Darwinian Selection Leads to Gaia

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The Gaia hypothesis, in its strongest form, states that the Earth's atmosphere, oceans, and biota form a tightly coupled system that maintains environmental conditions close to optimal for life. According to Gaia theory, optimal conditions are intrinsic, immutable properties of living organisms. It is assumed that the role of Darwinian selection is to favor organisms that act to stabilize environmental conditions at these optimal levels. In this paper, an alternative form of Gaia theory based on more traditional Darwinian principles is proposed. In the new approach, environmental regulation is a consequence of population dynamics, not Darwinian selection. The role of selection is to favor organisms that are best adapted to prevailing environmental conditions. However, the environment is not a static backdrop for evolution, but is heavily influenced by the presence of living organisms. The resulting co-evolving dynamical process eventually leads to the convergence of equilibrium and optimal conditions. A simple Daisyworld model is used to illustrate this convergence phenomenon. Sensitivity analysis of the Daisyworld model suggests that in stable ecosystems, the convergence of equilibrium and optimal conditions is inevitable, provided there are no externally driven shocks to the system. The end result may appear to be the product of a cooperative venture, but is in fact the outcome of Darwinian selection acting upon "selfish" organisms.

Introduction

It is widely observed that population growth is greatly influenced by environmental conditions. Some conditions, such as temperature, pH, and salinity, are found at levels quite suitable for life, and in some cases these levels are optimal, in the sense that other levels would lead to lower population growth rates. For example, there is evidence that optimal (and survivable) temperatures for extremophilic bacteria vary over a wide range, but are usually tightly coupled to those prevailing in their specific environments (Madigan, 2000). Assuming a common origin for prokaryotes, a Darwinian explanation for this phenomenon is that optimal conditions are heritable traits, subject to variation and selection, and evolution has favored species that are best adapted to their respective environments. According to Gaia theory (Lovelock & Margulis, 1974), adaptation is not the whole story. Natural selection also favors organisms that have the ability to stabilize the environment, and so maintain conditions that are compatible with life. Evidence in support of Gaia theory is summarized in James Lovelock's book, *The Ages of Gaia* (1995) and in a recent review article appearing in *Nature* (Lenton, 1998).

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One prerequisite for a self-regulating biosphere is that organisms must be able to affect their environment. The environment is undoubtedly influenced by the presence of life, if only because living organisms consume nutrients and expel waste materials on a large scale, and these activities influence many environmental parameters (Holland, 1984). Gaia theory argues that environmental regulation occurs because organisms that alter the environment in a way that is beneficial to themselves (and perhaps others) are preferentially selected. There is no need to postulate altruistic behavior on the part of organisms, or to apply group selection theory to explain self-regulation. In fact, Gaia researchers tend to shy away from group selection arguments since they are open to criticism by most biologists (e.g. see Dawkins, 1982). Instead, Gaia theory has been constructed on a foundation of individual selection. It is proposed that organisms that act on the environment in a beneficial way are preferentially rewarded over those that hitch a "free ride".

A prototype model, called Daisyworld (Watson & Lovelock, 1983), has heavily influenced the development of Gaia theory. In Daisyworld, two competing species of daisies, one black, the other white, affect the mean air temperature by altering the albedo (reflectivity) of the planet. Both species have optimal growth rates when the temperature is 22.5°C, but white daisies cool the air in their immediate vicinity, while black daisies warm the air in their immediate vicinity. The opposing tendencies of black and white daisies give rise to a self-regulating thermostat for the planet. For example, if the luminosity of the sun increases, causing an increase in the Earth's temperature, white daisies are favored, and the planet cools. Note that temperature diffusion must be limited so as to allow selection to occur at the individual level. If the temperature is uniform, regulation is absent. Daisyworld models that allow for color mutation are even more self-regulating (Stocker, 1995; Bloh et al., 1997; Lenton, 1998).

There are two problems with the current Daisyworld models. The first is that Darwinian adaptation acts to destroy the property of self-regulation (Saunders, 1994; Robertson & Robinson, 1998). Consider again the example of an increasing solar luminosity. In Robertson and Robinson's model, black mutant daisies are introduced that can survive the warmer temperatures, and the thermostat breaks down. In fact, the mutants keep mutating, and air temperature rises ever higher, resulting in a kind of never-ending prisoner's dilemma for the planet†. The essence of the problem is that cooperation and competition are not compatible behaviors. Lenton & Lovelock (2000) have pointed out that regulation can be reinstated in "Darwinian Daisyworld" if constraints are placed on temperature adaptation.

The second problem with the current models is the need for a mechanism that selectively rewards individuals that act to improve the environment. In the real world, it is much more likely that beneficial environmental conditions will be enjoyed by all. In Daisyworld, rewards are selective because atmospheric temperature is non-uniform. Most real-world examples of Gaian phenomena appear to be more global in nature (Volk, 1998). For example, one candidate for Gaian phenomena is the amplification of rock weathering by plants and bacteria (Lovelock & Watson, 1982; Schwartzman & Volk, 1989). Weathering is a long-term phenomenon that removes CO_2 from the atmosphere, balancing the input of CO_2 from metamorphic processes and volcanism. CO_2 stabilization leads to temperature regulation, because temperature is linked to CO_2 via the greenhouse effect. So plants and bacteria have an impact on atmospheric temperature. It has been estimated by Schwartzman & Volk (1989) that if there was no amplification of rock weathering by the biota, the Earth might be 30–45°C warmer than it is today. A Daisyworld-like model for enhanced rock weathering would have to include a localized feedback mechanism that links surface temperature with weathering activity for selective feedback to occur. Such a model would be

† A similar plight awaits the planet if the overall growth rate of black daisies is allowed to mutate upwards. Faster growing black daisies will be selected, and the equilibrium temperature point will move higher and higher, eventually leading to sub-optimum conditions and low population levels for all daisies. If the white daisies are also allowed to mutate, an "arms race" between black and white daisies may keep the planet in a well-regulated state.

difficult to justify given the global nature of the forces involved. It is more likely that there exists a large-scale feedback mechanism that limits weathering as a whole, and hence regulates temperature. What is left unanswered is why the resulting equilibrium temperature should be anywhere close to optimal for plants and bacteria.

Given the problems with existing models, there is a need for a new theoretical approach. In the present article, a new formulation of Gaia theory is presented, based on Darwinian selection. There are no localized reward mechanisms. Instead, optimal conditions are heritable traits, subject to variation and selection, and evolution favors species that are best adapted to their environment. At the same time, living organisms have a profound and widespread affect on the environment. The environment is in some sense a moving target for natural selection, and the main goal of the present study is to explain why optimal conditions should converge to prevailing environmental conditions. A mechanism is described which allows convergence to take place due to the stabilizing influence of population dynamics on the environment.

Adaptive Gaia

A recent review article distinguished several types of feedback mechanisms that could regulate the environment (Lenton, 1998). One type, called feedback on selection, sees the environment as a local extension of the organism. The original Daisyworld model (Watson & Lovelock, 1983) was constructed based on this type of feedback. The other type, which is the focus of this paper, is called feedback on growth, and is driven by population dynamics. Finite resources serve to regulate populations, or equivalently, living organisms regulate the environment, through their plundering of available resources (Tyrrell, 2002). Environmental characteristics that are affected by some species through this type of population dynamics are stable under perturbations of that species' population. For example, plants and CO_2 are involved in a short-term negative feedback cycle that limits both the amount of plant material in the biosphere, and the amount of CO_2 in the atmosphere (Kump

et al., 1999). Another example is the remarkable stability of nutrient ratios in the open ocean, which are regulated by the dynamics of phytoplankton and bacterial growth (Redfield, 1958; Lenton & Watson, 2000; Tyrrell, 1999). Environmental regulation is thus an emergent property of population dynamics, not an outcome of Darwinian selection (Wilkinson, 1999, 2002).

A theoretical argument shows how the combination of population dynamics and Darwinian selection can lead to organisms with optimal conditions (preferred habitats) coincident with environmental conditions. Environmental characteristics that are candidates for being optimal include temperature, salinity, and pH, as well as the concentrations of various substances, not including those for which demand is infinite (e.g. food or limiting nutrients). Consider the case of a bacterial species having a population growth rate that is dependent on temperature in a bell-shaped manner, such that the maximum growth rate occurs at some optimal temperature for the species. If optimal temperature is a heritable trait, subject to variation and selection, then any strain of bacteria having optimal temperature closer to the actual temperature will be selected. If the actual temperature is unaffected by bacterial populations, then according to the usual Darwinian argument, the optimal temperature will eventually converge on the actual temperature. On the other hand, if the bacterial population affects temperature, that dependence will either be related to some effect of bacterial metabolism, or will be related to levels of nutrients or waste products, both of which are dependent on bacterial population levels. In either case, after selection occurs, there will be a slightly higher level of population, a slight depletion of resources, and a corresponding shift in temperature. As evolution proceeds over time, more and more adaptation will be required to produce smaller and smaller increases in population, because the bacterial nutrients will become more and more depleted, limiting the ability of bacteria to expand their numbers. Hence there will be smaller changes in temperature as time goes by. So while the optimal conditions for organisms may evolve at any rate, subject to the dynamics of variation and selection, the rate of change of environmental conditions should

decrease over time, eventually leading to a convergence of optimal and environmental conditions, assuming no external forcing. The resulting environmental conditions will also be stable under perturbations of population. *In summary, Darwinian selection should lead to organisms that are well adapted to their environment, even when environmental conditions are affected by those very same organisms.*

A Daisyworld Model

It is useful at this stage to present a new version of Daisyworld, similar to the original version (Watson & Lovelock, 1983), but which illustrates the convergence of optimal conditions and equilibrium environmental conditions. The Appendix contains a more general mathematical discussion. In the new Daisyworld model there are only white daisies. White daisies reflect sunlight, limiting the amount of energy hitting the planetary surface. In the original Daisyworld model, there was competition between daisies for land. In this new model, the daisies compete for energy, which is treated as the limiting raw material for growth. As the white daisies proliferate, more and more sunlight is reflected back to space, leaving less energy for new daisies. The resulting population limit represents an equilibrium point for the system. The growth rate of daisies is a function of temperature, having the same form as the original model, but now temperature is uniform over the surface. Since every plant experiences the same temperature, there are no selective pressures favoring plants that alter the environment for their own benefit. Note that in a low temperature world it would be advantageous for daisies if their color could change to black, because black daisies would warm the planet. But since temperature is uniform, there are no selective pressures favoring black mutants. Although color mutation might lead to a mix of colored daisies through stochastic effects, the outcome is arbitrary. The present model has been kept simple by not allowing any color mutation.

White daisies have an assumed albedo (or reflectivity) of 0.75, whereas the ground is assumed to be dark, with an albedo of 0.25.

The albedo of the planet, A, is then given by

$$A(x) = A_g(1 - x) + A_d x, \qquad (1)$$

where $A_g = 0.25$, $A_d = 0.75$, and x is the proportion of the planet covered by daisies. The energy flux reaching the surface of Daisyworld is

$$E(x) = SL(1 - A(x)), \qquad (2)$$

where L is a dimensionless luminosity parameter for the sun (equal to 1 on Earth at the present time), and $S = 917 \, \text{W m}^{-2}$ is the solar flux constant. The planet is assumed to radiate heat according to the Stefan–Boltzman law. Balancing incoming and outgoing energy, we obtain an expression for temperature:

$$\sigma(T + 273)^4 = E(x) \qquad (3)$$

with Stefan's constant $(\sigma) = 5.67 \times 10^{-8}$ $\text{W m}^{-2} \text{K}^{-4}$. Population growth and decay are governed by the following equation:

$$\frac{\dot{x}}{x} = G(x) \equiv kE(x)\beta(T) - \gamma, \qquad (4)$$

where k is a constant (to be determined), $\gamma = 0.3 \, \text{yr}^{-1}$ is the death rate, and $kE(x)\beta(T)$ is the overall birth rate. $\beta(T)$ is a parabolic function of temperature:

$$\beta(T) = 1 - \left(\frac{T - T_0}{\lambda}\right)^2. \qquad (5)$$

The parameter λ is a measure of the width of the growth response as a function of temperature (here $\lambda = 17.5°\text{C}$), and T_0 is the optimum temperature for growth (preferred habitat). We are assuming that there are no time lags between the different processes. *In the present model, evolution occurs through variation in T_0.* An obvious extension of the model would be to allow variation in λ, but λ has been kept constant for now.

The dynamical equation (4) contains a resource factor, $kE(x)$, which replaces the $1 - x$ factor in the original model (Watson & Lovelock, 1983). Energy flux is now treated as the limiting resource, which is regulated by daisies, while temperature is the secondary characteristic,
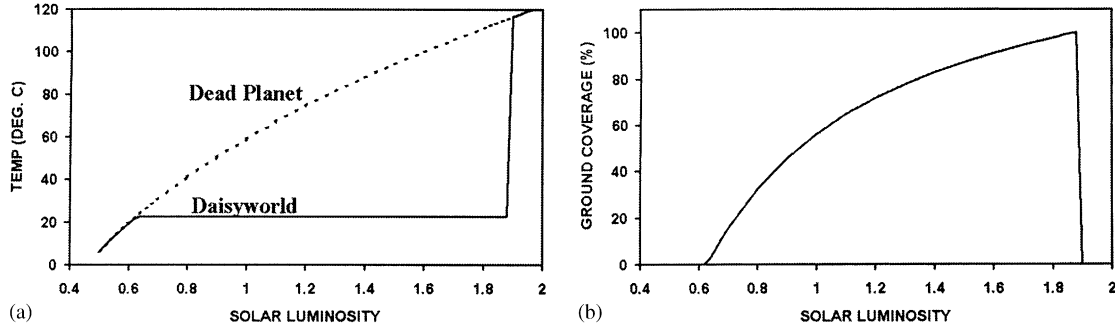
Fig. 1. Homeostasis on Daisyworld. (a) Temperature is well regulated as long as solar luminosity lies between 0.6 and 1.9. When luminosity is lower than 0.6, the presence of daisies cause the temperature to fall below the threshold for growth. When the luminosity rises above 1.9, daisies have already saturated the planet, and there is no room for more daisies to reflect the additional sunlight. Hence the temperature rises above the optimum 22.5°C, leading to a reduction in population, which leads to a warmer planet, quickly leading to the extinction of daisies. (b) The population of Daisies increases in tandem with increases in luminosity, so as to maintain net energy flow to the planet constant.

determined by energy flux. The parameter "k" represents the productivity of daisies, i.e. their ability to translate sunlight into population growth. The higher the value of "k", the higher the rate of population growth for a given amount of incident energy $E(x)$. It should be noted that all simple models of population dynamics as well as more sophisticated models that utilize the Michaelis–Menten formula contain such a parameter. The left-hand side of equation (4) has the units of yr^{-1}, which are matched by the units of kS on the right-hand side. The original Daisyworld model (Watson & Lovelock, 1983) implicitly contains a parameter having the units of yr^{-1} in the definition of β, although its value happens to be equal to 1, whereas in the present model β is kept dimensionless. We can arbitrarily choose a value of k by forcing the equilibrium solution of eqn (4) to occur at a temperature of 22.5°C when $L = 1$ and $T_0 = 22.5°C$ ($k = 6.94 \times 10^{-4}$ W^{-1} m^2 yr^{-1}). This equilibrium point occurs when $x = 0.56$, the planetary albedo is 0.53, and $kS = 0.636$ yr^{-1}. It is easily verified that the equilibrium point, x_f, satisfies the following stability criteria:

$$G(x_f) = 0, \text{ and } \left.\frac{\partial G(x)}{\partial x}\right|_{x=x_f} < 0. \quad (6)$$

Before delving into the dynamics of Darwinian selection, it is instructive to investigate the homeostatic properties of this model. It turns out that planetary temperature is regulated over a wide range of solar luminosities. If we slowly increase luminosity, and allow the system to come to equilibrium at each step, the daisy population grows just enough to reflect the excess energy, and so maintain the temperature at 22.5°C. As shown in Fig. 1, the equilibrium temperature is independent of L over a large range. Analytically:

$$T_{equil} = \left(\frac{\gamma}{k\sigma}\right)^{1/4} - 273. \quad (7)$$

It is possible that a system obeying eqns (1)–(5) could exist with any value of T_0. For example, since daisies are the only life form on Daisyworld, they must have originated at some time on a dead planet. It is reasonable to assume that the optimal temperature for growth at that time was the prevailing dead-planet temperature. At a luminosity of 1, the dead-planet temperature is 59°C and if we set $T_0 = 59°C$ and $L = 1$ in eqns (1)–(5), the equilibrium temperature turns out to be 49°C, which is below optimum for these proto-daisies.

The unique characteristic of the new Daisyworld model is that Darwinian selection inevitably drives the evolution of optimal and equilibrium temperatures down to 22.5°C. Consider what happens if we allow mutation of T_0. Equations (4) and (5) must be replaced by the

following system:

$$\frac{\dot{x}}{x} = kE(x + x')\beta(T) - \gamma,$$

$$\beta(T) = 1 - \left(\frac{T - T_0}{\lambda}\right)^2 \qquad (8a)$$

and

$$\frac{\dot{x'}}{x'} = kE(x + x')\beta'(T) - \gamma,$$

$$\beta'(T) = 1 - \left(\frac{T - T_0'}{\lambda}\right)^2, \qquad (8b)$$

where x, $\beta(T)$, and T_0 refer to the original population, while x', $\beta(T)$, and T_0' refer to the mutants. T is now a function of $x + x'$ through its dependence on $E(x + x')$ in equation (3). There are no fixed-point solutions of eqns (8a) and (8b) that allow for the coexistence of both types of daisies, so one of the types must be driven to extinction. If $T_0 = 59°C$ and T_0' is greater than T_0, then $\beta'(T) < \beta(T)$ for all values of T less than T_0, including at the equilibrium temperature of 49°C. The only stable solution of eqns (8a) and (8b) is $x' = 0$, hence these mutants cannot survive. However, if T_0' is less than T_0, $\beta'(T) > \beta(T)$ at the equilibrium temperature, and the mutants take over. These higher growth mutants cause the albedo to increase, further cooling the planet. If variation and selection is allowed to continue, both the optimum tempera-

ture T_0, and the equilibrium temperature continue to drop, until they are both equal to 22.5°C, after which there is no further evolution of temperature. Fig. 2(a) shows the time course of the optimal and equilibrium temperatures, assuming for the sake of argument that the optimal temperature mutates at a rate of 1°C per million years.

Sensitivity Analysis

The final point of convergence depends on the parameters of the dynamical system. In Daisyworld, the key determinant of the final temperature according to eqn (7) is k, which represents the productivity of daisies. We deliberately chose a value of k that led to a final temperature of 22.5°C. Other values of k lead to different final temperatures. Table 1 lists the outcome of several simulation runs, and shows how the final condition of the planet depends on k (kS for convenience), L, and the initial optimal temperature of daisies. Note that the final temperature is independent of L for a given value of k. For example, at $kS = 0.636$ (the value used in the previous section), if the luminosity is set to 1.2, the initial dead-planet temperature becomes 74.3°C, but the end-point temperature is still 22.5°C. Increasing the luminosity leads to an increase in final land coverage and albedo, which compensates for the added energy. In part (b) of Table 1, the ground albedo is raised to 0.45 and the daisy albedo is lowered to 0.55. The line in
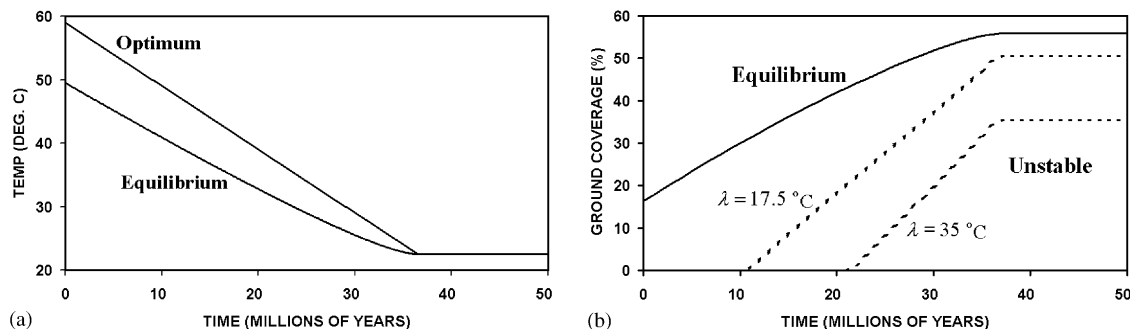

FIG. 2. Convergence of optimality and equilibrium. (a) At first there is a wide separation between the optimal and equilibrium temperatures. But natural selection favors variants with optimal points closer to the equilibrium point. As evolution proceeds, both points shift in value, but eventually, there is convergence. Note that in the real world, convergence may occur gradually as shown here, or in jumps due to evolutionary innovations. (b) The top line shows the equilibrium level of ground coverage (stable attractor). The lower two lines show the threshold for instability for two different λ parameters. If the population drops below these lines, regulation breaks down, and the population of daisies quickly goes to zero.

TABLE 1

Sensitivity of final convergence conditions to selected parameter values and initial conditions. (a) *Albedo values used in the initial Daisyworld model.* (b) *A smaller difference in albedo between ground and daisies leads to a smaller acceptable range of parameters*

KS (yr^{-1})	L	Initial Daisy optimal temperature (°C)			Final convergence conditions		
		Minimum	Dead planet	Maximum	Temperature (°C)	Land coverage	Albedo
(a) *Ground albedo = 0.25, Daisy albedo = 0.75*							
0.3	1.4	84.2	88.0	91.8	83.6	0.07	0.29
0.4	1.0	58.9	58.9	58.9	58.8	0.00	0.25
0.4	1.2	67.2	74.3	81.5	58.9	0.25	0.37
0.4	1.4	78.6	88.0	97.3	58.9	0.43	0.46
0.5	0.8	40.9	40.9	40.9	40.8	0.00	0.25
0.5	1.0	51.0	58.9	66.7	40.9	0.30	0.40
0.5	1.2	64.2	74.3	84.4	40.9	0.50	0.50
0.5	1.4	76.5	88.0	99.4	40.9	0.64	0.57
0.636	0.8	32.8	40.9	49.0	22.5	0.32	0.41
0.636	**1.0**	**48.2**	**58.9**	**69.5**	**22.5**	**0.56**	**0.53**
0.636	1.2	62.3	74.3	86.4	22.5	0.71	0.61
0.636	1.4	75.0	88.0	101.0	22.5	0.83	0.66
0.7	0.6	15.3	19.1	22.9	15.5	0.07	0.29
0.7	0.8	31.5	40.9	50.2	15.5	0.43	0.46
0.7	1.0	47.4	58.9	70.3	15.5	0.64	0.57
0.7	1.2	61.7	74.3	87.0	15.5	0.79	0.64
0.7	1.4	74.5	88.0	101.5	15.5	0.89	0.69
0.8	0.6	11.9	19.1	26.2	6.1	0.25	0.37
0.8	0.8	30.1	40.9	51.6	6.1	0.56	0.53
0.8	1.0	46.5	58.9	71.2	6.1	0.75	0.62
0.8	1.2	61.0	74.3	87.7	6.1	0.87	0.69
0.8	1.4	74.0	88.0	102.0	6.1	0.96	0.73
(b) *Ground albedo = 0.45, Daisy albedo = 0.55*							
0.4	1.4	58.2	61.1	63.9	58.9	0.14	0.46
0.5	1.2	43.2	48.4	53.7	40.9	0.50	0.50
0.636	**1.0**	**27.5**	**34.1**	**40.7**	**22.5**	**0.79**	**0.53**
0.7	0.8	14.6	17.4	20.3	15.5	0.14	0.46
0.8	0.8	10.7	17.4	24.2	6.1	0.81	0.53

bold contains the same values of kS and L that were used in the previous section, and the final temperature and albedo are the same as before, but the required land coverage is greater (0.79 instead of 0.56).

Not all values of kS and L lead to stability and convergence. If either of these two quantities is too low, then even if $\beta(T) = 1$ the growth rate may lie below threshold. The higher the ground albedo, the higher the required values of kS and/ or L, because there is less net energy available to the daisies. On the other hand, if kS or L is too large, the growth rate may be so high that the planet becomes saturated with daisies ($x = 1$) before equilibrium is achieved at the point of convergence [where $\beta(T) = 1$ also]. The lower the daisy albedo, the lower the maximum allowed values for kS and L, because low-albedo daisies require more land coverage in order to come to equilibrium. In a realistic model, other constraints on growth would probably cause the population to come to equilibrium before saturation of land is attained. The following lower and upper bounds on kSL are easily derived by setting eqn (4) to zero (with $\beta(T) = 1$) at $x = 0$ and 1, respectively.

$$\frac{\gamma}{1 - A_g} < kSL < \frac{\gamma}{1 - A_d}, \qquad (9)$$

where A_g is the ground albedo (0.25 in the initial discussion), and A_d is the daisy albedo (0.75 in the initial discussion). Equation (9) shows why there are less possible combinations of kS and L in part (b) of Table 1 than in part (a) because of the smaller difference between A_g and A_d.

Since the parameter k is a characteristic of daisies, it is possible that it could itself be subject to variation and selection pressure. In any competition between daisies, the species having the largest value of k will win, and so we expect that k will increase over time. Consider the case where the optimal and equilibrium temperatures have already converged, and some variant arises which has a larger value of k than the prevailing population. This variant will drive the other daisies to extinction, and cause the equilibrium temperature to drop. If a new variant now arises having the same value of k but a lower optimal temperature, it will be selected. Eventually, such rounds of variation and selection will once again lead to the convergence of equilibrium and optimal temperatures.

The third and fifth columns of Table 1 list the minimum and maximum values of initial optimal temperature of daisies. If the initial optimal temperature falls outside this range, the daisies cannot get off the ground because their growth rate is below the threshold of growth, due to the influence of the $\beta(T)$ function [see eqn (5)]. However, it is reasonable to expect that the initial optimal temperature would be equal to the dead-planet temperature, which is halfway between the minimum and maximum optimal temperatures. Note that the higher the λ value, the wider the range of allowed initial optimal temperatures.

The parameter λ does not have any affect on the temperature of convergence, but it does have a strong influence on the stability properties of Daisyworld. As already mentioned, the system is very stable under perturbations of luminosity over a wide range. However, the same cannot be said for perturbations of population. The system can handle any *increase* in population, since the white daisies will reflect more light and hence lower the growth rate. But the system is at risk whenever there is a reduction of population due to some external forcing. This vulnerability gets worse over time, as the daisies adapt to an environment that is dependent on the existing population of daisies. Early in the life of the planet, daisies are able to live in the hot environment of a near-dead planet. But as the planet cools, the daisies gradually "forget" how to live on a dead planet. If there is some externally caused drop in population, it is possible that the temperature might rise to such an extent that a catastrophic positive feedback scenario occurs, leading to the extinction of all life. We can compute the threshold for catastrophe by finding the unstable fixed point x_f, where

$$G(x_f) = 0 \text{ and } \frac{\partial G(x)}{\partial x}\Big|_{x = xf} > 0. \qquad (10)$$

Note that the stable point occurs at a larger population level than the unstable point, so the only region where instability can set in is when the population is below the unstable fixed point. Fig. 2(b) shows the evolution of population, coinciding with the evolution of temperature shown in Fig. 2(a). Included in Fig. 2(b) are two catastrophe threshold lines, one corresponding to $\lambda = 17.5°C$ (the present model), and other corresponding to $\lambda = 35°C$ for comparison. It is possible that in a fully stochastic model, where λ is subject to variation and selection, λ might evolve such that the population is immune to moderate fluctuations in population. Then the remaining risk would be from an unusual event that kills off a larger portion of the population.

As long as kS and L satisfy eqn (9), and as long as the initial optimal temperature allows for growth to get started, and there are no sudden reductions of population due to external causes, the system will come to equilibrium and the optimal temperature will converge to the equilibrium temperature. In other words, as long as the system can come to equilibrium, Darwinian selection will lead to the convergence of optimal and equilibrium temperatures.

Discussion

The Daisyworld model presented in the previous sections is simple enough that one is led to speculate that Gaian phenomena are ubiquitous on Earth. One of the prerequisites for Darwinian evolution is that there are

constraints on population growth. These constraints must be enforced by regulatory systems operating on the organisms and their environment. The Earth system probably contains many such regulatory systems, some of which are driven by resource limitations, others by environmental degradation effects due to population pressures (like the white daisies blocking the sun's energy). Regulation implies the existence of stable fixed points. One of the characteristics of systems exhibiting stable fixed points is that if there is any variation in growth rate, the fastest growing species will drive all others to extinction. Or in other words, if several species share an ecological niche, the one with the highest reproductive success will be the one to survive in the long run. Hence regulation leads to competition, and organisms that are best adapted to equilibrium conditions will be selected.

One proposed Gaian system that is similar to Daisyworld links marine plankton, sulphate aerosols, cloud formation and climate (Charlson et al., 1987). The Earth's albedo is largely determined by the amount of cloud cover (clouds have high albedo), and a large percentage of clouds are located over the oceans, which have low albedo. There is evidence to suggest that marine plankton affect the amount of cloud cover over the oceans, through the release and action of dimethyl sulfide (DMS), and hence act like white daisies. It may also be the case that dimethyl sulfide emissions are positively correlated with sunlight intensity (Bates et al., 1987; Simo & Pedros-Alio, 1999; Simo, 2001), in which case the present Daisyworld model should be applicable. Marine plankton may have first appeared when the Earth's temperature was higher than it is now, and they would have contributed to a cooling of the Earth, through the effect of DMS-induced cloud formation. This cooling effect would have occurred in conjunction with other environmental effects of marine plankton. There would have been selective pressure on subsequent generations of plankton to adapt to the cooler temperatures, leading to higher levels of plankton, and even cooler temperatures. One prediction of this scenario is that the current optimal temperature for plankton growth should either coincide with the current prevailing temperature, or lie at a

higher temperature, in which case the evolution of optimal temperature is ongoing.

Another candidate Gaia phenomenon is the amplification of rock weathering by plants and bacteria (Lovelock & Watson, 1982; Schwartzman & Volk, 1989). In this case, the regulatory mechanism is most likely related to a limited supply of elemental nutrients such as phosphorus (Lenton, 1998). A side effect of population growth is the enhancement of silicate weathering, which removes CO_2 from the atmosphere, cooling the Earth. One can imagine an evolutionary scenario much like that discussed in relation to marine plankton, except that in this case, enhanced rock weathering would lead to the cooler temperatures. In this scenario, early forms of bacteria thrive in a high-temperature environment. But as their numbers increase, atmospheric temperature is lowered due to weathering activity. The drop in temperature leads to sub-optimal growth conditions, limiting the spread of bacteria. After some time, strains of bacteria form that are more suited to the lower temperatures. The new strains beat out the older bacteria in the race for nutrients. The equilibrium population rises slightly, leading to further enhancement of rock weathering, and cooler temperatures.

Adaptive Gaia theory may serve as a good framework for understanding environmental issues. One of the major preoccupations of environmental researchers is to determine if the biosphere is at risk of self-destruction caused by human activity. The central theme of this paper is that organisms are adapted to survive in an environment that is heavily influenced by life itself. Although the Earth system is self-regulating to a large extent, organisms are still vulnerable to changing conditions because they are optimized to survive best near stable points. As Fig. 2(b) warns, the more time that evolution has to operate, the more vulnerable life is to shocks. If the Earth system is perturbed too heavily, negative feedback may turn into positive feedback, and the system will break down.

In conclusion, there is theoretical justification for believing that environmental conditions on Earth are maintained close to optimal for life by negative-feedback processes involving life itself. The original Gaia hypothesis suggested that

optimal conditions for life are pre-determined, and Darwinian selection favors organisms that help maintain those conditions. In this paper, an alternative explanation for Gaian phenomena has been presented, based on more traditional Darwinian principles. In the new approach, self-regulation is a natural outcome of population dynamics, and is a prerequisite for Darwinian selection, not the other way around. The role of Darwinian selection is to favor organisms that are most capable of surviving the conditions on Earth. But the Earth is strongly influenced by the presence of life. Hence life and its environment co-evolve until the optimal conditions for life coincide with equilibrium conditions.

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APPENDIX

The purpose of this Appendix is to illustrate the convergence of optimal and equilibrium environmental conditions in multi-species ecosystems, and to determine what restrictions are required of the dynamics. As will be shown, all that is required is that the dynamics be asymptotically stable, and that equilibrium properties be dominated by resource constraints. Consider an N species system interacting with M

varieties of non-biological materials. All species cooperate in a supply chain (e.g. food web), or other non-competitive relationship. For example, the system might consist of two types of organisms, one animal and the other plant, and two gases, carbon dioxide and oxygen. The dynamics can be written as follows:

$$\frac{\dot{x}_i}{x_i} = G_i(\lambda_i, \mathbf{x}, \mathbf{m}) \quad \dot{m}_j = F_j(\mathbf{x}, \mathbf{m}), \quad (A.1)$$

where $\mathbf{m}$ is the vector of material quantities ($j = 1 \ldots M$), $\mathbf{x}$ is the population vector of species ($i = 1 \ldots N$), and λ_i is a convenient parameter representing the individual fitness characteristics of each species i. Each species follows Malthusian growth, so G_i is finite and non-zero at $x_i = 0$. Since the non-biological materials do not replicate, they follow non-Malthusian dynamics. A fixed point $(\mathbf{x}_f, \mathbf{m}_f)$ is characterized by $G_i(\lambda_i, \mathbf{x}_f, \mathbf{m}_f) = 0$, and $F_j(\mathbf{x}, \mathbf{m}) = 0$ for all i, j. According to perturbation analysis, the fixed point is stable if all eigenvalues of the Jacobian matrix of eqn (A.1) have negative or zero real parts. If any eigenvalue has zero real part, then either there is some linear combination of population and material that is undetermined, or the system exhibits permanent oscillations, as in the Lotka–Volterra predator–prey system. *The present analysis only applies to systems that are asymptotically stable,* i.e. *all eigenvalues have negative real parts.* If it happens that a particular system of interest has eigenvalues with zero real parts, the following analysis may still be applied to the subspace of $(\mathbf{x}, \mathbf{m})$ that satisfies the conditions of asymptotic stability.

Now consider the situation where a variant of species k, labeled k', arises in direct competition with the original species k. The variants differ from the original organisms by having a different value of λ_k. The biological part of system (A.1) must then be replaced with:

$$\frac{\dot{x}_i}{x_i} = G_i(\lambda_i, \{x_l\}, x_k + x'_k, \mathbf{m}), \quad i, l \neq k, \quad (A.2.1)$$

$$\frac{\dot{x}_k}{x_k} = G_k(\lambda_k, \{x_l\}, x_k + x'_k, \mathbf{m}), \quad l \neq k, \quad (A.2.2)$$

$$\frac{\dot{x}'_k}{x'_k} = G_k(\lambda'_k, \{x_l\}, x_k + x'_k, \mathbf{m}), \quad l \neq k. \quad (A.2.3)$$

At equilibrium, all time derivatives are zero, but in general, the right-hand sides of eqns (A.2.2) and (A.2.3) cannot both be zero, so either $x_k = 0$, or $x'_k = 0$ (survival of the fittest). The species with the largest G_k wins, as can be verified using perturbation analysis. Let us assume that the variant win the contest. At first, the right-hand side of eqn (A.2.3) will be greater than zero. *But since the system is asymptotically stable, the population levels of all species will adjust until $G_k = 0$ once again (after x_k has diminished to zero).* We are assuming that there is no intermediate point along the path taken by $\mathbf{x}$ at which the original population of species k can coexist with the variant population. The total change in G_k will be zero by the time the system returns to equilibrium. So defining $\lambda'_k = \lambda_k + d\lambda_k$, we have

$$0 = dG_k = \frac{\partial G_k}{\partial \lambda_k} d\lambda_k + \sum_i \frac{\partial G_k}{\partial x_i} dx_i + \sum_j \frac{\partial G_k}{\partial m_j} dm_j$$

$$(A.3)$$

But the first term in eqn (A.3) is positive; otherwise the variants would not survive. Hence, the amount that the population vector $(d\mathbf{x}, d\mathbf{m})$ changes during the process of selection for species k satisfies the following inequality:

$$\sum_i \frac{\partial G_k}{\partial x_i} dx_i + \sum_j \frac{\partial G_k}{\partial m_j} dm_j < 0. \quad (A.4)$$

Now consider a new version of eqn (A.1) that explicitly separates the contributions of individual environmental fitness, and external resource constraints:

$$\frac{\dot{x}_i}{x_i} = G_i[f_i(\mathbf{x}, \mathbf{m}), r_i(\mathbf{x}, \mathbf{m})], \quad \dot{m}_j = F_j(\mathbf{x}, \mathbf{m}), \quad (A.5)$$

where

$$f_i(\mathbf{x}, \mathbf{m}) = e(\mathbf{x}, \mathbf{m}) - (e_0)_i.$$

$f_i(\mathbf{x}, \mathbf{m})$ is the individual fitness function, which is in turn expressed in terms of the difference between some environmental parameter, $e(\mathbf{x}, \mathbf{m})$,

(such as temperature) and the optimal environment for species i: $(e_0)_i$. $(e_0)_i$ replaces the parameter λ_i in eqn (A.1). The functional dependence of G_i on f_i is assumed to be bell-shaped, such that the closer $(e_0)_i$ is to e, the larger G_i becomes. $r_i(\mathbf{x}, \mathbf{m})$ is the resource contribution to growth, and dominates the equilibrium properties of the system.

In order for the convergence of equilibrium and optimality to occur, we must assume that resource limitations regulate the population of organisms no matter what their individual growth characteristics are. That is, condition (A.4) applies to the resource part of the dynamics during the process of selection:

$$\frac{\partial G_k}{\partial r_k}\left(\sum_i \frac{\partial r_k}{\partial x_i}\mathrm{d}x_i + \sum_j \frac{\partial r_k}{\partial m_j}\mathrm{d}m_j\right) < 0. \quad (A.6)$$

In practical application, eqn (A.6) must be verified using the equations of the system under study. We can now derive a condition on the evolution e_f in terms of $\mathrm{d}(e_0)_k$ by noting that

$$\mathrm{d}e_f = \sum_i \frac{\partial e}{\partial x_i}\mathrm{d}x_i + \sum_i \frac{\partial e}{\partial m_j}dm_j, \quad (A.7)$$

where $(\mathrm{d}\mathbf{x}, \mathrm{d}\mathbf{m})$ is the change in quantities during selection, after equilibrium has been restored. Applying conditions (A.3) and (A.6) to eqn (A.5), and using the expression for $\mathrm{d}e_f$ in eqn (A.7), we obtain the central result:

$$\frac{\partial G_k}{\partial (e_0)_k}(\mathrm{d}(e_0)_k - \mathrm{d}e_f) > 0. \quad (A.8)$$

This condition allows us to conclude that equilibrium and optimality will converge during the process of variation and selection. To show this, it is useful to define the parameter changes in terms of their end points: $\mathrm{d}(e_0)_k = (e_0)_k' - (e_0)_k$, and $\mathrm{d}e_f = e_f' - e_f$, and assume that all environmental quantities are positive. There are three cases to consider:

Case 1: $(e_0)_k < e_f$. In this case, $\mathrm{d}(e_0)_k$ must be positive to be selected, since that will take $(e_0)_k$ closer to e_f, and the growth rate of the variant will be larger than that of the original species k. Also, $\partial G_k / \partial (e_0)_k$ will be positive, and so $\mathrm{d}(e_0)_k - \mathrm{d}e_f > 0$, and hence $e_f' - (e_0)_k' < e_f - (e_0)_k$.

Case 2: $(e_0)_k > e_f$. In this case, $\mathrm{d}(e_0)_k$ is negative, and $\partial G_k / \partial (e_0)_k$ is negative, so $\mathrm{d}(e_0)_k - \mathrm{d}e_f < 0$, hence $(e_0)_k' - e_f' < (e_0)_k - e_f$.

Case 3: $(e_0)_k = e_f$. This is the end point of evolution as far as the present analysis is concerned. Any variant of species k with different $(e_0)_k$ will not be selected because its growth rate will be less than that of the prevailing population.

The above analysis applies to all species, so it is expected that the in the long run, $(e_0)_i$ will approach e_f for all i.