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Effects of simple environmental feedback on some population models

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ABSTRACT

Lovelock used a model of an idealised planet to demonstrate the stabilising effect of feedback on a population of daisies and environmental temperature. The equations he used represented a population model with only two steady states: no daisies present, or a stable population with monotonic damping. This paper investigates whether a similar result is obtained with a less stable population model. It was found that simple feedbacks, mediated by albedo and temperature, or by CO_2 and the "greenhouse" effect, did not alter the basic properties of population models but could alter the stability regime within which a certain set of population parameters operated. Models of populations with discrete generations tended to be less stable with feedback while those with continuous growth were more stable. This confirms that Lovelock's result is not highly dependent on the type of population model. Adding environmental feedback to simple population models does not alter the basic properties of the models themselves but leads to a stabilisation of the whole system of environment plus population.

1. Introduction

Lovelock (1983) and Watson and Lovelock (1983) showed how environmental feedback can lead to stabilization of the environment and of population size using a simple equation to represent population growth. The example used was of an imaginary planet, termed "daisyworld", not dissimilar to earth in terms of solar luminosity and temperature, but with just a single organism, a daisy. The colour of the daisies affects the albedo of the entire planet and therefore its temperature. With a temperature-dependent growth curve and species of different colours the planet's temperature and the size of the daisy population is controlled over a wide range of solar luminosities. By testing the effects of different types of environmental feedback on different population models, the present paper investigates how general is Lovelock's result.

2. Methods

The daisyworld model was extended to ensure that the system stabilised at each increment (upwards or downwards) of solar luminosity. Environmental feedback, using the same temperature equations as in daisyworld, were then added to different types of population model (May, 1981). Temperature feedback based on the effects of carbon dioxide released by the biota on greenhouse warming was also tested.

There are two basic types of model for single populations: those based on discrete growth, normally applied to insects which have non-overlapping generations, and those based on continuous increase, which have wider application. Simple examples of these are considered, as well as a model of competition between two species with continuous growth.

3. Results

3.1. Daisyworld

Some extensions of the basic results of the "daisyworld" model of Watson and Lovelock (1983) are given here, but for a full description of the model reference should be made to the original

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paper. The population growth is described by the equation:

$$dP/dt = P(\gamma G - \phi), \tag{1}$$

where γ is the growth rate, P is the proportion of the planet covered by daisies, G is the proportion of bare ground ($P + G = 1$), and ϕ is the death rate. The growth rate depends on the temperature of the daisies as follows:

$$\gamma = 1 - 0.003265\,(22 \cdot 5 - \text{temp})^2. \tag{2}$$

For a single population of daisies, the temperature of the daisies (temp) is determined by the solar luminosity (sol) and the albedo of the bare ground (alb_b) and of the daisies (alb_d):

$$\text{temp} = (\text{alb} - \text{alb}_d)\,20 + \text{temp}_t \tag{3}$$

where

$$\text{temp}_t = -273 + (1 \cdot 681 \times 10^{10}(1 - \text{alb})\,\text{sol})^{0 \cdot 25}, \tag{4}$$

$$\text{alb} = \text{alb}_b \cdot G + \text{alb}_d \cdot P, \tag{5}$$

where temp_t is the overall temperature of the planet.

In the model, it is assumed that there is a "sun" which gives rise to a luminosity at the surface of the planet with a similar value to the solar luminosity on the present-day earth. If this is taken to be equivalent to a value of 1.0 the solar luminosity in the model runs is varied between 0.5 and 1.8. Fig. 1a, b shows the results for black and white daisies for both increasing and decreasing luminosity. The response is not identical for these two directions of change; there are two regions of

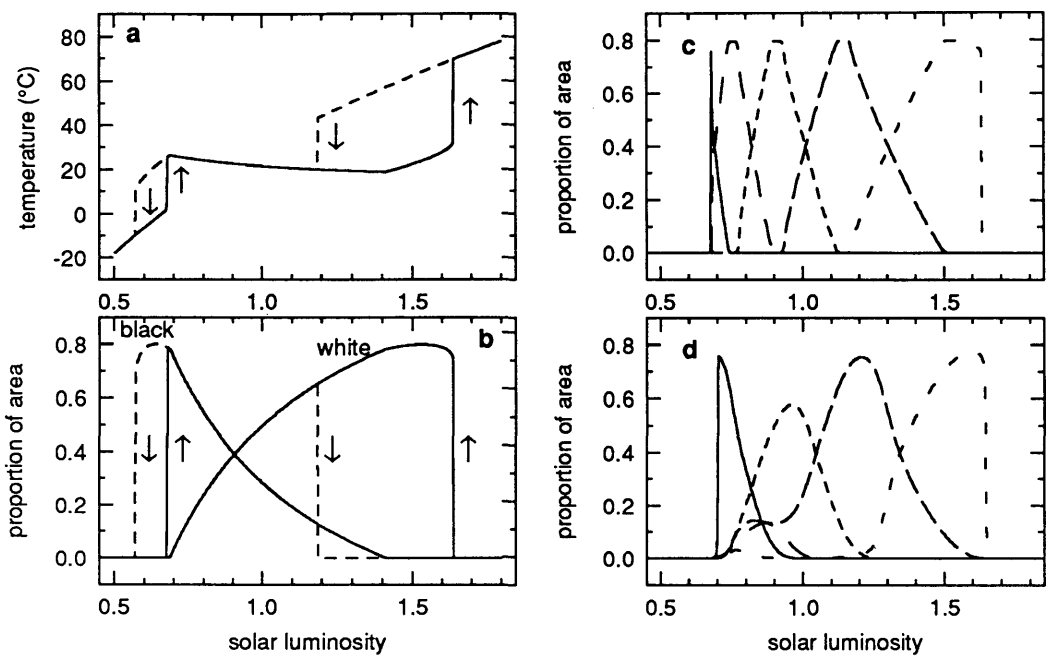

Fig. 1. Results of a daisyworld model (eq. (1–5)) as the solar luminosity rises from 0.5 to 1.8. Albedo of bare ground = 0.5, death rate, $\phi = 0.2$. (a) temperature and (b) area covered when black (albedo = 0.25) and white (albedo = 0.75) daisies are both present. The responses for rising (solid line) and falling (dashed line) luminosity are not identical and the direction of change is shown by arrows on the curves. (c&d) when five species are present together. Albedos of daisies: solid line, 0.25, pecked lines 0.375, 0.5, 0.625, 0.75. In (c) the model was allowed to reach equilibrium (500 iterations) for each of 500 values of solar luminosity between 0.5 and 1.8. In (d) only 5 iterations of the equations were calculated at each of the 500 values of solar luminosity, equivalent to the solar luminosity changing too rapidly for equilibrium to occur.

hysteresis in which the outcome depends on the past state of the model. The region at higher values of solar luminosity was described by Watson and Lovelock (1983) but that at lower values has not previously been demonstrated.

Stability analysis shows that there are two stable states for the model: with daisies absent, when $\gamma < \phi$ and with daisies present when $\gamma > \phi$. It is therefore possible to predict the range of solar luminosities for which daisies of a given albedo can exist on the planet, if the growth curve and temperature/albedo relationships are known, except within the region of hysteresis in which the species are interdependent.

Another result of interest is that with more than two species, each of different albedo, and changing luminosity, there will never be more than two species present at any one time (Fig. 1c), unless the luminosity changes so fast that the population never has time to stabilize (Fig. 1d).

It should be noted that although the daisies of different colours are referred to as "species" for convenience they do not in fact differ in any way except colour and should therefore perhaps more properly be considered variants of the same species.

3.2. *Discrete growth*

An example of a population model describing discrete growth is that used by Hassell et al. (1976):

$$N_{t+1} = \lambda N_t (1 + \alpha N_t)^{-\beta}, \tag{6}$$

where N_t is the size of the population at time, t, N_{t+1} is the population one generation later, and λ, α and β control the type of population growth. α determines the level of the population at equilibrium while λ and β affect its stability. Stability analysis (Hassell, 1975) shows that the model is stable only when $2 > \tilde{\boldsymbol{b}} > 0$, where

$$\tilde{\boldsymbol{b}} = \beta(1 - \lambda)^{-1/\beta}. \tag{7}$$

The relationship between the values of λ and β and the outcome of this model is given by Hassell et al. (1976). As β and λ increase the model becomes increasingly unstable, moving from a region of monotonic damping through damped oscillations to stable limit cycles, and finally to unpredictable chaotic oscillations.

Environmental feedback of the type used by Watson and Lovelock (1983) was added to the model:

$$N_{t+1} = \lambda N_t \gamma (1 + \alpha N_t)^{-\beta}, \tag{8}$$

where γ is the temperature-dependent growth rate as defined in eqs. (2–5). With a neutral albedo of 0.5 the growth rate, γ, was 0.83 and the results for different values of β (chosen to give the range of possible outcomes described by Hassell et al. (1976)) are shown in Fig. 2a–e. When the albedo of the plants was raised to 0.625 the population was less stable (Fig. 2f–i), although the growth rate was almost the same.

A slightly simpler model, with only two parameters, is obtained as β tends to infinity and α to zero with $\beta\alpha = \delta$ (Hassell et al., 1976):

$$N_{t+1} = \lambda N_t \exp(-\delta N_t) \tag{9}$$

with the stability criterion

$$\tilde{\boldsymbol{b}} = \ln \lambda. \tag{10}$$

In this case, the type of response depends only upon λ, but with a similar range of possibilities. When environmental feedback was added to this equation:

$$N_{t+1} = \lambda N_t \gamma \exp(-\delta N_t), \tag{11}$$

a similar result was obtained using the simpler equation.

3.3. *Continuous growth*

A continuous model based on a differential equation of the type

$$\mathrm{d}N/\mathrm{d}t = rN_t(1 - N_{t-T}/K) \tag{12}$$

always gives a monotonically damped solution unless a time-lag, T, is introduced into the density-dependent part of the equation. N_{t-T} is the population size at time $t - T$, K is the level of the stable population and r is the rate of increase. The stability depends on the length of the time lag.

Temperature feedback (eqs. (2–5)) was also added to this model:

$$\mathrm{d}N/\mathrm{d}t = rN_t(\gamma - N_{t-T}/K). \tag{13}$$

With neutral albedo, and therefore effectively no

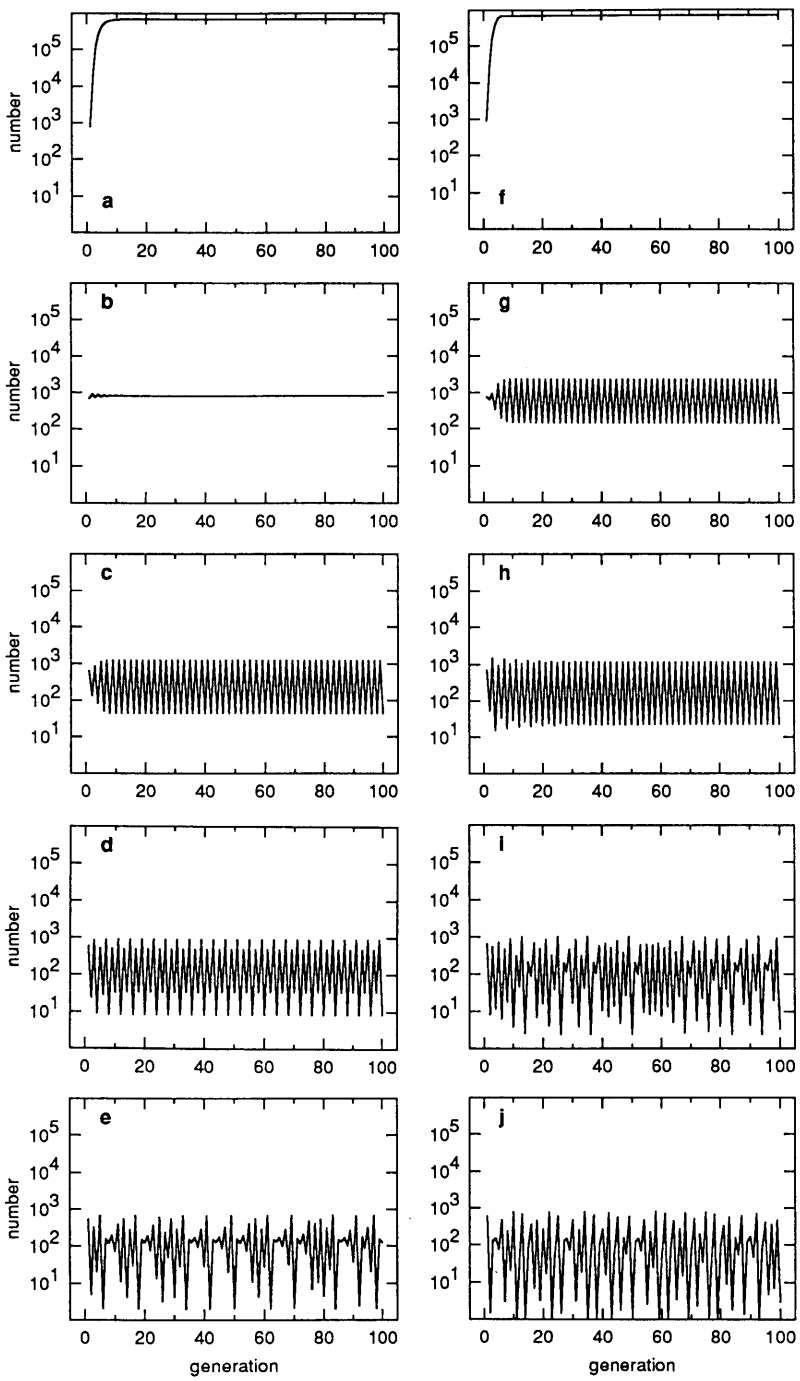

Fig. 2. Model of discrete growth of a single population with temperature feedback (eq. (8)). $\lambda = 100$, $\alpha = 0.01$; (a)–(e) with neutral (0.5) albedo; (f)–(j) with albedo = 0.625. Increasing values of β: 0.5 (a, f); 2.0 (b, g); 3.0 (c, h); 4.0 (d, i); 5.0 (e, j).

environmental feedback, the model gave a range of results with different values of time lag, T, (Fig. 3a–c). The temperature feedback led to stabilization of the population (Fig. 3d–f), so that the model behaved as if the time lag was smaller.

Daisyworld considers the case of a continuously varying environmental factor (solar luminosity) and such a condition was explored in the present models. The results are not presented in detail here as the effect was complex: as the luminosity changed steadily the model moved through several of its stability regimes.

3.4. *Carbon dioxide feedback*

A different type of environmental feedback was also included in the model of a continuously growing population. The growth rate of the plant again depended on temperature but in this case the temperature feedback was mediated not by albedo but by atmospheric CO_2 and the "greenhouse effect". Carbon dioxide is removed from the atmosphere by the plant and is related to the population size by the following equation (Lovelock, personal communication):

$$CO_2 = 4000/(1 + 50P), \tag{14}$$

where CO_2 is the concentration of atmospheric carbon dioxide in ppm., and varies between 4000 when there are no daisies, to about 100 when the daisies cover 80% of the planet's surface. The temperature of the planet is given by:

$$\text{temp}_t = -273 + (8.405 \times 10^9 \text{ sol})^{0.25} + {CO_2}^{0.34}. \tag{15}$$

This is the same as eq. (4) with an albedo of 0.5 and the addition of an extra term for the warming effect of carbon dioxide. It does of course assume that all the carbon extracted from the atmosphere

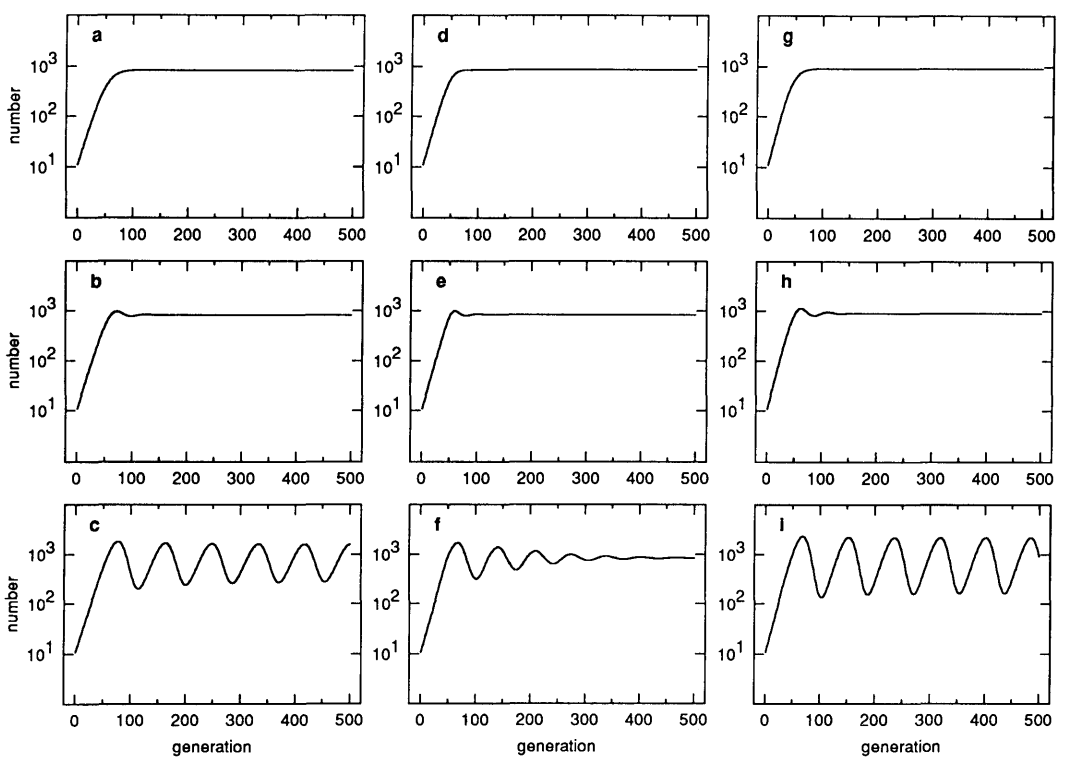

Fig. 3. Model of continuous growth of a single population (eq. (13)), $r = 0.8$, $K = 1000$: (a)–(c) with neutral albedo (0.5) and temperature feedback; (d)–(f) albedo = 0.6 with temperature feedback; (g)–(i) with CO_2 feedback (eq. (14–15)). Increasing time-lag: 0 (a, d, g); 10 (b, e, h); 20 (c, f, i).

by the plants is lost to the system by some form of carbon burial, and that other mechanisms for production and removal of CO_2 are independent of the atmospheric concentration. However this is a very much simplified model and is intended to show only that different types of environmental feedback can produce stabilization of a population and of its environment. The results for the same three time lags as used before (0, 10, 20) are shown in Fig. 3g–i and it can be seen that the population is indeed more stable than in the model with no environmental feedback (Fig. 3a–c), but less stable than that with the feedback via albedo (Fig. 3d–f). However, the oscillations in temperature are smaller for the equivalent oscillations in the population size and are also less symmetrical. This is of course due to the mathematical relationship used in the two cases.

3.5. Competition

A pair of differential equations, very similar to those described above for continuous growth, gives a simple example of competition (May, 1981):

$$dN_1/dt = r_1 N_1(1 - (N_1 + \alpha_{12} N_2)/K_1), \quad (16)$$

$$dN_2/dt = r_2 N_2(1 - (N_2 + \alpha_{21} N_1)/K_2), \quad (17)$$

where α_{12} and α_{21} are the interactions between the two species, and K_1 and K_2 are the carrying capacities of the environment for the two species (equivalent to the maximum number of each species which can be supported). Only when α_{12} and α_{21} are both less than unity is stable equilibrium possible, with both species coexisting.

Adding temperature feedback as before (eqs. (2–5)):

$$dN_1/dt = r_1 N_1(\gamma_1 - (N_1 + \alpha_{12} N_2)/K_1), \quad (18)$$

$$dN_2/dt = r_2 N_2(\gamma_2 - (N_2 + \alpha_{21} N_1)/K_2), \quad (19)$$

and giving each species a different albedo alters the balance of the two species (Table 1). If $\alpha_{12} = \alpha_{21}$, this model approximates to daisyworld although the temperature changes are not quite so smooth. When one species was independent of temperature it affected the level of both populations, tending to lead to an increase in the one which was no longer temperature-dependent, but both species continued to coexist, even when the other was penalized by reducing its γ value to 0.8.

Table 1. *Results of models of two competing populations with different values of* α *and albedo (eqs. (18, 19)), and different degrees of temperature feedback; albedo of bare ground* $= 0.5$; $r_1, r_2 = 0.8$; $K_1, K_2 = 1000$

α_{12}	α_{21}	alb_1	alb_2	N_1^*	N_2^*	$N_1^* + N_2^*$
0.25	0.75	0.5	0.5	763	254	1017
0.75	0.25	0.5	0.5	254	763	1017
0.5	0.5	0.5	0.5	551	551	1112
0.25	0.75	0.25	0.75	511	616	1127
0.75	0.25	0.25	0.75	340	803	1143
0.5	0.5	0.25	0.75	460	748	1208
0.5	0.5	0.5	0.75	750	491	1241
†0.5	0.5	0.5	0.75	755	490	1245
‡0.5	0.5	0.5	0.75	825	351	1176

† $\gamma_1 = 1.0$, growth-rate of species 1 independent of temperature.

‡ $\gamma_1 = 1.0$, γ_2 reduced to 80%.

4. Discussion

The results of the models presented here show that the daisyworld result is not unique to the equations and parameters chosen but can be considered of more general application to different population equations and types of feedback. Such feedbacks do not alter the range of responses of such models to different values of the population parameters, but can shift the boundaries of the response obtained in a given situation.

Models with no density-dependent feedback allow unlimited growth of the population and are therefore unrealistic in most situations. There are phases of certain population life histories (of which phytoplankton in a developing bloom may be one) where this type of exponential increase can occur for a short time. The models with very high values of the growth rate and chaotic fluctuations are examples of populations in which the control is out of balance with the reproduction.

Density dependence could be considered a type of environmental feedback, in that the use of a resource, such as space or nutrients, is the factor limiting the growth of the populations. If the population growth slows down before all the

space or nutrients are exhausted this will prevent the entire population dying out. There are many behavioural mechanisms which help to prevent such catastrophic events, as well as the more direct ones whereby it becomes increasingly difficult for an individual to obtain enough food to continue growing and reproducing.

These relationships are however quite different from the type of environmental feedback considered here and our feedbacks may shift the whole population into a region where the outcome of the model is different, but it will not fundamentally alter the shape of the growth with time as the other density-dependent mechanisms will still be operating. In other words the feedback is via a non-expendable resource. The organisms are able to buffer their own environment against changes on a larger scale, imposed from outside. Such mechanisms must be working on a scale smaller than that at which the imposed changes are occurring, e.g., in our particular example the changing luminosity of the sun. One could also consider changes in climate caused by changes in the earth's orbit, Milankovitch cycles, interacting with the biota to cause ice ages (Watson and Maddock, 1991) to be an example of such a system, or on a very much smaller scale, the maintenance of a stable microclimate within the soil, despite large changes in the weather.

It therefore appears that daisyworld is a general result and not highly specific to the particular equations used. It describes a generally stable situation in which strong feedback between the environment and the biota leads to a *stable system.* It is difficult to look at either part in isolation without coming to erroneous conclusions about the control mechanisms involved. This has important implications for the modelling of all types of ecosystems and their evolution. At present there are probably few, if any, examples of ecosystems for which enough information is available to construct a realistic model. However, the development of more detailed theoretical models using the systems approach could lead to important insights into real situations.

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