

Evolution without Natural Selection: Further Implications of the Daisyworld Parable

PETER T. SAUNDERS

Department of Mathematics, King's College, Strand, London WC2R 2LS, U.K.

(Received on 18 March 1992, Accepted in revised form on 3 April 1993)

Daisyworld is a model dynamical system in which very simple mechanisms interact to produce complex behaviour. It was devised to show how regulation can arise without natural selection. Here we investigate the model in greater detail. We analyse the possible steady states and study the response of the system under different conditions, we consider the implications of the hysteresis which is found in this and many other non-linear systems, and we compare the properties of the model with those of systems that evolved solely by natural selection.

Natural selection inherently concentrates on local optimization and immediate advantage rather than on robustness and long-term benefit. This makes some features of organisms hard to explain within the synthetic theory. The model suggests that the solution may simply be that natural selection was not the crucial factor in their evolution.

When a system that has previously responded to challenge counter-intuitively or apparently not at all subsequently begins to react in the way one would expect, this should be taken as a warning that it is a regulated system and that the regulation may be about to break down. If that happens, there is likely to be a catastrophic change as the system either collapses altogether or else moves rapidly to the state it would have been in without regulation. Recovery, if possible at all, is likely to be unexpectedly difficult.

Introduction

The Gaia hypothesis (Lovelock, 1972, 1979, 1988) arose out of the problem of determining whether there is life on Mars. In thinking of experiments for the Viking probes to carry out, Hitchcock & Lovelock (1966) realized that it was not actually necessary to go to Mars. All that was needed was to determine the composition of its atmosphere. If there is no life on Mars, the atmosphere should be at or near chemical equilibrium, as in fact it is. If, on the other hand, the atmosphere were not near equilibrium, as the Earth's is not, this would be very strong evidence in favour of the existence of life.

The recognition that a good indicator of life on a planet would be the general activity of the planet itself led Lovelock to revive the old idea that the Earth should be thought of as an organism. There is, to be

sure, no firm definition of life to use as a criterion, but it is generally agreed that among the characteristic properties of living things are respiration, metabolism, self-regulation, irritability and reproduction. The Earth can be said to possess all of these except the last. Whether we choose to call it an organism is perhaps a matter of taste (and not, in fact, crucial to Lovelock's chief concern, which is ecological) but it does have many of the properties which organisms have.

One of the objections that has been raised to the Gaia hypothesis is based on evolution theory. The Earth, so it is argued, cannot be an organism because organismic properties arise only through natural selection. Since the Earth has been the same entity all the time, natural selection could not have operated. There is thus no mechanism whereby the Earth could have become able to maintain optimal conditions for the biota that are part of it, and there is consequently

no need to consider the matter further. (See, for example, Dawkins, 1982; Maynard-Smith, 1988.)

This is not the first time that such an argument has been used in a debate about evolution. Throughout the first half of the nineteenth century, more and more evidence was accumulating to support the view that the Earth has undergone many changes since it was first formed, and that in particular the species which we now observe are not the same as lived in the distant past. The strongest scientific objection to the idea of evolution was the argument from design. Without assuming either a Creator or some sort of life force there seemed no way of explaining how organisms can function as well as they do.

The breakthrough came when Charles Darwin suggested a plausible scientific mechanism for adaptation. Even though he was unable to prove that evolution had occurred in the way that he proposed (cf. Mayr, 1988: 201), once he had shown how it *could* happen, scientists were prepared to accept the evidence that it had. Unfortunately, the idea that defeated the dogma became a dogma itself. Any feature of an organism that cannot be explained by natural selection cannot exist, or, in the unlikely event that it does, it must be an epiphenomenon, something accidental and outside the chain of causation. Certainly we would not expect that anything of vital importance to an organism can arise other than by selection.

As Darwin demonstrated, an effective way to counter such an argument is to propose a mechanism, and so Lovelock put forward the model he calls Daisyworld to demonstrate how regulation can appear in a system simply through the interaction of two separate mechanisms, one with positive feedback and one with negative. There is no need for either design or selection. The aim is not to deny that selection occurs nor that it can have significant effects, but rather to show what can be accomplished without it.

The model is kept as simple as possible in order to make it possible to see clearly how the regulation arises. It is not intended as a model of the real Earth, but it is based on well-known physical principles and involves a mechanism similar in principle to those which probably do regulate much of our environment (see Lovelock, 1988). This makes it appropriate for studying some of the principles of the evolution of the Earth and also of other dynamic self-regulating systems, including those we customarily call organisms (cf. Saunders, 1993).

Daisyworld

Daisyworld is a hypothetical planet in orbit around a star very much like our own sun. Its entire biota

consists of two species of daisies, one black and one white. Apart from their colour, the two kinds are identical. This simplifies the model by reducing the number of ways in which the daisies interact, thus allowing us to see more clearly the consequences of the effects we are studying. It does, however, leave for further investigation the ways in which these effects combine with others. One example is considered later in this paper.

The daisies grow in large patches of either one kind or the other; they do not intermingle. They grow best at one particular temperature, which is taken to be 22.5°C, less well at temperatures that are warmer or cooler, and not at all below 5°C or above 40°C. The daisies are also affected by crowding; as their numbers increase they spread into unoccupied regions of the planet, and as less space is available they grow more slowly. Naturally, the daisies also die, and if they are dying faster than they are growing, the area they cover will diminish.

The temperature of Daisyworld depends on the solar luminosity and on the planet's albedo, i.e. its reflectivity. Black daisies have a lesser albedo and so absorb more heat than bare earth. Hence for a given solar luminosity a planet covered in black daisies will be warmer than a lifeless one. A planet covered in white daisies has a greater albedo and will be cooler. If both species are present, it is warmer where there are black daisies than where there are white ones.

It turns out that these very ordinary properties have remarkable consequences. If black daisies appear on a planet that is only just warm enough for them to grow at all, they will reduce its albedo and so make it warmer. This will increase their growth rate, so they will cover more of the planet and reduce its albedo even further, making the planet even warmer, and so on. This does not, however, go on indefinitely, because there is progressively less space for the daisies to expand into and this tends to slow their growth rate. Eventually the two effects balance each other, and the daisy population stabilizes.

At the same time, the temperature of the planet also stabilizes, and well above the value it would have if there were no daisies. What is more, if the luminosity now changes even over a comparatively wide range, neither the daisy population nor the temperature changes anywhere near proportionately.

It is not hard to see how this can happen. The growth in the daisy population is subject to two influences. One, the dependence on temperature has a positive feedback. The other, the dependence on space, has a negative feedback. The combination of the two leads to regulation.

There seems no particular reason to invoke natural

selection to explain either feedback process separately. It is not in the least difficult to understand why plants should grow best at some particular temperature and less well when they are overcrowded. But whatever the view we take on this, once the two processes exist and interact, they produce regulation. As a result, regulation, one of the most fundamental and necessary properties of organisms, appears without being selected for. What is more, it appears as a property not of the daisies, on which natural selection may have acted, but of the planet, on which, as Dawkins rightly points out, it could not.

The Daisyworld Model

While Daisyworld is only a parable, the equations and physical constants have been chosen to be realistic. Where phenomenological equations are used, the results are not qualitatively sensitive to small changes in their forms.

The basic equations are (Watson & Lovelock, 1983):

$$d\alpha_w/dt = \alpha_w(x\beta_w - g) \quad d\alpha_b/dt = \alpha_b(x\beta_b - g) \quad (1)$$

$$x = 1 - \alpha_b - \alpha_w \quad (2)$$

$$\beta_i = 1 - 0.003265(295.5 - T_i)^2 \quad 278 < T_i < 313 \\ = 0 \quad \text{otherwise} \quad (3)$$

Here α_w and α_b are the areas covered by white and black daisies, x is the area left bare, β_i is the growth rate per unit area and g the (constant) death rate, both per unit time. (Since Daisyworld is a mathematical model planet, it naturally has unit area.) T_i is the local temperature in degrees K. The subscripts i denote either w or b depending upon which kind of daisy is meant. The form of β_i is chosen to make the growth rates rise from zero at 5°C to unity at 22.5°C and decrease to zero again at 40°C. In numerical calculations, g is taken to be 0.3.

The radiation emitted by the planet must equal that absorbed:

$$\sigma T_e^4 = SL(1 - A), \quad (4)$$

where $\sigma = 5.75 \times 10^{-5}$ is Stephan's constant, L is the luminosity of the sun and S is a constant which has the units of flux and is later taken to be 9.17×10^5 for convenience: this choice makes L approximately unity. A is the mean albedo of the planet, i.e. the weighted average of the albedos of bare earth (denoted by subscript g), black daisies and white daisies:

$$A = \alpha_g A_g + \alpha_b A_b + \alpha_w A_w. \quad (5)$$

Clearly $A_b < A_g < A_w$, and for the model we take $A_b = 0.25$, $A_g = 0.5$, $A_w = 0.75$.

We ignore the effect of latitude on temperature because it contributes nothing significant to the model, but we must allow for heat flow between the regions. To do this without making the mathematics excessively complicated, we suppose that the local temperatures T_i are related to the effective planetary temperature T_e by the equation

$$T_i^4 = q(A - A_i) + T_e^4. \quad (6)$$

This relation preserves the energy balance of the planet since, as is easily verified, $\sum \sigma \alpha_i T_i^4 = \sigma T_e^4$. The constant q measures the degree of redistribution of solar energy. If $q = 0$, all local temperatures are equal to the mean temperature, whereas if $q > SL/\sigma$ the heat flow is against the temperature gradient. Lovelock sets $q = 2.06 \times 10^9$, which is well below the critical value.

Equation (6) is apparently unrealistic in that it predicts that even a single black daisy on Daisyworld will create a microclimate for itself which is about 5°C warmer than the rest of the planet. If, however, there are hills and valleys on Daisyworld, some small areas will be warmer than others, like the south-facing slopes on which European vineyards are often located. Small numbers of black daisies will appear in these areas before they can survive elsewhere, and the dynamic then determines whether or not they spread. Similarly, white daisies will appear first in shaded areas.

Suppose that the luminosity of the sun is very low and that Daisyworld is consequently very cold, and that there are in the ground seeds for one or both kinds of daisies. Suppose also that the sun then becomes brighter (as a main sequence star like our sun will tend to) and that while this happens a bit faster than for our own sun, the rate is still slow enough that the planet is always very close to equilibrium. Then to follow what happens we have to find the equilibrium values of the temperature T_e corresponding to different values of L .

There are four cases, depending on which kinds of seeds we have. The simplest is if there are none at all, or if the daisies do not affect the temperature, either because they are "grey", i.e. with the same albedo as bare earth, or because we choose to ignore physics. In this case eqn (4) gives us immediately

$$T_e^4 = SL/2\sigma. \quad (7)$$

This is illustrated in Fig. 1(a) and is just as we would expect; as the luminosity steadily increases so does the temperature of the planet.

Next, suppose that there are seeds for black daisies

but not for white ones. In that case eqn (1) implies that at equilibrium

$$\beta_b = g/x = g/(1 - \alpha_b) \quad (8)$$

and that consequently, using (3),

$$T_b = 295.5 \pm 17.5 \left[\frac{\alpha_b + g - 1}{\alpha_b - 1} \right]^{1/2}. \quad (9)$$

The albedo of the planet is

$$A = 0.25\alpha_b + 0.5(1 - \alpha_b) = 0.5 - 0.25\alpha_b. \quad (10)$$

Equation (6) becomes

$$T_b^4 = 0.25q(1 - \alpha_b) + T_e^4, \quad (11)$$

and when we eliminate T_e from (4) and (11) and use (10) we obtain

$$\sigma T_b^4 = 0.25\sigma q(1 - \alpha_b) + SL(0.5 + 0.25\alpha_b). \quad (12)$$

We can now solve (9) and (12) for T_b and α_b as functions of the luminosity, L . This enables us to find the equilibrium values of the planetary temperature T_e as a function of L , and the result is shown in Fig. 1(b).

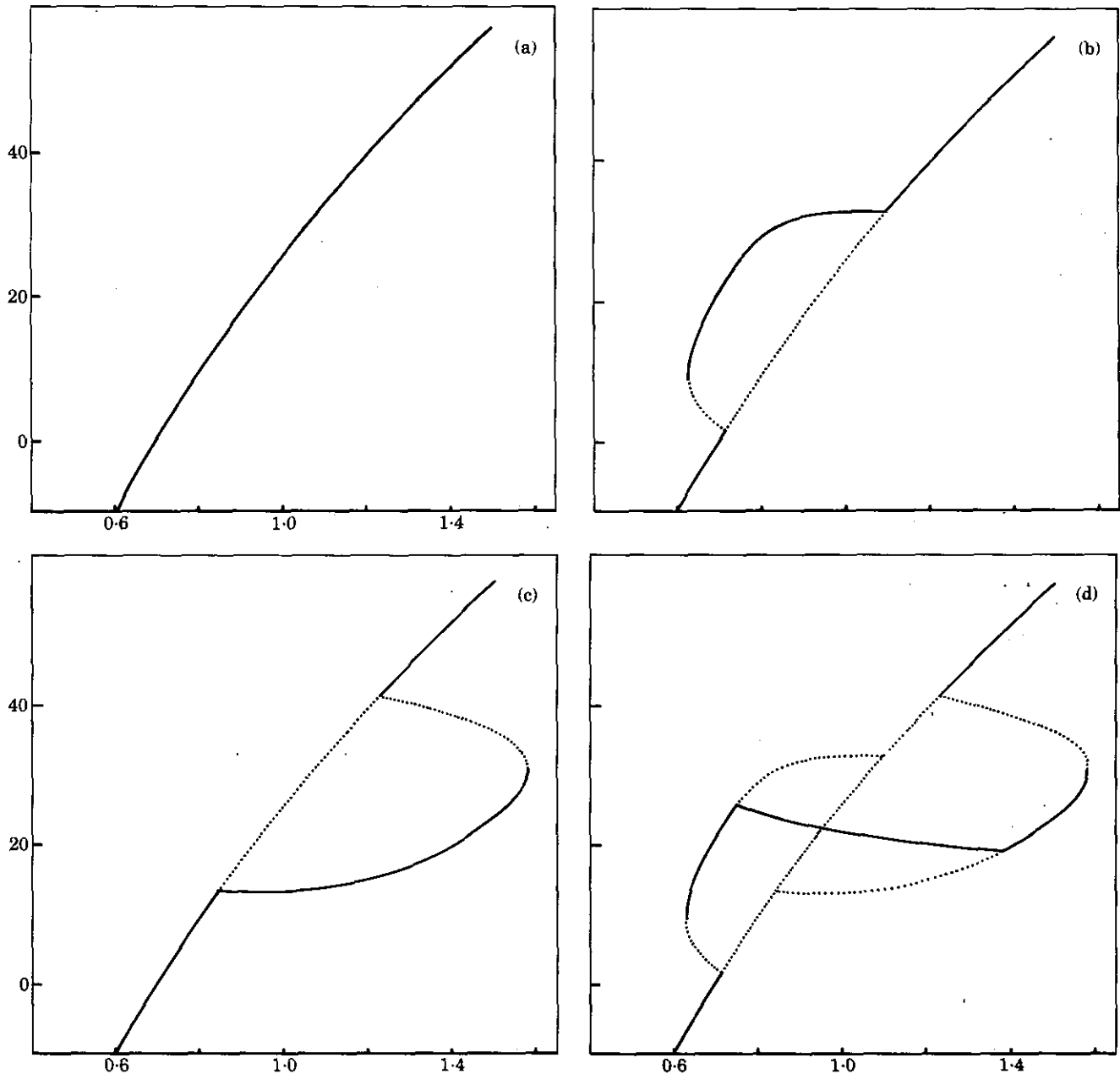


FIG. 1. Effective planetary temperature T_e as a function of solar luminosity L with (a) no daisies (or "grey" ones only), (b) only black daisies, available, (c) only white daisies available, (d) both black and white daisies available. In all cases there are ranges with no daisies and in (d) ranges with only black or only white. Dotted lines denote unstable equilibria.

The curve $T_e^4 = SL/2\sigma$ still corresponds to possible steady states of Daisyworld, those in which no daisies are present. Stable and unstable equilibria have been distinguished on the diagram, and we can therefore read off directly what will happen as L varies.

If L is increased slowly from a low value, when it reaches the critical value 0.72, the equilibrium given by $T_e^4 = SL/2\sigma$ becomes unstable. The system moves to the other stable equilibrium available for the same value of L and the temperature therefore increases rapidly from 2°C to 24°C. If L increases further, there is very little change in T_e . Instead, the number of black daisies reduces, thus increasing the albedo of the planet and preventing the temperature from rising. By $L = 1.10$ the black daisies have disappeared altogether, and from that point on the temperature, which is only 32.7°C, increases with L according to eqn (7).

The situation is slightly different if there are seeds for white daisies but not black ones. In this case, the white daisies initially spread slowly, because when they first appear they cool the planet, making it less favourable for themselves. As L increases, however, the white daisies do better and occupy more of the planet, keeping the temperature below what it would be if they were not there. Eventually the limited space means that there cannot be enough white daisies to hold the temperature to a suitable level. They start to die, which warms the planet, which in turn makes it even less suitable for them, and so they rapidly become extinct.

The lack of symmetry is due to the direction of the change in luminosity. If L is gradually decreased from a high value, white daisies appear suddenly and disappear slowly, whereas black daisies appear slowly and disappear rapidly. Note that for the black daisies to become extinct L must be reduced to significantly below the level at which they would appear if L were increasing from a low value. Conversely, if white daisies exist they persist to higher values of L than that at which they would appear if L were decreasing from a high value.

An important consequence of this hysteresis is that it makes Daisyworld more stable. If L is increased to just 0.72, over half the surface will be rapidly covered by black daisies. If L is then reduced to below that figure, the daisies do not disappear as quickly as they came. Not only do they persist, the area covered will actually increase slightly as more black daisies are needed to maintain a suitable temperature.

If both species are present, eqn (1) implies that $\beta_w = \beta_b$ and so in the rest of this section we will refer to either of them simply as β . Then from (3), since $T_b > T_w$,

$$T_b - 295.5 = 295.5 - T_w,$$

i.e.

$$T_b + T_w = 591. \quad (13)$$

Subtracting eqn (11) for w from the same equation for b gives

$$T_b^4 - T_w^4 = q(A_w - A_b) \quad (14)$$

and using (13)

$$T_b^4 - (591 - T_b)^4 = q(A_w - A_b). \quad (15)$$

Thus the local temperatures depend only on the albedos of dark and light daisies and on the value of q , not on the initial conditions nor on the solar luminosity, L . The mean temperature of the planet will depend on L but not strongly, because the variation is due only to the changing proportions of the planet covered by different coloured daisies. Since the local temperatures are independent of L , so too is β and therefore also x . Thus the total area covered by daisies is constant so long as both species are present.

Because the fourth order terms cancel, eqn (15) is a cubic, and for all plausible values of the constants it has only one real root, which for the given parameter values is $T_b = 300.5$. We then find that $T_w = 290.5$, $\beta = 0.918$, and $\alpha_b + \alpha_w = 0.673$. [The reduction in the degree of (15) comes about because β is by hypothesis symmetric. If β is not symmetric but still vanishes at 5°C and 40°C or thereabouts and has a single maximum in between, (15) has two real roots, but the other one is large in absolute value and corresponds to an unstable equilibrium. The unique stable equilibrium is not moved appreciably and so the predictions of the model are not greatly affected. Indeed the fourth order terms in the model, which appear on account of the Stefan-Boltzmann law, are of no special importance to it. If we were to use a linear relation in (6) instead, the results would be very much the same. This can be seen by following through the calculations, or just by noting that the curve in Fig. 1(a) is very nearly a straight line.]

With the given values of the albedos A_i , eqn (5) becomes

$$A = 0.668 - 0.5\alpha_b \quad (16)$$

and we now use (4) and (6) to obtain, with $S = 9.17 \times 10^5$,

$$\alpha_b = \frac{12.2}{14.7L - 1.90} - 0.663 \quad (17)$$

and

$$T_e = 299((\alpha_b + 0.668)L)^{1/4}. \quad (18)$$

These results are illustrated in Fig. 1(d). Again all the curves that were drawn previously are present, though the ranges of stability are different. This is because when we say that something is or is not stable, we have to specify the sorts of perturbations that are possible. The entire upper portion of the curve that first appears in Fig. 1(b) is stable against small variations in the solar luminosity or the number of black daisies. Much of it is not, however, stable against the appearance of even a small number of white ones.

This is an important point in modelling: if we come to the confident conclusion that a system is stable, this may mean only that we have not allowed for all possible perturbations. Of course we cannot be expected to think of everything, still less include it in a model, but we should at least be aware of the possibility, especially if we are doing something like introducing a new species (here, white daisies) to an ecosystem.

Figure 1(d) allows us to read off directly what will happen under a variety of circumstances. Let us consider just one, L increasing slowly from a low value. Until $L = 0.72$ no daisies can grow; even if a few black ones appear they will soon vanish. At $L = 0.72$, however, black daisies appear and rapidly cover about two thirds of the planet. As L increases, the area occupied by daisies slightly decreases, until $L = 0.75$, when the first white daisies appear. From then until $L = 1.37$ the two species coexist. The white daisies gradually replace the black ones and, though this is not obvious from the figure, the total area occupied by daisies remains constant. The white daisies then increase slowly until $L = 1.50$, then decrease until $L = 1.58$. If L increases further, the daisies disappear.

What is especially remarkable is that during this process the planetary temperature T_e remains remarkably constant. So long as there are daisies on the planet, even if the solar luminosity varies over a range from 0.7 to 1.5 the temperature remains within the range 21°C to 26°C. If there were no daisies, the temperature would vary from 0°C to 52°C.

This is obviously very important for evolution. Imagine two planets, one with daisies, one without, both orbiting a sun whose luminosity is gradually increasing. Any organisms on the daisy-free planet would have to adapt to a change in temperature from the freezing point of water to one that is too hot for humans. Those on Daisyworld would be guaranteed a stable environment in which to live and evolve, stable in terms of the temperature range they would have to live in, and also in terms of all the other things that are affected by temperature: other organisms,

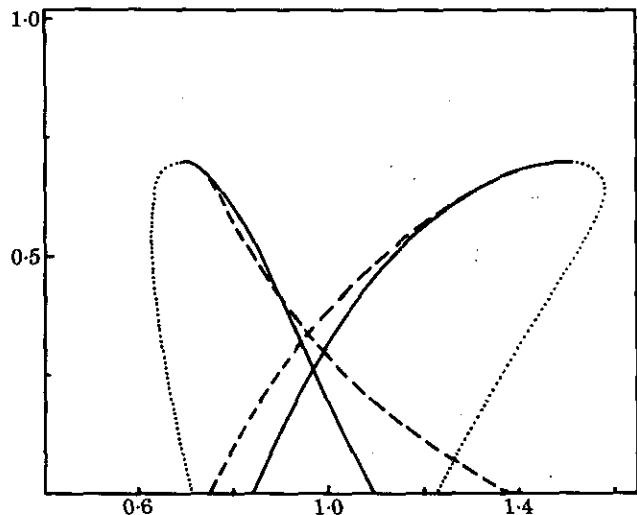


FIG. 2. The area covered by daisies as a function of luminosity. Dotted lines denote unstable equilibria. The curve on the left is for black daisies and that on the right is for white daisies. For both the dashed line indicates the area covered when both species are present and the solid line indicates the area when the other is absent.

climate, sea levels, and so on. Thus an important part of the "fitness of the environment" (Henderson, 1913) would be due to the daisies.

To see how different the situation on Daisyworld is from that envisaged in neo-Darwinist evolutionary theory, imagine that an inter-planetary expedition is sent from the Earth to Daisyworld. The astronauts would report that they had found a planet with a mean temperature of about 22.5°C and that all that seemed to grow on it were two species of daisies. Since there was no other life on the planet, they would have plenty of time to study the daisies in detail and they would find that both species grew fastest at a temperature of 22.5°C. And they would almost certainly conclude that here was a clear example of natural selection. Obviously the daisies had become adapted to the prevailing conditions on the planet.

That is not, of course, what actually happened. In particular, the number 22.5 is a property of the daisies, not the planet. The daisies did not adapt to the environment. They adapted the planet to suit themselves. We can account for the fit between organism and environment in terms of simple physical laws; there is no need to postulate a mutation that causes appropriate adaptations to appear. In fact, even if such changes were possible, there was no pressure for them. Once the planet was even marginally suitable for the daisies they immediately adjusted it to near-optimal conditions for themselves. And, in so doing, they turned the planet into an active system capable of maintaining its

temperature at a remarkably constant level while its environment, i.e. the luminosity of its sun, is changing significantly.

Figure 2 illustrates that when both species of daisy are present each occupies an area which is never much less, and sometimes significantly greater than the area it would occupy at the same luminosity if the other species were not there. There is competition (and, consequently, natural selection) on Daisyworld, because the daisies both depend on a common and limited resource, space. As a factor in the evolution of the planet, however, it is less important than how the two species co-operate to maintain a temperature that they both find suitable. Daisyworld is not a utopian paradise in which everything strives for the common good without thought for itself, but it is also not a world based on and driven by selfishness. One may at least hope that it is in this respect a good description of the real world.

The Breakdown of Regulation

One consequence of thinking of the Earth as alive is that it leads us to ask whether it might die. Put another way, if the Earth were an inert platform on which organisms interacted among themselves, then we would not have to be concerned about the effect those interactions might have on the Earth. If, however, we accept that many of the conditions necessary for life may depend on regulation, we ought to ask how this regulation might fail. The Daisyworld parable provides clues to what we might watch out for.

Consider the following example. Suppose, as before, that the solar luminosity is gradually increasing, only now imagine that there are intelligent beings on Daisyworld who have discovered how to control the sun. Naturally, this is very expensive to do, so their government is reluctant to act unless it is absolutely necessary.

Now for a long period of time the increasing brightness of the sun will not make Daisyworld warmer. On the contrary, it will actually become slightly cooler. When L reaches 1.38, however, the temperature of the planet, which is then only about 19°C, will start to rise. If there are "green" Daisyworlders, they will start to agitate for something to be done about this. Others, however, will be more worried about the cost. They will point out that the increase is relatively small and that the temperature is still not as great as it was many centuries before, when L was roughly half what it is now. Since the temperature has been falling for some time, if it is now rising

that is surely on account of some cyclical phenomenon. True, there are no longer any black daisies, but there are still plenty of white ones, and those are the important kind that do the cooling. Why spend large amounts of the taxpayers' money just to preserve biological diversity?

But consider what may happen if nothing is done. As L continues to increase, so will the temperature, though still not so much as to make the planet unbearably hot. If L is allowed to reach 1.58, however, the daisies will suddenly disappear and the temperature will rise abruptly from 31°C to 62°C. The Daisyworlders may not survive this, and even if they do, to restore the temperature regulating system they will have to reduce the luminosity to 1.22, which will presumably cost them much more than it would have done to have held it at about 1.5.

A system that is apparently resistant to perturbations may be inert, but it may also be being regulated. If it responds to change in a counter-intuitive way, then it is almost certainly the latter. If such a system starts to respond to change in the way that you would expect, this should be taken as a warning that the regulation is breaking down and that there is likely to be an abrupt change as the system moves to where it would have been without regulation. It may not be possible to recover from this, and even if it is, hysteresis will make recovery much more costly and difficult than one might expect.

This result gives us only an indication of serious trouble ahead, not a firm prediction. As the Daisyworlders in the parable discovered, however, and as we on the real Earth may also discover if we act unwisely, that is not a reason for ignoring it. By the very nature of catastrophes the only way to be absolutely sure that one is imminent is to let it happen, at which point it is generally too late to do anything about it.

Darwinian Evolution on Daisyworld

The temperature is not the same everywhere on Daisyworld because the local environment of black daisies is warmer than that of white ones; in the two species model above we found $T_b = 300.5$ and $T_w = 290.5$. Since these local temperatures are maintained as long as both species are present, i.e. over a range $0.75 < L < 1.38$, we might suppose that the daisies will evolve to make these their optimum growth temperatures.

Let us suppose that the appropriate mutants appear. Then because they are fitter, i.e. because they grow faster at those temperatures, they will replace

the original ones. To see the effect of this, we repeat the calculations of the previous section with the growth functions

$$\begin{aligned}\beta_b &= 1 - 0.003265(300.5 - T_b)^2, \\ \beta_w &= 1 - 0.003265(290.5 - T_w)^2.\end{aligned}\quad (19)$$

We still require $\beta_b = \beta_w$, which now implies

$$(290.5 - T_w)^2 = (300.5 - T_b)^2 \quad (20)$$

i.e.

$$T_b + T_w = 591 \quad (21)$$

or

$$T_b - T_w = 10. \quad (22)$$

Substituting either (21) or (22) into (14) yields $T_b = 300.5$, $T_w = 290.5$, as in the previous case. Then since $\beta_w = \beta_b = 1$, eqn (1) implies $x = 0.3$, i.e.

$$\alpha_b + \alpha_w = 0.7. \quad (23)$$

Equation (5) becomes

$$A = 0.675 - 0.5\alpha_b \quad (24)$$

and so, using (4) and (6),

$$\alpha_b = \frac{3.80}{4.58L - 0.594} - 0.65 \quad (25)$$

and

$$T_e = 299((\alpha_b + 0.65)L)^{1/4}. \quad (26)$$

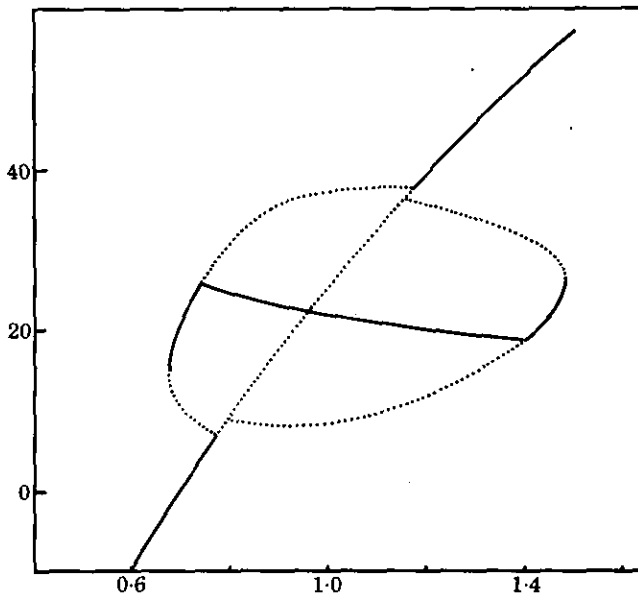


FIG. 3. Effective planetary temperature T_e as a function of solar luminosity L . Both black and white daisies are available and each species has its maximum growth rate at the local temperature. Dotted lines denote unstable equilibria, and the cases of no daisies or one species only can be read off by comparison with Fig. 1.

These results are illustrated in Fig. 3. It is striking how little is gained by adaptation. The proportion of the planet covered by daisies when both species are present increases only from 0.67 to 0.70. The temperature regulation is not improved at all. The most significant difference is that the range of stability is decreased by about 16%. The original daisies could regulate the temperature throughout the range $0.63 < L < 1.58$; their successors can do it only for $0.68 < L < 1.48$. The reason for this is that the black daisies, which are responsible for the regulation at lower luminosities, have adapted to grow better at higher ones than before, and the white ones, which do the regulating at higher luminosities, now grow better at lower ones.

Imagine our astronauts coming upon the original Daisyworld (i.e. the daisies have not evolved in the way described in this section), and suppose that its sun is subject to occasional large fluctuations in luminosity. If the visitors were to study the system carefully, they would discover that by not having adapted themselves precisely to their local temperatures, and thus having foregone the small short-term gain in population, the daisies had significantly improved their long-term chances of survival.

This would be very difficult to explain within the synthetic theory. One can imagine that it might even become known as the central theoretical problem of Daisyworld. The explanation, of course, is that just as the daisies did not adapt to the planet in the first place, but adapted it to suit themselves, so the ability to withstand a greater variability is not the result of Darwinian adaptation. On the contrary, it exists because of the absence of Darwinian adaptation.

Similar explanations might well apply to phenomena like altruism and sex, where short-term disadvantages appear to be in conflict with long-term benefits. If we do not insist on accounting for everything in terms of natural selection, the paradoxes evaporate.

Conclusion

Daisyworld is a simple and immediately intelligible model based on conventional mechanisms, not on arbitrary equations carefully contrived to produce unusual behaviour. It therefore demonstrates what a very simple system can do naturally, i.e. without either conscious design or natural selection. We may use it as a null hypothesis, an indication of how we expect systems to behave unless there is a reason why they should do otherwise.

The model demonstrates how regulation can result from the interaction of positive and negative feedbacks. These can easily arise individually, and all that

is then needed is for them to interact appropriately. Hence, when we observe regulation, we should not jump to the conclusion that it was created by natural selection. Indeed, since regulation is a systems property which typically involves the interaction of different processes, it is not obvious how it could be created by selection. What use is half a regulatory system? Of course it can be selected for once it appears, and selection can tune it and refine it, but that does not explain how it got to be there in the first place.

This result is important from an ecological point of view because when a regulated system fails it is likely to do so catastrophically, in both the technical and common senses of the word. If we are so convinced that the Earth cannot be being regulated that we do not even ask whether it is, still less whether the regulation is in danger of breaking down, we may be running unnecessary risks.

It may seem surprising that such an obviously useful property as regulation could arise without natural selection, but there are many things in the universe which appear to be essential for life and yet were clearly not created by selection. It is difficult to see how life could exist if the law of gravity were much different from what it is, if the crucial resonances of C^{12} and O^{16} were at only slightly different energies from where they happen to be, if water did not have the peculiar properties it does, and so on. Not everything that is to our advantage is the product of selection. It may just be how things naturally are. (For more examples and a discussion of the issues they raise, see Barrow & Tipler, 1986.)

It is sometimes said that natural selection is a mechanism for generating the improbable. What this means is that organisms are unnatural, because they are not what we would expect Nature to produce. Yet there are many indications that organisms are more natural than some evolutionists think. For instance, D'Arcy Thompson (1917) gave many examples to show that the forms we observe in organisms are often determined more by physics than by selection, and the roles of both physics and chemistry have been investigated by many authors since, especially following Turing (1952).

The Daisyworld parable not only supports this view, it also reminds us that what is natural is more likely to be robust. The model illustrates this by the way that natural selection reduces the range of stability, but there are many real examples. Some are

familiar from everyday life, like sophisticated machinery that can only perform under perfect conditions and when carefully tuned. Engineers have also found that over-optimization tends to produce structures with potentially dangerous instabilities (cf. Thompson & Hunt, 1973). What is especially interesting for biology is that the problems arise when we try to optimize simultaneously two connected features of a structure. They will therefore not be revealed by a research strategy which seeks to account for organisms by decomposing them into individual traits which, so it is assumed, are acted on separately by natural selection.

There is much to be said for fitting naturally into the universe instead of trying to screw every ounce of advantage out of it. Above all, it reduces the danger of compromising the future for the sake of a small short-term advantage—what we might call the “Esau effect”, after the man who traded his birthright for a mess of pottage, i.e. to satisfy an immediate need. The Daisyworld parable demonstrates how organisms may be less prone to this mistake than the synthetic theory of evolution suggests.

REFERENCES

- BARROW, J. D. & TIPLER, F. J. (1986). *The Anthropic Cosmological Principle*. Oxford: Oxford University Press.
- DAWKINS, R. (1982). *The Extended Phenotype*. Oxford: Freeman.
- HENDERSON, L. J. (1913). *The Fitness of the Environment*. New York: Macmillan.
- HITCHCOCK, D. R. & LOVELOCK, J. E. (1966). Life detection by atmospheric analysis. *Icarus* 7, 149–159.
- LOVELOCK, J. E. (1972). Gaia as seen through the atmosphere. *Atmospher. Environ.* 6, 579–580.
- LOVELOCK, J. E. (1979). *Gaia: A New Look at Life on Earth*. Oxford: Oxford University Press.
- LOVELOCK, J. E. (1988). *The Ages of Gaia*. Oxford: Oxford University Press.
- MAYNARD-SMITH, J. (1988). Evolutionary progress and levels of selection. In: *Evolutionary Progress* (Nitecki, M. H., ed.) pp. 219–230. Chicago, IL: University of Chicago Press.
- MAYR, E. (1988). *Toward a New Philosophy of Biology*. Cambridge, MA: Harvard University Press.
- SAUNDERS, P. T. (1993). The Organism as a Dynamical System. In: *Thinking About Biology, SFI Studies in the Sciences of Complexity, Lecture Notes Vol. III* (Varela, F. & Stein, W., eds.) pp. 41–63. New York: Addison Wesley.
- THOMPSON, D'A. W. (1917). *On Growth and Form*. Cambridge: Cambridge University Press.
- THOMPSON, J. M. T. & HUNT, G. W. (1973). *A General Theory of Elastic Stability*. London: Wiley.
- TURING, A. M. (1952). The Chemical Basis of Morphogenesis. *Phil. Trans. R. Soc.* B237, 37–72.
- WATSON, A. J. & LOVELOCK, J. E. (1983). Biological homeostasis of the global environment: the parable of Daisyworld. *Tellus* 35B, 284–289.