A numerical model for biodiversity

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SUMMARY

A numerical model is presented based on Alfred Lotka's notion that the mathematics of evolutionary models would be simpler, not more complex, if the evolution of the organisms and of their physical environment was considered as a single process. The model is concerned with the climate and the community ecology of an imaginary planet, Daisyworld, in orbit around a star like the Sun. The stabilizing influence of environmental feedback is used to enable experiments in community ecology that might otherwise be impossible. The model planetary ecosystem is populated with numerous types of organism distributed in up to three trophic levels. There follows a preliminary report of an exploration of this model planet and an account of its biodiversity and species richness.

1. INTRODUCTION

In their text on community ecology, Begon *et al.* (1990) thoughtfully say 'We turn to some central questions which present themselves not only to community ecologists but to anybody who observes and ponders on the natural world. Why do some communities contain more species than others? Are there patterns or gradients of species richness? If so, what are the reasons for these patterns. There are plausible and sensible answers to these questions, but conclusive answers are virtually lacking'. Their statement was echoed by Ehrlich & Wilson (1991) in a serious and impassioned plea for the sustenance of biodiversity. Like most scientists they expressed the intuitive belief that biodiversity has an intrinsic value but offer no theory of the natural world by which the value and significance of species richness and diversity can be quantified.

Mathematical models aimed at the understanding of biodiversity require mechanisms for the coexistence of a number of species. Levin (1981) listed mechanisms such as density dependency, where the growth rates of types of organism are dependent upon the density of each type itself, or frequency dependency, where the growth rates of types are sensitive to the relative frequency of types. Frequency-dependent selection, acting to favour rare phenotypes, is an important factor in maintaining genetic polymorphisms and Clarke *et al.* (1988) propose it as a general phenomenon of predator behaviour, with negative frequency dependence a mechanism for the maintenance of diversity over evolutionary time. None of these approaches so far has provided a mathematical theory that could account, in quantitative terms, for the phenomena of diversity and species richness.

A barrier to the understanding of biodiversity is the insoluble nature of the ensembles of differential equations that attempt to define population and community ecology. May (1972) analysed the population dynamics of systems where the physical environment was not involved and concluded that the systems of equations used to describe communities of live organisms are inherently unstable. The instability can be so profound that the investigation of representations of single populations is now part of the history of a new mathematical endeavour, the theory of deterministic chaos (May 1974). These conclusions echo the prophesy of the pioneer population biologist, Alfred Lotka, who in 1925 wrote:

> this fact deserves emphasis. It is customary to discuss the 'evolution of the species of organisms'. As we proceed we shall see many reasons why we should take in view the evolution, as a whole, of the system (organisms plus environment). It may appear at first sight as if this should prove a more complicated problem than the consideration of the evolution of a part only of the system. But it will become apparent, as we proceed, that the physical laws governing evolution in all probability take on a simpler form when referred to the system as a whole than to any portion thereof.

What follows is an attempt to reduce Lotka's suggestion to practice. To show that the intractability of the mathematics of population biology problem is lessened if we address the whole system, organisms and their material environment, not either of these parts separately. In traditional ecology the tendency is to take as the environment, the milieu of other organisms. The material environment is regarded as a given state, which does not respond to the growth of the organisms and to which the organisms do or do not adapt. When Lotka used the term 'environment' he meant the physical and chemical environment, and he thought of it as responsive to the organisms, not as a constant. Hutchinson (1954) in his chapter on the

biochemistry of the Earth drew the first quantitative conclusions on the interaction between organisms and their chemical and physical environment. He laid the foundations of biogeochemistry but this science has remained separated from community ecology. Odum (1983) was almost alone in recognizing the ecosystem as an entity and Tilman (1988) appears to be the only community ecologist to consider coupled systems of organisms and their material environment. His experiments with algae and models of resource limited systems led to conclusions similar to those I shall now describe.

2. DAISYWORLD

This is the model of an imaginary planet populated by numerous types of organisms in stable coexistence. The species richness and biodiversity within the system will be examined under conditions where the evolution of the types of organisms and of their physical environment proceeds as a single tightly coupled process. The wisdom of Lotka's advice to include the physical environment was confirmed by the stability of the new class of mathematical model. The first of this kind was described (Lovelock 1982; Watson & Lovelock 1983). The environment was represented by a single variable climate, with temperature the parameter, and the organisms, by the population of a single plant, daisies.

The logic of self regulating systems is notoriously unfamiliar yet key to the understanding of the biodiversity models of this paper. The section that follows is therefore devoted to a detailed explanation of the mechanism of the generic model Daisyworld, which is the mathematical basis of geophysiology.

Daisyworld is a model planet, like the Earth but with less ocean, orbiting a star like the Sun and at the same orbital distance as the Earth. Its whole surface is assumed to be fertile and to be sown uniformly with the seeds of two daisy species, one dark (albedo 0.25) and one light (albedo 0.65). The star is assumed to increase in luminosity as it evolves moving from a luminosity of 0.6 to one of 1.2, compared with the present luminosity of the Sun, taken as 1.0. The object of the model when first constructed was to demonstrate that the self regulation of climate, over a wide range of stellar luminosities, can be an automatic process requiring no foresight or planning by the system.

Daisyworld is a zero-dimensional flat Earth model. The experiments that follow begin with the model planet populated by one plant only, daisies. The inherent stability of Daisyworld allows the modelling of many trophic levels and later experiments include herbivores and carnivores as well as daisies. Although more than one environmental variable could also have been accommodated, this series is restricted to temperature change.

The equations of Daisyworld are:

$$T_e = (SL(1-A)/\sigma)^{0.25} - 273, \quad (1)$$

$$A = xA_g + (a_1A_1 + a_2A_2 + \ldots + a_kA_k), \quad (2)$$

$$T_i = q(A - A_i) + T_e, \quad (3)$$

$$\beta_i = (1 - 0.00326(22.5 - T_i)^2), \quad (4)$$

$$da_i/dt = a_i(x\beta_i - \gamma_i), \quad (5)$$

$$x = 1 - (a_1 + a_2 + \ldots + a_k). \quad (6)$$

Where (k) is the number of daisy types, each having constant albedo (A_i), death rate (γ_i), variable growth rate (β_i), Temperature (T_i) in °C, and fractional area coverage of the planet (a_i). The planet has an average albedo (A) and effective temperature (T_e). The fraction of the planet that is bare ground and where plants do not grow is (x) the total planetary surface area is taken as unity. The albedo of bare ground is (A_g), (S) is the stellar constant, (σ) the Stefan–Boltzmann constant (L), is the relative solar luminosity, and (q) a constant, equal to 20, relating individual daisy temperature to its albedo and the effective temperature of its environment.

The growth equation (5) was taken from Carter & Prince (1981) who modelled the spread of plants like daisies. If this equation is replaced with any of the commonly used growth equations, including the Lotka equation and its descendants, the numerical solutions show only slight quantitative differences. Part of the stability of the model comes from the inclusion of equation (6) which introduces density, or more strictly, area dependence.

The mathematical basis of the Daisyworld model and the methods for the solution of the ensemble of equations are described further in Watson & Lovelock (1983) and Maddock (1991). The model is robust and can accommodate equations in their natural nonlinear form; unlike many models of community ecology, or of biogeochemical cycles, it is remarkably insensitive to the initial conditions and resilient to perturbation. A useful feature of geophysiological models is their ability to provide continuous verification by the expression of the environmental variable, and in all of the model experiments that follow, this variable,

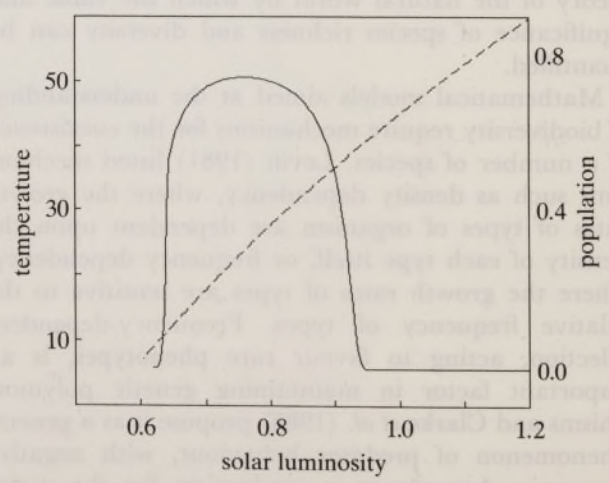

Figure 1. Model of the evolution of Daisyworld according to the conventional wisdom that there is no more than loose coupling between the physical and the biological processes of evolution. The humped curve illustrates the growth of daisy population in arbitrary units; the dashed line, the rise in temperature in °C. Going from left to right along the horizontal axis the star's luminosity increases from 60 to 120% that of our own Sun.

temperature, stays close to the optimum set for plant growth 22.5°C while the daisies are alive.

Figure 1 shows conventional wisdom about the rise of temperature and the growth of organisms on Daisyworld as its star evolves and the flux of radiant heat increases. Here the physical processes that determine the radiation balance are assumed to be quite independent of the biological processes that determine the growth of the organisms. The near linear increase of effective temperature as the star warms is shown as a dashed line and is the graphical expression of the Stefan–Boltzmann equation (1). The solid line shows the population of daisies expected if their growth rates varied according to the simple parabolic function, equation (4). Daisy population increasing as the planet warms from 5°C, the lower limit of temperature for growth, to comfortable temperatures near 22°C and then declines again as the upper limit of temperature, 40°C, is approached. The two curves represent the geophysical and biological views of the evolution of climate, and of the growth of organisms on the imaginary planet, and are what would happen if the growth of organisms was not tightly coupled to the physical evolution of the environment.

Figure 2 illustrates the effects of coupling physical and biological evolution on Daisyworld, and comes from the reiterated solution of equations (1–5) during the progressive rise of luminosity of Daisyworld's star. The dashed line represents the rise in mean surface temperature as the stellar luminosity increases and when the climatic effects of daisy growth are taken into account. The solid lines illustrate the rise and fall of population of the two daisy types, on the left of the diagram are dark daisies and on the right are light daisies.

The operation of the model can be explained as follows: when the surface temperature reaches 5°C daisy seeds commence to germinate. After their emergence, dark coloured daisies would be at an advantage because in the feeble sunlight they alone would be warm enough to grow. The few seeds left at the end of a season would nearly all be of dark daisies. At the start of the next season dark daisies would dominate and soon begin to spread, warming themselves and the area they occupied. Then, with explosive positive feedback, temperature and daisy growth would rise until a large proportion of the planetary surface was covered by dark daisies. Their growth would not continue indefinitely for two reasons: firstly, too high a temperature suppresses growth, and secondly, on a warm planet there would be competition for space from light coloured daisies. As the star warmed, the planetary ecosystem would change from one dominated by dark daisies to domination by light coloured daisies. Once equilibrium is established and light coloured daisies are now able to grow and compete for space the system enters a prolonged spell of negative feedback. The surface temperature of the model planet stays close to the optimum for daisy growth. It is the nature of stars to grow hotter as they age and eventually the ecosystem of daisies would collapse when a total planetary surface cover of light daisies was insufficient to keep the planet cool. The significant difference between these two models is that in the first the physical and biological evolutionary processes are independent of each other and merely coevolve, while in the second, Daisyworld, they are close coupled.

Figure 3 is a graphical illustration of the solution of the Daisyworld equations. The inverted U-shaped curve shows how the planetary area covered by a single species of light coloured daisies varies with temperature. The dashed line illustrates the planetary mean temperature for different extents of cover with this light coloured daisy specie. These two curves intersect at the point where the system settles down to

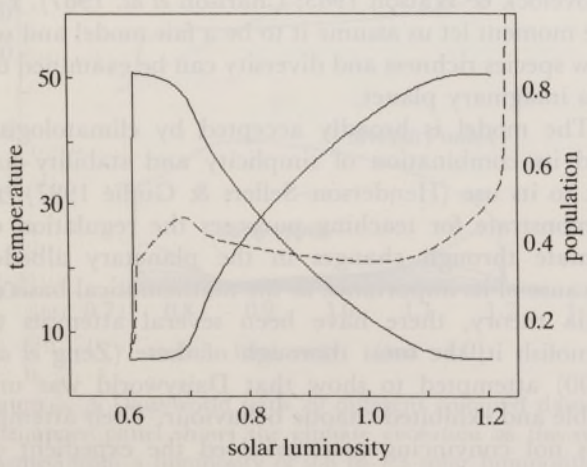

Figure 2. Model of the evolution of Daisyworld according to geophysiology and when the physical and biological processes of evolution are tight coupled. The populations of dark (left) and light (right) coloured daisies are shown as solid curves. The rise in temperature is shown as a dashed curve.

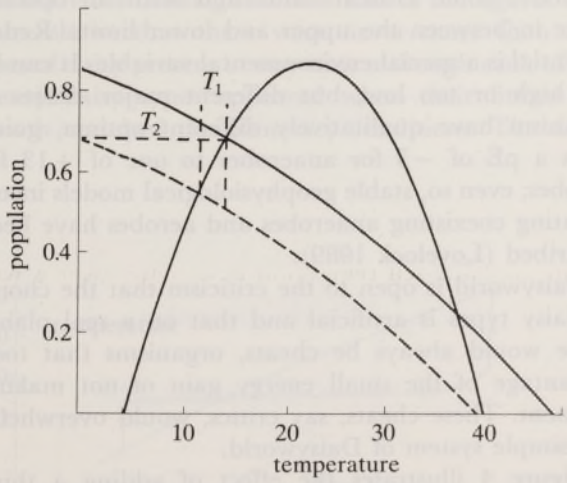

Figure 3. The Daisyworld mechanism. The inverted U-shaped curve shows the changes in area covered by daisies with temperature. The two convex curves show the response of the planetary temperature to the area covered with light coloured daisies for two different solar luminosities. The intersection points of these curves on the left hand side of the diagram mark the dynamically stable states of population and temperature. Note how the horizontal difference between the two intersection points is less than the horizontal distance between the two convex curves. These differences represent the temperature changes for a decrease in solar output with and without regulation.

its dynamic equilibrium for temperature and daisy population. Imagine the star to suddenly decrease its output of heat. The resulting new equilibrium is indicated by the point of intersection of the lower line with the curve illustrating daisy cover. If there were no self regulation the temperature decrease would simply be the horizontal distance between the two parallel dashed lines representing the variation of temperature with daisy abundance. With self regulation the temperature change is the horizontal distance between the two intersection points. This difference is less and illustrates how the system is able to reduce the change of temperature due to a change of solar output.

The model is quite general and is stable for other functions than parabolic. For example, if the parabola, equation (3) was instead a function that rose to an asymptote at 22.5°C and was horizontal for higher temperatures, light coloured daisies would regulate as before but dark ones would not. The exact shape is unimportant so long as the slope of the curve depicting daisy area cover with temperature, figure 3, does not approach zero at the point of intersection. Daisyworlds have been assembled and shown to regulate when the organisms change the extent of cloud cover, or the abundance of greenhouse gases. The humped curve of the growth rate can also relate to some other variable than temperature. Regulation can be modelled for other environmental properties, like redox potential, or the abundance of atmospheric gases (Lovelock 1989; Maddock 1991). Main stream biological systems operate within a limited range of physical and chemical environments. It can be too hot or too cold, too wet or too dry, too fresh or too salt, too acid or too alkaline. The functions relating these variables to growth usually take the form zero below or above some critical value and with an optimal value in between the upper and lower limits. Redox potential is a special environmental variable. It can be too high or too low, but different major classes of organism have qualitatively different optima, going from a pE of -5 for anaerobes to one of $+13$ for aerobes; even so, stable geophysiological models incorporating coexisting anaerobes and aerobes have been described (Lovelock 1989).

Daisyworld is open to the criticism that the choice of daisy types is artificial and that on a real planet there would always be cheats, organisms that took advantage of the small energy gain of not making pigment. These cheats, say critics, would overwhelm the simple system of Daisyworld.

Figure 4 illustrates the effect of adding a third neutral coloured type to Daisyworld, one which cheats by occupying space without contributing to regulation. Cheating is made tangible by a 5% bonus of growth rate for not making pigment. The system with three types of daisy is seen to be stable and able to regulate as well as the two type model. Cheating does not happen on Daisyworld because only dark daisies are fit to grow at low temperatures, and only light daisies fit to grow at high temperatures. The growth of the neutral coloured daisies is restricted to stellar luminosities where regulation is not needed.

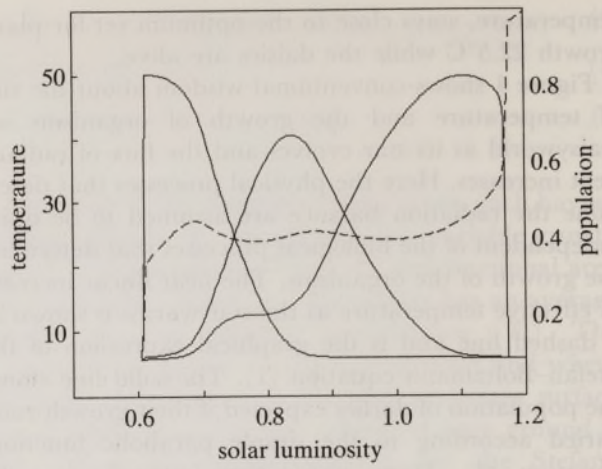

Figure 4. The evolution of climate and population on a three types Daisyworld with dark, neutral and light coloured daisies present. The temperature evolution is shown as a dashed curve.

The stability and indifference to initial conditions make Daisyworld a candidate for model experiments in population biology, and for the preliminary investigation of biodiversity. What we have in Daisyworld is something quite different from the well known damping effect of density dependence (Hassel 1975). Daisyworld is a tightly coupled system made stable by a combination of environmental feedback and density dependence, in it unrestrained growth does occur, but only when positive feedback serves to bring the system rapidly to its stable state. This is illustrated in figure 2 by the rapid rise of temperature and daisy population at the start of life on Daisyworld, and the same would be true of a model where the solar heat was declining. It may be some time before evidence and observation confirms or denies the existence of self regulation for the Earth, although it is already possible to argue, from the geochemistry of rock weathering, and from the association between climate, clouds and marine algae, that this mechanism operates for the long-term regulation of atmospheric carbon dioxide and climate (Lovelock & Watson 1983; Charlson *et al.* 1987). For the moment let us assume it to be a fair model and see how species richness and diversity can be examined on this imaginary planet.

The model is broadly accepted by climatologists and its combination of simplicity and stability has led to its use (Henderson–Sellers & Guffie 1987), to demonstrate for teaching purposes the regulation of climate through changes in the planetary albedo. Because of its importance as the mathematical basis of Gaia theory, there have been several attempts to demolish it; the most thorough of these (Zeng *et al.* 1990) attempted to show that Daisyworld was unstable and exhibited chaotic behaviour. Their attempt was not convincing as it involved the expedient of introducing a time lag between the sensing of a change of heat input and the response of the system. Engineers and physiologists familiar with the properties of feed-back control systems know that such an act is itself a recipe for instability and chaos in otherwise stable systems. Perhaps the most intriguing adaptation

of the model is as part of a computer game called SimEarth. As in climatology teaching, Daisyworld provided a stable and well behaved platform on which to build more intricate model scenarios. Daisyworld must be judged by its likeness as a caricature of the real world.

3. THE BIODIVERSITY MODELS

The model I have most used to examine biodiversity is one populated by many daisy types differing only in their colour or albedo. The model was made to include up to 100 types with the albedos of the different types of daisy ranged in evenly spaced steps from 0.25 to 0.6. The planetary surface albedo in the absence of daisies was 0.4 and the natural death rate of the daisies 0.3. The radiation of the star heating the model planet was assumed, as with the earlier models, to increase linearly from 0.6 to 1.2 times the luminosity of the Sun. The biodiversity was expressed using the Shannon index:

$$H = \Sigma(p_i)\ln(p_i). \tag{7}$$

I share Robert May's instinct to prefer some function of the variance as an index of biodiversity, but started my models with the Shannon index as the first encountered. For this series of models the qualitative conclusions do not seem to depend significantly on which index of diversity is used.

Figure 5 shows the evolution of the climate, and of the diversity index for a community of 20 daisy types, differing only in the shade of their colour. The index is greatest when the system is least stressed, namely at the time when the solar output is such that the temperature would be comfortable even with no regulation taking place. Diversity is least when the system is furthest from this comfortable zone, whether too hot or too cold. A response that resembles the well known decrease of diversity with altitude or latitude on the Earth.

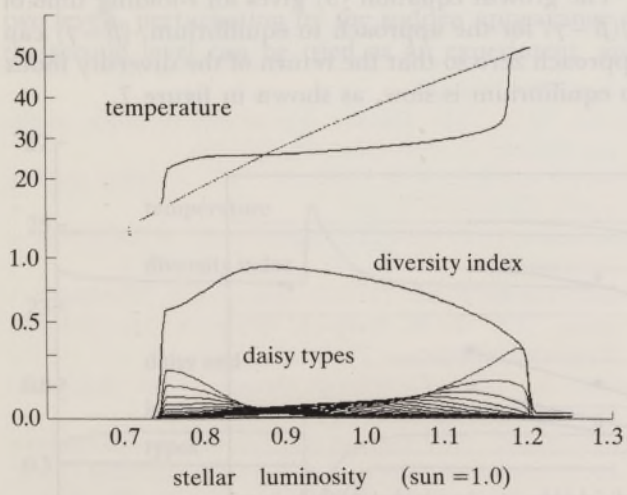

Figure 5. A Daisyworld with 20 different coloured daisies. The upper panel shows the climate evolution as the star warmed from a luminosity of 0.6 to 1.3 solar luminosities; the rise in temperature on a control lifeless model is shown as a dashed line. The lower panel shows the populations of the different coloured daisies, and the diversity index. In this model only two integration cycles took place for each of the 200 temperature increments going from left to right along the horizontal axis.

Daisyworld as a demonstration model for climatology is usually run under conditions where the rate of change of solar heat input is rapid, that is changing significantly during the generation time of the organisms. Maddock (1991) observed that when the system was allowed to approach equilibrium at constant solar input, the number of types of daisy slowly declined until there were, at any time, never more than two present. I had failed to notice this in my earlier experiments with Daisyworld because my interest was in climate regulation, not biodiversity; moreover, I had noticed that changing the number of types initially available to the model, and changing the solar heating rate, had only a slight effect on the ability of the system to regulate. Looking more closely at both regulation and biodiversity we now see that although thermostasis is not much determined by the number of types present at any given time, it is dependent upon the potential of the system to provide different daisy types when needed. In the model, seeds of all types of daisy are assumed always to be present. The run down of the number of species when the model is allowed to equilibrate appears to confirm the conclusion (May 1972) that complex systems are unstable. Looked at however as physiological models the stability of daisyworlds, measured by their resistance to perturbation, is not lessened as the number of species increases.

The experiment illustrated in figure 6, was run with the heat received from the star changing so slowly that the daisies were always in equilibrium with their environment. This was done in the model by using 10 000 integration steps for each of the 200 temperature increments along the time axis of the figure. The figure shows that there were never more than two types of daisy present at any time although each of the twenty daisy types appeared when their fitness for growth matched the planetary conditions. The slope

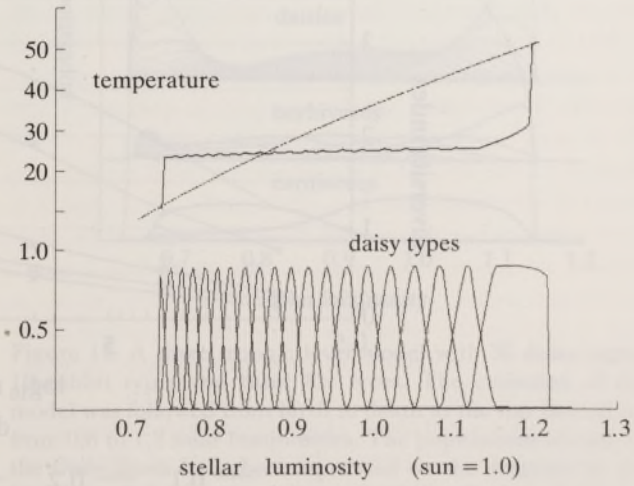

Figure 6. The model exactly as in figure 5, but with 10 000 integration cycles for each temperature increment. Note the presence of only one or two daisy types at any time.

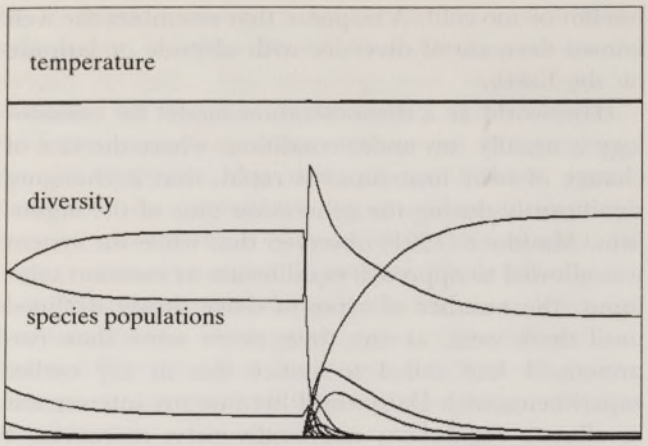

Figure 7. The perturbation of a 100 types daisyworld carrying daisies that differed in colour by evenly spaced intervals from an albedo of 0.25 to 0.65. The system was run through several million integration cycles until close to equilibrium and then perturbed by a 4% increase in solar luminosity. Note the large increase of the diversity index that accompanied a barely perceptible rise in temperature. Note also the presence of only two types before the disturbance and the relaxation to two types again afterwards.

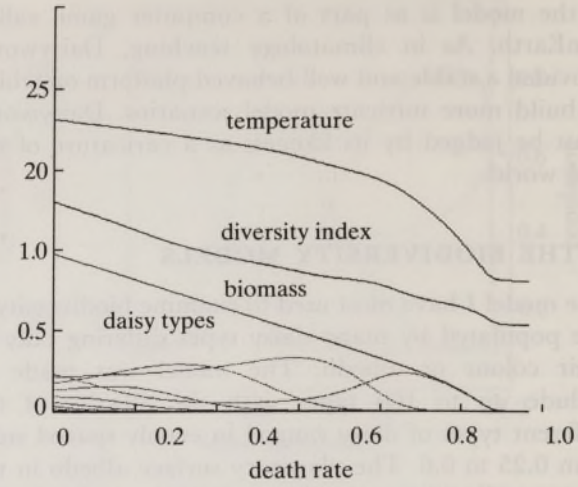

Figure 9. The effect of a progressively increasing death rate on a 10 species Daisyworld when the solar luminosity is constant at 0.7. The upper panel illustrates temperature regulation and the lower panel biomass, and diversity index. The death rate was taken to increase from 0.05 to 1.0 along the horizontal axis.

of the temperature curve is less than that in figure 6 indicating a more efficient temperature regulation.

Figure 7 illustrates the effects of a small perturbation of the radiant flux on the diversity index of a model containing 100 different types of daisy at equilibrium with a constant solar luminosity ($L=0.76$). The perturbation was a sudden increase of luminosity of 4%, comparable with a change in solar luminosity that would be expected to change the Earth's effective temperature from glacial to interglacial. Before the perturbation the system had settled down with only two types of daisy keeping a comfortable régime even though there were 100 species potentially available. The small sudden heat increase induced the flowering of many daisy types, followed by a slow return to a sparsity of types at the new slightly higher equilibrium temperature.

The experiment was repeated over a range of different rates of perturbation. To do this the 4% increase of solar heat was applied over different numbers of integration cycles going from one to 300 cycles. The lower the number of cycles the more abrupt the perturbation; the experiment in figure (7) was for a rapid perturbation applied over 3 integration cycles. In a further series of experiments these observations were repeated with a range of natural death rates for daisies going from 0.1 to 0.8. Figure 8 summarises the results of these experiments and shows how the diversity index varies with the logarithm of the rate of application of the perturbation. The effect of different natural death rates for the daisies is illustrated in the figure as a parameter.

The growth equation (5) gives an *e*-folding time of $1/(\beta-\gamma)$ for the approach to equilibrium. $(\beta-\gamma)$ can approach zero so that the return of the diversity index to equilibrium is slow, as shown in figure 7.

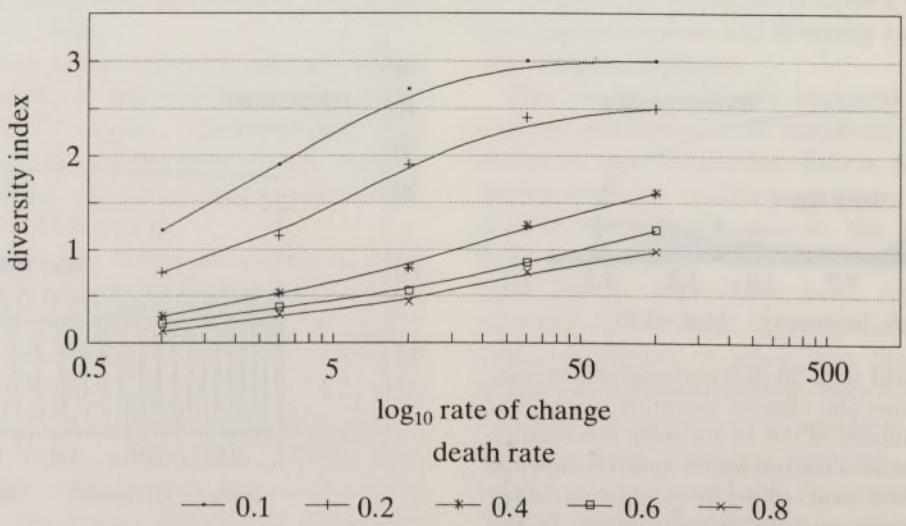

Figure 8. The relationship between the Shannon diversity index and the logarithm of the rate of change of solar luminosity going from 1.0 to 100.0 milli-luminosity units per integration cycle. Each line on the diagram is for a different death rate going from 0.1 to 0.8.

Figure 9 illustrates the effect on the diversity index of a deteriorating environment where the natural death rate of the daisies is increasing. Here a system of ten daisies was run at constant solar input but with an increasing rate of natural death, such as by a progressive increase in abundance of some toxic material. The model shows that temperature regulation persists until almost all the daisies have died; the total population and the diversity index both decline as the model develops.

The models so far have been limited to one trophic level. Figures 10–12 illustrate models with two or three trophic levels. As with the single level model there seemed to be no limit to the number of types that could be included. Practical considerations of computing time limited the models to 30 types of daisy, grazed by up to 15 types of herbivore, that in turn were the prey of up to four types of carnivore. The growth equations that introduced the types of the two new trophic levels were based on equation (5) as follows:

$$\mathrm{d}a_i/\mathrm{d}t = a_i(\beta_{ia}x_a - \gamma_{ia} - B) \quad \text{plants,} \tag{8}$$

$$\mathrm{d}b_i/\mathrm{d}t = b_i(A\beta_{ib}x_b - \gamma_{ib} - C) \quad \text{herbivores,} \tag{9}$$

$$\mathrm{d}c_i/\mathrm{d}t = c_i(B\beta_{ic}x_c - \gamma_{ic}) \quad \text{carnivores.} \tag{10}$$

Where (A, B and C) are the populations of each of the three trophic levels, and (x_a, x_b, x_c) the space unoccupied by each of these populations. The other symbols are as for equation (5). Environmental feedback was applied at all three levels. Preliminary experiments showed that the upper trophic levels could be populated by homeotherms without sacrificing model stability, but this variation was not investigated further.

Figure 10, illustrates a two trophic level model perturbed by a 4% increase of solar luminosity. The response to perturbation is very similar to that for the single level model with daisies alone, figure 7. With two levels, perturbation by the sudden appearance of the second level can be tried as an experiment, and

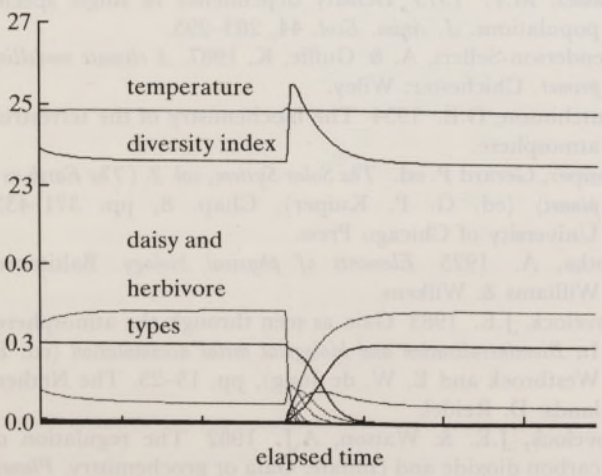

Figure 10. A Daisyworld populated by 30 different coloured daisy types, and 8 different coloured rabbit types. The model was allowed to approach equilibrium, left-hand side, and then perturbed during three iteration cycles by a 4% increase of solar luminosity. The response is similar to that for one level, figure 7.

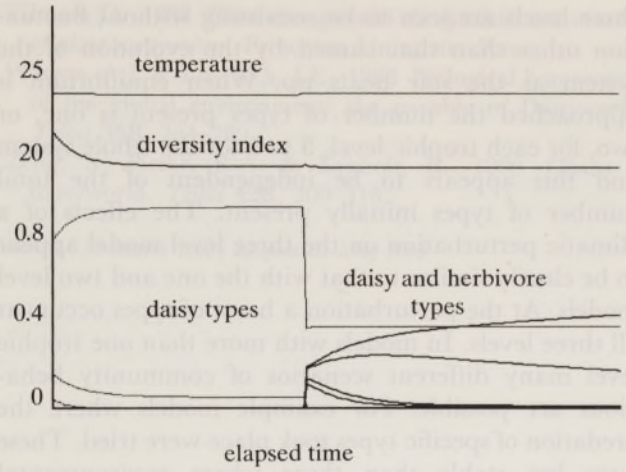

Figure 11. The same model as in figure 10 but with a constant solar luminosity of 0.76 but perturbed by the sudden appearance of herbivores. Note the fall in the diversity index of the abundant daisy species.

this is illustrated in figure (11). The model was started running with 20 daisy types at a constant solar luminosity of (0.76), half way through, three herbivore species were introduced. In this experiment there was no burst of types, only a decline in the diversity index of the daisies. The test was made with the solar luminosity at its most comfortable. This was done to separate the effects of a predation disturbance from a climatic one. If the model was perturbed by the appearance of herbivores at higher or lower solar luminosities than (0.76), there was a brief disturbance of the planetary temperature as well as an increase of the diversity index. This increase of diversity was equal to that expected of a climate change alone.

Figure (12) shows the populations of a three trophic level model that had not yet reached equilibrium. The

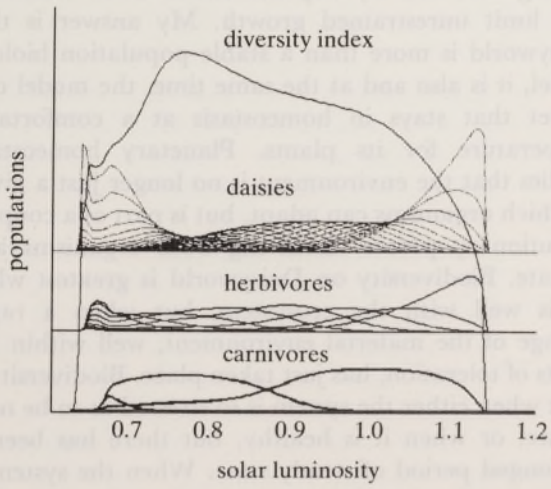

Figure 12. A three trophic level model with 30 daisy types, 10 rabbit types and three fox types. The evolution of the model was followed from birth to death as the star heated up from 0.6 to 1.2 solar luminosities. The populations of each of the three levels have been separated on the diagram in the interests of clarity. Note the peak of the diversity index at the solar luminosity (0.76) where the system is most stable. Temperature regulation, not shown, was very similar to that illustrated in figures 5 and 6.

three levels are seen to be coexisting without fluctuation other than that caused by the evolution of the system as the star heats up. When equilibrium is approached the number of types present is one, or two, for each trophic level, 3 to 5 for the whole system and this appears to be independent of the total number of types initially present. The effects of a climatic perturbation on the three level model appear to be closely similar to that with the one and two level models. At the perturbation a burst of types occurs at all three levels. In models with more than one trophic level many different scenarios of community behaviour are possible. For example models where the predation of specific types took place were tried. These were less stable than those where environmental feedback was dominant but did look promising for the modelling of frequency dependence.

Other complex models with feedback from several different environmental variables applied simultaneously have been tried and found stable (Lovelock 1989). The next step will be to see what effect increasing the complexity of the material environment has on the behaviour of these model communities and their species richness.

4. CONCLUSIONS

Daisyworld was the first numerical model for geophysiology. A way of viewing the world as a tightly coupled self-regulating entity and as the mathematical basis of Gaia theory. Whether right or wrong it has been a source of stimulation for new thoughts and experiments. If we can assume that the real world regulates to some extent like Daisyworld, then it provides some insight into the environmental problem of biodiversity. The most frequent criticism from biologists of the material presented in this paper is that it has all been said before by population biologists dealing with density dependence or other feedbacks that limit unrestrained growth. My answer is that Daisyworld is more than a stable population biology model, it is also and at the same time, the model of a planet that stays in homeostasis at a comfortable temperature for its plants. Planetary homeostasis implies that the environment is no longer just a given to which organisms can adapt, but is part of a coupled evolutionary process involving both organisms and climate. Biodiversity on Daisyworld is greatest when all is well with the ecosystem, but when a rapid change of the material environment, well within the limits of toleration, has just taken place. Biodiversity is least when either the system is so stressed as to be near failure, or when it is healthy, but there has been a prolonged period of steady state. When the system is rich in species the relaxation time after a perturbation is very long in terms of the generation time of individual species.

Does this say anything about our present condition? We usually regard the great diversity of organisms, especially in equatorial regions, as a steady natural state. I wonder if instead we should regard this great diversity as an indication that the ecosystem or the Earth itself although healthy is continuously perturbed. Even the single environmental variable, climate, considered in this paper is perturbed on the short timescale of day and night, and of the seasons. The geophysical record suggests that glaciations and warm periods have alternated for the past few million years and that similar fluctuations may have occurred at all times in the past. If this view is right then biodiversity is a symptom of change during a state of health. What seems important for sustenance is not so much biodiversity as such, but potential biodiversity, the capacity of a healthy system to respond through diversification, when the need arises. In the Amazon and other regions under threat, destroying biodiversity will reduce the reservoir of apparently redundant, or rare species. Among these may be those able to flourish and sustain the ecosystem when the next perturbation occurs. Environmental stress that is mild and does not decrease the biomass, such as a small change in temperature, increases biodiversity, when it is potentially available. Pathological stress, as by an increase of death rate, or by predation, reduces biodiversity unconditionally. The loss of biodiversity rarely occurs alone, it is a part of the destructive process of converting natural ecosystems to farm land. It is the whole process, the loss of biodiversity and the loss of the potential of the region to sustain biodiversity that makes the clearance of tropical forests so dubious an act.

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REFERENCES

Carter, R.N. & Prince, S. D. 1981 Epidemic models used to explain biogeographical distribution limits. *Nature, Lond.* **213**, 644–645.

Hassel, M.P. 1975 Density dependence in single species populations. *J. Anim. Ecol.* **44**, 283–295.

Henderson-Sellers, A. & Guffie, K. 1987. *A climate modelling primer*. Chichester: Wiley.

Hutchinson, G.E. 1954 The biochemistry of the terrestrial atmosphere.

Kuiper, Gerard P. ed. *The Solar System, vol. 2.* (*The Earth as a planet*) (ed. G. P. Kuiper), Chap. 8, pp. 371–433. University of Chicago Press.

Lotka, A. 1925 *Elements of physical biology*. Baltimore: Williams & Wilkens.

Lovelock, J.E. 1983 Gaia as seen through the atmosphere. In *Biomineralisation and biological metal accumulation* (ed. P. Westbroek and E. W. de Jong), pp. 15–25. The Netherlands: D. Reidel.

Lovelock, J.E. & Watson, A.J. 1982 The regulation of carbon dioxide and climate: Gaia or geochemistry. *Planet. Spa. Sci.* **30**,795–802.

Lovelock, J.E. 1989 Geophysiology: the science of Gaia. *Rev. Geophys.* **27**, 215–222.

Lovelock, J.E. 1989 *The ages of Gaia*. New York: Norton.

Maddock, L. 1991 Environmental feedback and population models. *Tellus* **43B**, 331–337

May, R.M. 1972 Will a large complex system be stable? *Nature, Lond.* **238**, 413–414.

May, R.M. 1974 Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science, Wash.* **186**, 645–647.

May, R.M. 1981 *Theoretical ecology*. (Oxford: Blackwell Scientific Publications.

Odum, E.P. 1983 *Basic ecology*. Philadelphia: Saunders College Publishing.

Tilman, D. 1988 *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press.

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

Zeng, X, Pielke, R.A. & Eykholt, R. 1990 Chaos in daisyworld. *Tellus* **42B**, 309–318.

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