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Darwinian Evolution Does Not Rule Out the Gaia Hypothesis

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This study explores so-called Darwinian Daisyworlds mathematically rigorously in detail. The original Daisyworld was introduced by Watson & Lovelock (1983) to demonstrate how two species of daisies regulate the global temperature of their planet through competition among these species against the rising solar luminosity, i.e. the Gaia hypothesis. Its variants are Darwinian Daisyworlds in which daisies can adapt themselves to the local temperature. Robertson & Robinson (1998) insist their Darwinian daisies lose the ability for temperature regulation on the basis of their spreadsheet simulations. Lenton & Lovelock (2000) point out that the constraints on adaptation recovers Darwinian daisies' ability of temperature regulation on the basis of their Euler-code simulations. The present study shows there exist the exact and closed-form solutions to these two Daisyworlds. The results contradict the former studies: Robertson and Robinson's daisies do regulate the global temperature even longer than non-adaptive daisies; Lenton and Lovelock's daisies are less adaptive than Robertson and Robinson's daisies because of the constraints on adaptation; the introduction of weak adaptability drives species into a dead end of evolution. Thus, the present results confirm that the Gaia hypothesis and Darwinian evolution can coexist.

Introduction

Watson & Lovelock (1983) proposed a model called Daisyworld to demonstrate how the life on a planet can regulate the global environment via competition among species, i.e. the Gaia hypothesis. Later Saunders (1994) investigated Daisyworld mathematically rigorously and derived several formulas to describe the steady-state Daisyworld. He is the first to use the word Darwinian Daisyworld by which he pointed out the adaptation to local temperatures might decrease daisies' ability of regulating the global temperature. Robertson & Robinson (1998) presented their Darwinian Daisyworld and concluded that the adaptive evolution of daisies eliminates their ability for regulating the environment. Lenton & Lovelock (2000) rebutted against them by introducing the constraints on adaptation into the former Daisyworld model. They showed that species with the constrained adaptation do regulate the global environment, while freely adaptive species cannot do that. The aim of this study is first to show that there exist the exact and closed-form one-line formulas for the equilibrium in Darwinian Daisyworlds. These formulas reveal the true nature of Darwinian Daisyworlds that contradicts the former studies.

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Formulation

BASIC EQUATIONS

I shall describe the full set of the basic equations introduced by Watson & Lovelock (1983), Robertson & Robinson (1998) and Lenton & Lovelock (2000).

The total area of Daisyworld is a_e having unity as its value, while a_b and a_w represent the area covered by black and white daisies, respectively. The growth of a_b and a_w, or the population dynamics, is governed by a variant set of Haale's ordinary differential equations in terms of time t:

$$\frac{\mathrm{d}a_b}{\mathrm{d}t} = a_b\{(a_e - a_b - a_w)\beta_b - \gamma\}, \tag{1}$$

$$\frac{\mathrm{d}a_w}{\mathrm{d}t} = a_w\{(a_e - a_b - a_w)\beta_w - \gamma\}, \tag{2}$$

where the death rate γ is 0.3 for both species; β_b and β_w are the growth rates of black and white daisies, respectively, which I will describe in detail later.

The Stefan–Boltzmann law determines the average global temperature T_e as well as the local temperatures T_b for black daisies and T_w for white daisies in terms of solar flux and albedos:

$$(T_e + 273)^4 = (1 - A)SL/\sigma, \tag{3}$$

where σ is Stefan's constant, i.e. $5.6697 \times 10^{-8}\,\mathrm{W\,m^{-2}\,K^{-4}}$; albedos are given by

$$\begin{aligned} A &= A_g + (A_b - A_g)\frac{a_b}{a_e} + (A_w - A_g)\frac{a_w}{a_e} \quad \text{global average,} \\ A_g &= 0.5 \quad \text{for bare ground,} \\ A_b &= 0.25 \quad \text{for black daisy area,} \\ A_w &= 0.75 \quad \text{for white daisy area;} \end{aligned} \tag{4}$$

solar flux is expressed as the product of today's value $S = 917\,\mathrm{N\,m^{-2}\,s^{-1}}$ and L, a non-dimensional constant called solar luminosity. The local temperatures are expressed by use of the term q representing the effect of heat diffusion with the value $2.06425 \times 10^9\,\mathrm{K}^4$:

$$(T_i + 273)^4 = (1 - A)SL/\sigma + (A - A_i)q, \tag{5}$$

where the subscript i denotes either b or w depending on which species of daisies is meant.

Both the population dynamics and the thermodynamics are interrelated by the growth rates of daisies:

$$\beta_i = \max\left[0, m(T_{opt,\,i})\left\{1 - \left(\frac{T_i - T_{opt,\,i}}{17.5}\right)^2\right\}\right], \tag{6}$$

where the function m represents the constraints on adaptation:

$$m(T_{opt,\,i}) = \begin{cases} 1 & \text{for Robertson and Robinson model,} \\ 1 - \left(\dfrac{T_{opt,\,i} - 22.5}{77.5}\right)^2 & \text{for Lenton and Lovelock model.} \end{cases} \tag{7}$$

In the original Daisyworld the optimum temperatures $T_{opt,\,i}$ are fixed at 22.5. In Darwinian Daisyworlds $T_{opt,\,i}$ is subject to the adaptation process against the solar luminosity increasing in geological time. Robertson & Robinson (1998) introduced the relation

$$L = \left(1 - \frac{0.38t}{4.55}\right)^{-1}, \tag{8}$$

where t is measured by the Gyr. They also described the adaptation process to the change in the local temperatures by the following model:

$$T_{opt,\,i}(t + \Delta t) = T_{opt,\,i}(t) + a\big(T_i(t) - T_{opt,\,i}(t)\big), \tag{9}$$

where a is a relaxation factor taking values in (0,1]; Robertson & Robinson (1998) adopted 40 Myr as the time step Δt.

Thus solving the full set of the basic equations, we shall ask: how two daisies grow by changing their environment through the corresponding albedos; how the growth rates are changed by their environment; what will become of the global temperature. This is Daisyworld.

ASSUMPTION ON TIME-SCALES

To eliminate any ambiguity on the time-scale in eqn (8) I will introduce an assumption as follows.

In the original Daisyworld L is a parameter, but in Darwinian Daisyworlds L depends on the time with its typical time-scale Δt as extremely large as 40 Myr. Nevertheless, we have already one particular time-scale in the form of the growth rate β_i and the death rate γ. Since Daisyworld was first introduced as a parable, there was no explicit description about the particular measure of β_i and γ. But it is obvious:

$$\Delta t^{-1} \ll \beta_i \text{ and } \Delta t^{-1} \ll \gamma.$$

How many times do daisies repeat their life cycles during Δt? The equilibrium of the population dynamics is obtained by tending t to infinity, but this infinity is not the geological eternity but a mathematical metaphor of sufficiently large time for that phenomenon. The population dynamics reaches the equilibrium almost instantly compared to Δt.

In short my concern is the equilibrium.

Derivation of the Exact Solutions

INITIAL STATE IN DARWINIAN DAISYWORLDS

Robertson & Robinson (1998) started their simulation from $t = -3.5$ Gyr, while Lenton & Lovelock (2000) started their simulation from $t = -4.0$ Gyr. Around these ages life on the earth are supposed to appear. In any Daisyworld both daisies can exist even as early as $t = -4.0$ Gyr. This fact will be verified later by use of our formulas. So we shall start with the case of two-species Darwinian Daisyworlds.

The initial stage is the same as the original Daisyworld. I will derive the results after Saunders (1994). Let t_0 be the initial time, and the following holds between the initial optimum temperatures:

$$T_{opt,\,b}(t_0) = T_{opt,\,w}(t_0) = 22.5. \tag{10}$$

Since daisy populations stop growing in equilibrium, the left-hand sides of eqns (1) and (2) are equal to zero. Therefore,

$$a_b\{(a_e - a_b - a_w)\beta_b - \gamma\} = 0, \tag{11}$$

$$a_w\{(a_e - a_b - a_w)\beta_w - \gamma\} = 0. \tag{12}$$

We are not interested in the single-species solutions or the trivial solution, i.e. $a_b = a_w = 0$, so we insist the following must hold:

$$\beta_b = \beta_w. \tag{13}$$

From eqns (6), (7) and (10) and the relation above, we arrive at the relation:

$$(T_b - 22.5)^2 = (T_w - 22.5)^2.$$

Introducing a positive constant α_0, we shall equate the both sides of the relation above with α_0^2. Then the following holds:

$$T_b = 22.5 + \alpha_0, \tag{14}$$

$$T_w = 22.5 - \alpha_0, \tag{15}$$

because the local temperature of black daisies is higher than that of white daisies. This α_0 is shown to be a universal constant in the following. Subtracting eqn (5) of white daisies from eqn (5) of black daisies, we obtain the relation:

$$(T_b + 273)^4 - (T_w + 273)^4 = 0.5q. \tag{16}$$

Substituting eqns (14) and (15) in eqn (16), a bit of algebra leads us to the cubic equation in terms of α_0:

$$\alpha_0^3 + 295.5^2\alpha_0 - \frac{q}{4728} = 0.$$

This has one and only real root:

$$\alpha_0 = 4.998568\cdots$$

Saunders (1994) rounded this figure to obtain 5.

TWO-SPECIES STATE IN DARWINIAN DAISYWORLDS: TEMPERATURES

Let us examine how daisies adapt themselves to the local temperatures in the next stage $t = t_0 + \Delta t$.

Substituting eqns (10), (14) and (15) in eqn (9), we obtain

$$T_{opt,\,b}(t_0 + \Delta t) = 22.5 + a\alpha_0, \qquad (17)$$

$$T_{opt,\,w}(t_0 + \Delta t) = 22.5 - a\alpha_0. \qquad (18)$$

To become in equilibrium, eqn (13) must hold again. Noting the relations (17) and (18), Lenton and Lovelock's m functions of eqn (7) satisfy the equality at $t = t_0 + \Delta t$:

$$m(T_{opt,\,b}) = m(T_{opt,\,w}) = 1 - \left(\frac{a\alpha_0}{77.5}\right)^2.$$

Therefore condition (13) is reduced to the following form for both Darwinian Daisyworlds:

$$\{T_b - (22.5 + a\alpha_0)\}^2 = \{T_w - (22.5 - a\alpha_0)\}^2.$$

Equating both sides of the relation above with the square of a positive constant α_1, we can lead the relations:

$$T_b = 22.5 + (a\alpha_0 + \alpha_1),$$

$$T_w = 22.5 - (a\alpha_0 + \alpha_1).$$

Since these temperatures must satisfy relation (16), we become aware

$$a\alpha_0 + \alpha_1 = \alpha_0.$$

That is

$$\alpha_1 = (1 - a)\alpha_0,$$

and hence

$$T_b(t_0 + \Delta t) = 22.5 + \alpha_0,$$

$$T_w(t_0 + \Delta t) = 22.5 - \alpha_0.$$

Although the daisies have evolved, the local temperatures stay the same as before. This fact holds true as far as the two daisies coexist in any Daisyworld. Saunders (1994) proved that for the original Daisyworld, so in case of Darwinian Daisyworlds I shall show that the following relations hold for $n \geqslant 1$ with the aid of mathematical induction.

$$T_b(t_0 + n\Delta t) = 22.5 + \alpha_0, \qquad (19)$$

$$T_w(t_0 + n\Delta t) = 22.5 - \alpha_0, \qquad (20)$$

$$T_{opt,\,b}(t_0 + n\Delta t) = 22.5 + \{1 - (1 - a)^n\}\alpha_0, \qquad (21)$$

$$T_{opt,\,w}(t_0 + n\Delta t) = 22.5 - \{1 - (1 - a)^n\}\alpha_0. \qquad (22)$$

I have already shown that the relations above hold for $n = 1$.

Suppose these relations hold in case of $n = k$, then the optimum temperature for black daisies at $t = t_0 + (k + 1)\Delta t$ is given as follows:

$$\begin{aligned} T_{opt,\,b}(t_0 + (k+1)\Delta t) &= T_{opt,\,b}(t_0 + k\Delta t) \\ &\quad + a\big\{T_b(t_0 + k\Delta t) - T_{opt,\,b}(t_0 + k\Delta t)\big\} \\ &= 22.5 + \big\{1 - (1 - a)^k\big\}\alpha_0 \\ &\quad + a\big[22.5 + \alpha_0 - 22.5 - \big\{1 - (1 - a)^k\big\}\alpha_0\big] \\ &= 22.5 + \big\{1 - (1 - a)^{k+1}\big\}\alpha_0, \end{aligned}$$

and in the same manner

$$\begin{aligned} &T_{opt,\,w}(t_0 + (k+1)\Delta t) \\ &= 22.5 - \big\{1 - (1 - a)^{k+1}\big\}\alpha_0. \end{aligned}$$

Therefore, eqns (21) and (22) hold true in the case of $n = k + 1$ and hence for any $n \geqslant 1$. Because of these relations, Lenton and Lovelock's m functions satisfy the following relation:

$$\begin{aligned} &m(T_{opt,\,b}) = m(T_{opt,\,w}) \\ &= 1 - \left[\frac{\big\{1 - (1 - a)^{k+1}\big\}\alpha_0}{77.5}\right]^2, \end{aligned}$$

and hence we obtain the reduced form of the requirement of the equilibrium (13) in the case of $n = k + 1$ for both Darwinian Daisyworlds as follows:

$$\left\langle T_b - \left[22.5 + \left\{1-(1-a)^{k+1}\right\}\alpha_0\right]\right\rangle^2$$

$$= \left\langle T_w - \left[22.5 - \left\{1-(1-a)^{k+1}\right\}\alpha_0\right]\right\rangle^2.$$

Equating both sides of the relation above with the square of a positive constant α_{k+1}, we can lead the relations:

$$T_b(t_0 + (k+1)\Delta t)$$

$$= 22.5 + \left[\left\{1-(1-a)^{k+1}\right\}\alpha_0 + \alpha_{k+1}\right],$$

$$T_w(t_0 + (k+1)\Delta t)$$

$$= 22.5 - \left[\left\{1-(1-a)^{k+1}\right\}\alpha_0 + \alpha_{k+1}\right].$$

Therefore, applying the very same argument over the derivation of α_1, we obtain

$$\alpha_{k+1} = (1-a)^{k+1}\alpha_0$$

and

$$T_b(t_0 + (k+1)\Delta t) = 22.5 + \alpha_0,$$

$$T_w(t_0 + (k+1)\Delta t) = 22.5 - \alpha_0.$$

Therefore, eqns (19) and (20) hold true in case of $n = k+1$ and hence for any $n \geqslant 1$.

As a matter of course

$$\lim_{n\to\infty} T_{opt,\,b} = 22.5 + \alpha_0$$

and

$$\lim_{n\to\infty} T_{opt,\,w} = 22.5 - \alpha_0,$$

so the daisies' optimum temperatures tend to the local temperatures as expected.

Thus, the adaptation of the daisies does not affect the local temperatures. Now I shall show that even the global temperature is not affected by their adaptation.

Solving eqn (5) of black daisies in terms of $1 - A$, we obtain

$$\begin{aligned} 1 - A &= \frac{(T_b + 273)^4 - 0.75q}{SL/\sigma - q} \\ &= \frac{(\alpha_0 + 295.5)^4 - 0.75q}{SL/\sigma - q}. \end{aligned} \qquad (23)$$

Substituting eqn (23) in eqn (3), we obtain

$$T_e = \left[\frac{(\alpha_0 + 295.5)^4 - 0.75q}{1 - \sigma q/SL}\right]^{1/4} - 273.$$

Therefore, the global temperature T_e is a function of L only. This is exactly the same result as in the original Daisyworld (Saunders, 1994) and this implies the very important fact that adaptive daisies do not lose their ability for regulating the global temperature.

TWO-SPECIES STATE IN DARWINIAN DAISYWORLDS: FRACTIONAL COVERS

In order to know what the adaptation affects, it is necessary to obtain the formulas for fractional covers, i.e., a_b/a_e and a_w/a_e. To do so we take one equation from eqn (11) or (12):

$$\frac{a_b}{a_e} + \frac{a_w}{a_e} = 1 - \frac{\gamma}{a_e\beta_n}, \qquad (24)$$

where β_n is the growth rate at n-th time step and given by

$$\boxed{\beta_n = \begin{cases} 1 - \left\{\dfrac{(1-a)^n\alpha_0}{17.5}\right\}^2 & \text{for Robertson and Robinson model,} \\ \left\langle 1 - \left[\dfrac{\{1-(1-a)^n\}\alpha_0}{77.5}\right]^2\right\rangle \left[1 - \left\{\dfrac{(1-a)^n\alpha_0}{17.5}\right\}^2\right] & \text{for Lenton and Lovelock model.} \end{cases}}$$

Another equation to be solved is given by substituting eqn (4) in eqn (23):

$$\frac{a_b}{a_e} - \frac{a_w}{a_e} = 4\,\frac{(\alpha_0 + 295.5)^4 - 0.75q}{SL/\sigma - q} - 2. \qquad (25)$$

Solving eqns (24) and (25) in terms of a_b/a_e and a_w/a_e, we find the fractional covers:

$$\frac{a_b}{a_e} = 2\,\frac{(\alpha_0 + 295.5)^4 - 0.75q}{SL/\sigma - q} - \frac{1}{2} - \frac{\gamma}{2a_e\beta_n} \tag{26}$$

and

$$\frac{a_w}{a_e} = \frac{3}{2} - \frac{\gamma}{2a_e\beta_n} - 2\,\frac{(\alpha_0 + 295.5)^4 - 0.75q}{SL/\sigma - q}. \tag{27}$$

Thus the adaptation, symbolized by the factor a, affects the population dynamics through β_n. Since β_n is greater than the growth rate found in the original Daisyworld, i.e.

$$1 - \left(\frac{\alpha_0}{17.5}\right)^2 \leqslant \beta_n,$$

black daisies in both Darwinian Daisyworlds survive against stronger L than non-adaptive daisies in the original Daisyworld.

The emergence of white daisies means the beginning of the two-daisies era. This can be estimated by equating the left-hand side of eqn (27) with zero and solving it with respect to L with the initial value of β_n. Therefore two daisies can coexist, if

$$L \geqslant 0.7387,$$

that is

$$t \geqslant -4.235\,\text{Gyr},$$

for any Daisyworld. That is why our analysis starts with the two-species state.

In the same way, the extinction of black daisies indicates the end of the two-daisies era. This differs from one Daisyworld to another. Equating the left-hand side of eqn (26) with zero and solving it with respect to L, we find that two species coexist if

$$L \leqslant \begin{cases} 1.359 \\ \quad \text{for non-adaptive daisies,} \\ 1.383\text{–}1.384 \\ \quad \text{for Robertson and Robinson model,} \\ 1.383 \\ \quad \text{for Lenton and Lovelock model.} \end{cases}$$

These correspond to

$$t \leqslant \begin{cases} 3.163\,\text{Gyr} \\ \quad \text{for non-adaptive daisies,} \\ 3.317\text{–}3.324\,\text{Gyr} \\ \quad \text{for Robertson and Robinson model,} \\ 3.317\,\text{Gyr} \\ \quad \text{for Lenton and Lovelock model.} \end{cases}$$

I have calculated these upper bounds by using $a = 0.02$ and 0.5, but the results are identical within three significant digits because of the 182 to 183 time step adaptation starting from $t_0 = -4$ Gyr.

Lenton and Lovelock's black daisies become extinct earlier than Robertson and Robinson's black daisies, in case of the same a, because of the constraints on adaptation. The most important consequence of this subsection is the fact that adaptive daisies can regulate the global temperature longer than non-adaptive daisies.

WHITE DAISIES IN DARWINIAN DAISYWORLD

After the extinction of the black daisies, the global temperature is regulated by the white daisies alone. The equilibrium is described by use of eqn (12) with $a_b = 0$. Solving eqn (12) in terms of β_w, we have

$$\beta_w = \frac{\gamma}{a_e - a_w}. \tag{28}$$

Equating the right-hand side of eqn (6) with the right-hand side of eqn (28), we have the relation between a_w and T_w:

$$m(T_{opt,\,w})\left\{1 - \left(\frac{T_w - T_{opt,\,w}}{17.5}\right)^2\right\} = \frac{\gamma}{a_e - a_w},$$

which has two possibilities, but we are interested in the relation available at the higher temperature.‡ Therefore, a bit of algebra leads us to the result:

$$T_w = T_{opt,\,w} + 17.5\sqrt{1 - \frac{\gamma}{m(T_{opt,\,w})(a_e - a_w)}}. \tag{29}$$

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‡ In the original Daisyworld we have to consider both possibilities, because the fractional cover of white daisies does not reach its maximum at the extinction of black daisies.

Substituting eqn (29) in eqn (5), we arrive at the formula:

$$\left\{T_{opt,\,w}+273+17.5\sqrt{1-\frac{\gamma}{m(T_{opt,\,w})(a_e-a_w)}}\right\}^4 = \left(0.5-0.25\frac{a_w}{a_e}\right)SL/\sigma-0.25\left(1-\frac{a_w}{a_e}\right)q. \qquad (30)$$

It is easy to find a_w for given L in some way or other, although eqn (30) is implicit. Substituting L and a_w, the solution of eqn (30), in eqn (3), we obtain the global temperature.

The adaptation process goes like this:

$$T_{opt,\,w}(t+\Delta t) = T_{opt,\,w}(t)+a\left\{T_w(t)-T_{opt,\,w}(t)\right\} = T_{opt,\,w}(t)+17.5a\sqrt{1-\frac{\gamma}{m(T_{opt,\,w})(a_e-a_w)}}.$$

This means white daisies try to adapt themselves to higher temperature until they die away. Noting the effect due to the term related to a, it is obvious that poorly adaptive daisies die away earlier than highly adaptive ones. The function m for Robertson and Robinson is unity, and hence this is always larger than Lenton and Lovelock's m. Therefore, Lenton and Lovelock's white daisies become extinct earlier than Robertson and Robinson's, in case of the same a.

Results and Discussion

Figure 1 shows the global temperatures in several Daisyworlds plotted against time. Figure 2 shows the histories of the corresponding fractional covers in Daisyworlds.

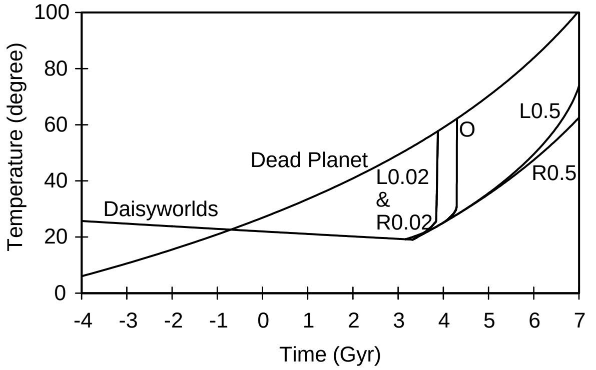

FIG. 1. Global temperatures vs. time. On a dead planet the global temperature keeps rising, while in Daisyworlds two species of daisies regulate the global temperature. After black daisies die away, phenomena bifurcate depending on models and the adaptation rate *a*. Symbols adjacent to lines denote as follows: O denote the original Daisyworld; R the Robertson and Robinson model; L the Lenton and Lovelock model; numbers correspond to the value of *a*. The present resolution shows the identical results for L0.02

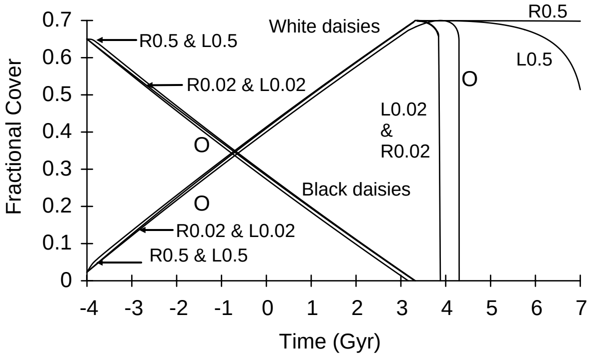

FIG. 2. Fractional covers vs. time Symbols denote the same as in Fig. 1. Daisies with unconstrained adaptation attain their maximum growth rates faster than daisies with constrained adaptation. Initially, the adaptation rate affects the fractional covers little, but it determines the extinction of white daisies. Daisies with $a = 0.02$ become extinct earlier than non-adaptive daisies, because they are trapped in a dead end of evolution.

Figure 1 reveals the biological homeostasis of the global temperature in any Daisyworld. This homeostasis is the consequences of the harmony between symmetry and asymmetry in the formalism of Daisyworlds: asymmetry in the difference between the albedo of land covered by daisies and that of the bare ground; the parabolic distributions of the growth rates in terms of the respective local temperatures; the same initial optimum temperature; the same adaptation rate for both species. As far as equilibrium (13) reduces to the following form, i.e.

$$(T_b-T_{opt,\,b})^2 = (T_w-T_{opt,\,w})^2,$$

along with the initial condition (10), the local temperatures remain the same as in the original Daisyworld. Therefore, contrary to the conclusion of Robertson and Robinson (1998), Darwinian daisies do not lose their ability of regulating the global temperature. They and I used the very same set of equations but reached the contradicting conclusions. The one and only black box is their spreadsheet simulation. The most probable source of the discrepancies lies in the method of numerical integration. Did they obtain the equilibrium of population dynamics at every forcing of the solar luminosity?

Lenton & Lovelock (2000) also obtained the result that follows Robertson & Robinson (1998): the adaptive daisies lose their ability of regulating the global temperature. Therefore, Lenton and Lovelock reached the erroneous conclusion that the constraints on adaptation *recover* daisies' ability of regulating the global temperature. Darwinian daisies with $a = 0.5$ can, however, regulate the global temperature for longer time than non-adaptive daisies, and the constraints on adaptation decrease Darwinian daisies' ability of temperature regulation. Judging from the text and figures (Lenton & Lovelock, 2000), they tried to reproduce Robertson and Robinson's results with the very special initial condition: the black daisies appear first and adapt themselves very quickly to the available environment; the black daisies become adaptive to higher temperature rather than regulate the global temperature; after several forcing of the solar luminosity the white daisies appear but the black daisies are too dominant for the white daisies to compete with; without co-evolution of two species, no temperature regulation becomes effective. Thus, their initial condition broke the harmony between symmetric and asymmetric structures of Robertson and Robinson's Darwinian Daisyworld. Two species, however, coexist from the start as I showed in the previous section, and hence they can co-evolve to regulate the global temperature.

The constraints on adaptation reduce the life expectancy of species, but their effects are very subtle. With the resolution of Figs 1 and 2 it is impossible to show the differences between freely adaptive daisies and daisies with constrained adaptation except the cases with $a = 0.5$ after the extinction of the black daisies.

The importance of the constraints is to reproduce more realistic life. The present calculation shows the results: freely adaptive daisies with $a = 0.5$ die away just after $t = 10.28$ Gyr in the local temperature as high as 167.7°C; daisies with constrained adaptation disappear as the local temperature rises more than 74.6°C by the time $t = 7.08$ Gyr. Although Daisyworld is an imaginary planet, life in burning atmosphere is nonsense.

The constraints on adaptation weaken the adaptability of species. This also implies that the constraints prevent one species from becoming too dominant over others. That is why Lenton & Lovelock (2000) report their daisies with constrained adaptation could regulate the global temperature even with the very special initial condition mentioned above.

Let us take a close look at the effects of a values, i.e. adaptation. Figure 2 shows the upper lines for black and white daisies' time history of fractional covers corresponding to those of the adaptive daisies with $a = 0.5$. The lower bounds correspond to those of the non-adaptive daisies. In two-daisies era the adaptive daisies with $a = 0.5$ become optimal very quickly. Both black and white daisies make most of resources and hence the sum of their fractional covers is almost 0.7. Even if a is as small as 0.02, the two-daisies era of 7 Gyr is long enough for both species to attain their growth rates as large as 0.992–0.994. Since the adaptive black daisies live 60 Myr longer than the non-adaptive black daisies, the temperature regulation lasts longer in Darwinian Daisyworlds than in the original Daisyworld.

After the extinction of the black daisies, Daisyworlds bifurcate. The adaptive white daisies with $a = 0.02$ die away earlier than the non-adaptive white daisies, but the adaptive white daisies with $a = 0.5$ survive far longer than the non-adaptive white daisies.

To understand this bifurcation we shall note the difference between the two-daisies state and the white-daisies state. The rate of change in the solar luminosity becomes larger as time passes, and hence the white daisies are exposed to the local temperature rising very fast compared to the constant local temperature in the two-daisies era. On the other hand the optimum temperature of the adaptive daisies is 4–5°C lower than that of the non-adaptive daisies. In other words the non-adaptive daisies are well prepared to the higher local temperature to come in the future.

In such circumstances the adaptive white daisies with $a = 0.02$ cannot catch up with the rapid rise in the local temperature and die away even faster than the non-adaptive white daisies. These white daisies are poorly adaptive and come to a dead end of evolution. In this context I would like to mention that Saunders' (1994) Darwinian Daisyworld is an extreme example of weakly adaptive daisies, because all he did is to replace the optimum temperatures of his daisies with the respective local temperatures in the two-species state. That is why his Darwinian Daisyworld becomes a dead planet earlier than the original Daisyworld.

Even in the same circumstances the very adaptive white daisies, i.e. in case $a = 0.5$, can get out of this dead end of evolution and keep on adapting themselves to the rising local temperature.

Conclusions

Basically, Darwinian daisies do not lose the ability of temperature regulation. The constraints on adaptation decrease the adaptability of daisies. The co-evolution of both daisies contributes to the regulation of global temperature, while the adaptation extends the duration of temperature regulation in the two-species state. After the extinction of black daisies, the future of Daisyworld depends on the adaptation rate and the constraints on it: the weak adaptation leads white daisies to a dead end of evolution resulting in the early extinction; the strong adaptation makes white daisies survive longer than non-adaptive daisies. All these aspects fit quite well to our orthodox understanding of both Darwinian evolution and the Gaia hypothesis.

In summary, Darwinian evolution does not rule out the Gaia hypothesis.

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