white clouds and a colder planet.

Fig. 2 shows the steady state output derived under this assumption. White daisies were not deliberately suppressed, but became extinct of their own accord. White daisies fail because, in the battle for survival of the fittest, they are now distinctly less fit than the black daisies. An increase in either species now tends to cool the planet, but black daisies, being warmer than the mean, thrive better at low temperatures. However, although the white daisies tend to be eliminated under the new conditions, an effective homeostasis is nevertheless maintained. It is clear that however we change the directions of the feedbacks, the worst that can happen is that we lose the less well-adapted species. The remaining daisies are still capable of homeostasis. *Regardless of the directions of the feedbacks, the model always shows greater stability with daisies than it does without them.* This result arises because the temperature versus growth curve is peaked, decreasing towards zero both above and below an optimum temperature. So whichever direction the life of the planet drives the temper-

ature, it ultimately reaches a region where a greater abundance of daisies results, via the temperature feedback, in a slower growth rate. A stable point will exist in this region. The stable state is buffered against external variations because the growth rate itself is a rather sensitive function of temperature and feeds back on any change.

5. Relevance to the earth

Extrapolation from daisyworld to the earth is, to say the least, rather tenuous at this stage. However, a peaked growth versus temperature curve is a universal property of living things. Furthermore, the biota may have a substantial influence on the earth's temperature via the abundance of greenhouse gases in the atmosphere. Recently, Owen et al. (1979) and Walker et al. (1981) have speculated that the abundance of atmospheric CO_2 may have been dominant in determining the mean temperature of the earth through geological time, in which case the biota as a whole would appear to be depressing the mean temperature below that of the "sterile earth" by tending to reduce atmospheric CO_2 pressures (Lovelock and Watson, 1982). In the present context, neither the direction nor the mechanism whereby life affects the temperature are of themselves important—only the assumption that the biota influence the temperature is required. For the sake of illustration, however, let us suppose that the net effect of life on Earth is to reduce atmospheric carbon dioxide, and that the biota are temperature limited. Thus a decrease in temperature would lead to an extension of the barren polar regions and would decrease the average level of biological activity over the earth as a whole, while a temperature increase would have the opposite effect. But a decrease in biological activity as a whole would presumably also decrease those activities which tend to reduce atmospheric CO_2. Thus carbon dioxide would increase to oppose the original change. We then have the rudiments of a temperature stabilization system for the earth analogous to that on daisyworld. We can speculate that some such mechanisms may have played a part in regulating the temperature and other environmental variables over the long history of the earth.

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