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Consequences of inter-specific competition among multiple adaptive species in Daisyworld

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With 5 Figures

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Summary

We investigate the consequences of Darwinian selection in a daisymodel with uniform temperature, inter-specific competition and multiple daisies. The assumption of a higher competition between species than within them allows for the coexistence of more than two species in equilibrium. Thus, it is the first time that a high biodiversity with equal environment-altering traits at the same trophic level in a daisymodel is reported under stationary conditions. Adaptation in the biota occurs through mutations, leading to changes in the optimum temperature in order to achieve the maximum growth rate at the individual level. We study the planetary sensitivity (i.e. the variation of the global mean temperature due to a 1% change in solar radiation) as a function of the strength of the inter-specific competition and of the number of different species that grow in the model. We find the following: 1) by fixing the parameter that defines the strength of the inter-specific competition, the planetary sensitivity increases as biodiversity increases; 2) by keeping constant the number of different species in the planet, the planetary sensitivity also increases as competition between species increases. In any case, however, the planetary sensitivity associated with adaptive daisies is much greater than that obtained from non-adaptive species. However, the range of mean solar radiation where biota grows in the planet is substantially larger for adaptive species than for non-adaptive ones. This result suggests that adaptation of multiple species with the same environmental-altering traits may not imply a strong regulation of the mean planetary temperature, which differs with recent studies that analyse adaptation of single species.

Similar results are obtained by using a constrained adaptation and non-uniform temperatures.

1. Introduction

The Gaia theory asserts that feedback mechanisms between the physical environment and the biosphere keep the planet in habitable conditions (e.g. Lovelock, 1989; Lenton, 1998). Several ‘Gaian’ processes have been proposed for the Earth system, such as the amplification of rock weathering by living organisms (e.g. Schwartzman and Volk, 1989) and the variation of cloud cover linked to the release of dimethyl sulfide by marine plankton (e.g. Bates et al., 1987). The regulatory ability of the Earth system has been also investigated by means of conceptual models that include simplified coupling mechanisms between life and the environment (e.g. Watson and Lovelock, 1983; Svirezhev and von Bloh, 1996; Lenton, 1998). Special attention has been devoted to the model Daisyworld since, in its original version, it showed a very robust stabilisation of the planetary temperature due to the effects of the biota (Watson and Lovelock, 1983), thereby providing a lucid illustration of the propositions stated by the Gaia theory.

Biota in Daisyworld follows a simple meta-population dynamics equation applied to several species (daisies) that may differ in colour. Then, changes in the amount of biota alter the albedo (i.e. reflectivity to solar radiation) of the physical environment. On the other hand, the environmental temperature affects the biota since it modifies the growth rate. Most versions of Daisyworld do not explicitly deal with Darwinian selection since they do not include any adaptation of living organisms to local environmental conditions, neither do they assume possible random mutations of characteristic traits of the biota. In the latter case, and in comparison with the classical model without mutations, recent studies show that mutation in albedo (i.e. colour of daisies) enlarges the range of solar luminosity from which the planetary temperature is strongly regulated by the existence of the biota (e.g. Stöcker, 1995; von Bloh et al., 1997; Lenton, 1998).

In classical daisymodels, adaptation, via mutations, of the growth rate function to prevailing environmental conditions may destroy the temperature stabilisation of the planet (Robertson and Robinson, 1998) unless reasonable constraints limiting the growth rate are assumed (Lenton and Lovelock, 2000). Recently, Staley (2002) has described a mechanism whereby Darwinian selection acting on living organisms that co-evolve with the environment leads to an equilibrium condition that is optimal for life. The main point in Staley's theory is that optimal conditions are heritable traits, subject to variation (through mutations) and natural selection. The fact that Darwinian selection leads to Gaia is illustrated by a simplified Daisyworld model with mutation of the optimum temperature of growth (Staley, 2002). Also recently, Sugimoto (2002) has shown that Darwinian selection in two adaptive species with the same value for the growth rate function leads to the Gaia hypothesis.

Our aim is to extend Staley's analysis by assuming that competition between species (i.e. inter-specific) is stronger than within them (i.e. intra-specific), as observed in some real plant communities (see the discussion in Cohen and Rich, 2000). As pointed out by Lenton and Lovelock (2001), inter- and intra-specific competition are given equal weighting in Daisyworld models. The unique exception is due to Maddock (1991) and Cohen and Rich (2000) who analyse

the effects of high inter-specific competition in a daisymodel consisting of two species without mutation nor adaptation. Cohen and Rich find that high inter-specific levels of competition may decrease the stabilisation of the mean planetary temperature obtained in the original Daisyworld model.

One important consequence of assuming different rates of inter- and intra-specific competition is the possible coexistence of multiple species (more than two) with the same albedo and of the same trophic level in equilibrium with equal death rate and the same growth rate function. This possibility was ignored in former Daisyworld studies and it is here explored in detail. The consequence of the coexistence of multiple species in equilibrium and non-equilibrium daisymodels including several trophic levels may be found elsewhere (Loevelock, 1992; Harding and Lovelock, 1996; Harding, 1999). Note that the models employed there reduce to the two species case when the equations for the dynamics of daisies are allowed to reach the equilibrium and herbivores and carnivores are removed.

The solution of Staley's daisymodel for a single non-adaptive species is shown in Section 2. The results for adaptive daisies with high inter-specific competition are obtained in Section 3. Section 4 takes into account the constraints on adaptation suggested by Lenton and Lovelock (2000) in a model with high inter-specific competition. Section 5 discusses the results found here. Conclusions appear in Section 6.

2. Single non-adaptive species

In the analysis of Darwinian selection in daisymodels, Staley (2002) provides a clever approach by ignoring the selective rewards associated with the non-uniform distribution of temperatures. Since both biota and bare earth have the same temperature, changes in colour do not lead to any reward at the individual level (Staley, 2002). However, individual rewards may be obtained through adaptation to the environmental conditions by changing the optimum temperature of growing.

In the daisymodel employed here, the physical environment follows a classical energy balance equation widely used in energy balance climate

models (see, e.g. North et al., 1981; and the references therein). In stationary conditions at the planetary scale, the energy balance condition reads

$$SL(1 - A(x)) = BT + C, \quad (1)$$

where the l.h.s. in Eq. (1) represents the short-wave energy radiation absorbed by the planet whereas the r.h.s. is the long-wave energy radiation that escapes to the space. For the latter expression, we make use of a linear parameterisation in terms of the surface temperature T commonly used in simple climate models (North et al., 1981) and first applied to Daisyworld by Weber (2001). The values of the constants $B = 2 \text{ W m}^{-2} \text{ K}^{-1}$ and $C = -416 \text{ W m}^{-2}$ follow Weber (2001). In the l.h.s. in Eq. (1), S is the area-averaged incoming solar radiation, whose value matches that observed at current Earth's orbit ($S = 340 \text{ W m}^{-2}$) and L is a dimensionless measure of the solar luminosity (i.e. brightness of the star). As shown in Eq. (1), not all the incoming solar radiation SL is absorbed by the planet since a fraction $A(x)$ is reflected back to the space. The albedo $A(x)$ depends on the fractional cover occupied by the species x in the form

$$A(x) = A_g(1 - x) + A_dx, \quad (2)$$

where $A_g (= 0.25)$ is the albedo of bare earth (i.e. of the fractional cover not occupied by biota; $A = A_g$ for $x = 0$) and $A_d (= 0.75)$ is the albedo of daisies ($A = A_d$ for $x = 1$).

Changes in the fractional cover occupied by daisies x follow the classical equation of metapopulation dynamics (Watson and Lovelock 1983; Hanski and Gilpin, 1991)

$$\frac{x'}{x} = (1 - x)\beta(T) - \gamma, \quad (3)$$

where x' is the dimensionless time derivative of x , γ is the constant dimensionless death rate ($= 0.3$) and $\beta(T)$ is the dimensionless growth rate function that follows a parabolic dependence on temperature T (Watson and Lovelock, 1983)

$$\beta(T) = 1 - \frac{(T_{\text{opt}} - T)^2}{\lambda^2}, \quad (4)$$

where T_{opt} is the optimum temperature of growth ($\beta(T_{\text{opt}}) = 1$) and λ is a measure of the width of the inverted parabola that follows β , here taken as 17.5 K (Staley, 2002).

In stationary conditions, $x' = 0$ and Eqs. (1) and (3) form a set of two equations (physical environment plus population dynamics) with two unknowns (T and x) once the solar luminosity L and the optimum temperature of daisies T_{opt} have been fixed. The solution may be found analytically since the substitution of Eq. (3) into (1) leads to a cubic equation in T . Classical stability analysis applied to the roots of this cubic equation shows that only one solution with biota is stable against small perturbations for a given value of L and T_{opt} . The results for the stable solutions that include biota as a function of L and T_{opt} are shown in Fig. 1, where the solid contours refer to the planetary temperature T and the dashed contours indicate the fractional cover occupied by daisies x . It is important to note that the trivial solution with no biota not shown in Fig. 1 is also stable.

From Eq. (4), the maximum possible value of β is $\beta = 1$. Thus, according to Eq. (3), the maximum daisy cover is $x = 0.7$. This maximises the radiation reflected back to space (l.h.s. in Eq. (1)). Therefore, the case $x = 0.7$ must correspond to the maximum possible value of L with biota in the planet. This is why, in the lower right corner in Fig. 1, the boundary between the sterile planet region (i.e. no daisies allowed to grow) and the

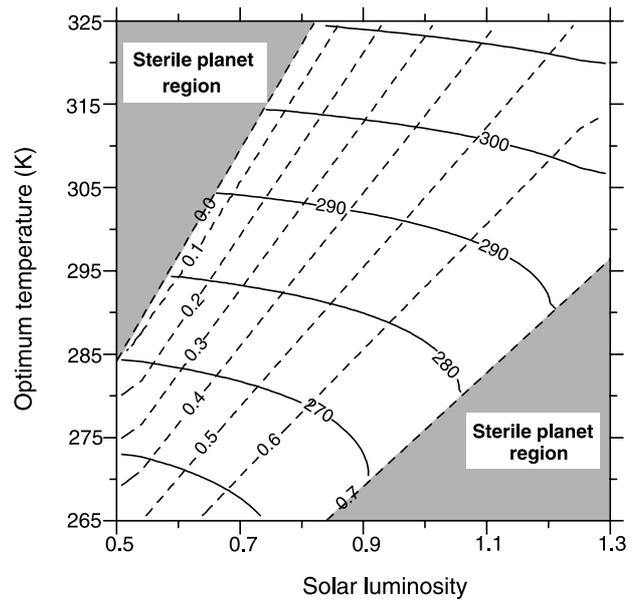


Fig. 1. Planetary temperature T (solid contours) and fractional cover of biota x (dashed contours) as a function of the optimum temperature T_{opt} and solar luminosity L for a non-adaptive single species

region with biota coincides with the solution for the maximum amount of daisies colonising the planet ($x = 0.7$; $\beta(T) = 1$; $T_{\text{opt}} = T$). Similarly, in the upper left corner in Fig. 1, the boundary between the sterile planet region and the region with biota follows the condition of vanishing daisy cover in both Eqs. (1) and (3) ($x = 0$; $\beta(T) = 0.3$; $T_{\text{opt}} = T + \lambda\sqrt{0.7}$). (The solution $T_{\text{opt}} = T - \lambda\sqrt{0.7}$) corresponds to the unstable root not shown in Fig. 1).

In climate models, the fundamental sensitivity of the planet Γ is defined as the change in mean planetary temperature T due to a 1% change in solar luminosity L (see, e.g. North et al., 1981)

$$\Gamma_x = \frac{1}{100} \frac{dT}{dL} = \frac{S(1 - A(x))}{100B}, \quad (5)$$

where the last equality in Eq. (5) follows from Eq. (1), and the subscript x in Γ_x refers to the sensitivity associated to a planet with a fractional cover of biota x . Results from energy balance models for Earth's current conditions obtain a range $0.8 \text{ K} < \Gamma < 3.4 \text{ K}$ (North et al., 1981). For a planet free of biota, $x = 0$ and Eq. (5) gives the value of the planetary sensitivity of a sterile planet $\Gamma_0 = 1.27 \text{ K}$. Note that $100 \Gamma_0$ is the slope of the boundary line labelled $x = 0$ in Fig. 1, so the planetary sensitivity obtained for a fixed value of the optimum temperature is smaller than Γ_0 .

In the classical version of Daisyworld, the optimum temperature T_{opt} is fixed at 295.5 K (Watson and Lovelock, 1983), so the range of luminosity L with biota on the planet lies between 0.57 and 1.29 (see Fig. 1). Note that then, the planetary temperature T varies only between 281 K and 295.5 K (Fig. 1). In contrast, without biota ($x = 0$), Eq. (1) implies that T varies from 281 K up to 372 K (for the same range of L). Thus, daisies strongly regulate the planetary temperature (by reflecting more sunlight if the solar luminosity increases). This regulation is the essence of the Gaia theory. In the next section, we will extend this approach to the more realistic case of several adaptive daisy species which compete against each other to colonise the planet.

3. Adaptive daisies with inter-specific competition

The assumption of a fixed value of T_{opt} ignores the possible ability of daisies to adapt to the

prevailing environmental conditions. Saunders (1994) analyses the effect of Darwinian evolution in the classical version of Daisyworld by setting the optimum temperatures T_{opt} equal (and constant) to the temperatures reached by daisies when evolution is ignored. Later, Robertson and Robinson (1998) assume that T_{opt} is an adaptive variable in the classical version of Daisyworld, so it equals the environmental temperature T at any value of solar luminosity L . In essence, this assumption implies a maximum value of the growth rate $\beta(T = T_{\text{opt}}) = 1$ (see Eq. (4)). Then, and from Eq. (3) at the steady state, the fractional cover of the biota reaches its maximum value ($x = 1 - \gamma = 0.7$). In this case, and from Eq. (5), the planetary sensitivity is $\Gamma_{0.7} = 0.68 \text{ K}$. Note that $100 \Gamma_{0.7}$ is the slope of the boundary line labelled $x = 0.7$ in Fig. 1. Although smaller than Γ_0 , $\Gamma_{0.7}$ is substantially greater than the planetary sensitivity observed without adaptation (i.e. at constant values of T_{opt}). Staley (2002) has recently analysed the consequences of adaptation in optimum temperatures in a daisy model similar to that described in Section 2. Here, we extend Staley's analysis by assuming inter-specific competition.

For a biota consisting of N species with the same death rate, the evolution equation describing the dynamics of the i -th species reads

$$\frac{x_i'}{x_i} = \left(1 - x_i - \sum_{\substack{j=1 \\ j \neq i}}^N \delta_{ij} x_j \right) \beta_i - \gamma; \quad i = 1, 2, \dots, N \quad (6)$$

where x_i is the fractional cover occupied by the i -th species, δ_{ij} is the inter-specific parameter that accounts for the inhibitory effect of species j on species i , and β_i is the growth rate function of the i -th species that follows

$$\beta_i = 1 - \frac{(T_{\text{opt},i} - T)^2}{\lambda^2}, \quad (7)$$

where $T_{\text{opt},i}$ is the optimum temperature of growth for the i -th species. For a single species ($N = 1$), Eqs. (6)–(7) become Eqs. (3)–(4), as they should. Equation (6) for $N = 2$ with $T_{\text{opt},1} = T_{\text{opt},2} \equiv T_{\text{opt}}$ has been analysed by Cohen and Rich (2000) in a Daisyworld model without adaptation (i.e. with a constant value of T_{opt}) (see, also, Maddock, 1991).

In Eq. (6), $\delta_{ij} \geq 1 \forall i, j$. Values of δ_{ij} greater than 1 tend to reduce the 'area' for colonising

available to the i -th species. For $\delta_{ij}=1$, Eq. (6) reverts to the equation employed in the classical version of Daisyworld (inter- and intra-specific competition with equal weight). Note that since the N species differ in their optimum temperature only (they do not differ in colour), the energy balance Eq. (1) is still valid by defining $x = \sum_{i=1}^N x_i$ as the fractional cover occupied by all species.

In stationary conditions, $x_i' = 0$ for $i = 1, 2, \dots, N$. We then add Eq. (6) from $i = 1$ to $i = N$. The result reads

$$x = \frac{N - \gamma \sum_{i=1}^N \frac{1}{\beta_i}}{1 + \delta(N-1)}, \quad (8)$$

where, for simplicity, we have assumed a constant value of the inter-specific parameter $\delta_{ij} = \delta$ for $i, j = 1, 2, \dots, N$, and $x = \sum_{i=1}^N x_i$. For $N=1$, Eq. (8) reverts to (3) at the steady state, as it should.

For a fixed value of the solar luminosity L and optimum temperatures $T_{\text{opt},i}$, Eqs. (1) and (8) form a set of two equations with two unknowns (T and x). For simplicity, we use discrete values of optimum temperatures with a 1°C interval ranging between -55°C and 100°C (these are extremely generous bounds for the existence of living organisms because they apply to extremophile bacteria and not to plants; see Lenton and Lovelock, 2000). Then, the maximum value of N is 155. However, physically admissible values of N lie well below this limit since the temperature T and the fractional covers x_i must satisfy the condition $0 < x_i < 1$ and $0 < \beta_i$ for $i = 1, 2, \dots, N$ in Eqs. (6) (with $x_i' = 0$) and (7), respectively.

Adaptation of the species following Darwinian selection implies a tendency (via mutations) of the optimum temperature $T_{\text{opt},i}$ to reach the environmental temperature T (see, e.g. Staley, 2002). In other words, adaptation of the i -th species leads to maximise its growth rate function β_i (see Eq. (7)). However, different species cannot simultaneously reach the maximum possible value for the growth rate function ($\beta=1$) since they have different optimum temperatures (see Eq. (7)). Then, the strategy to maximise the individual growth rate β_i in a planet with an odd number of species N , for example, is such that requires optimum temperatures $T_{\text{opt},i}$ to satisfy $\beta_{(N+1)/2} \approx 1, \beta_{(N-1)/2} =$

$\beta_{(N+3)/2} \approx 1 - 1^2 / \lambda^2, \beta_{(N-3)/2} = \beta_{(N+5)/2} \approx 1 - 2^2 / \lambda^2, \dots, \beta_1 = \beta_N \approx 1 - ((N-1)/2)^2 / \lambda^2$. From Eq. (7), this leads to optimum temperatures $T_{\text{opt},1} = T - (N-1)/2, T_{\text{opt},2} = T - (N-3)/2, \dots, T_{\text{opt},(N-3)/2} = T - 2, T_{\text{opt},(N-1)/2} = T - 1, T_{\text{opt},(N+1)/2} = T, T_{\text{opt},(N+3)/2} = T + 1, \dots, T_{\text{opt},N} = T + (N-1)/2$. This will be the selected distribution of optimum temperatures obtained by natural selection at the individual level.

We point out that the above expressions are approximated since the growth rates here computed use optimum temperatures between -55°C and 100°C with a 1°C interval, so they can only match integer values of the environmental temperature T . The above strategy has been corroborated by simulations of Eqs. (1), (6) and (7) with fixed values of solar luminosity L and number of species N using optimum temperatures T_{opt} ranging from 218 K to 373 K at 1 K interval. In these simulations, the N species use N successive values of T_{opt} (e.g. $T_{\text{opt},1} = T_0, T_{\text{opt},2} = T_0 + 1 \text{ K}, T_{\text{opt},3} = T_0 + 2 \text{ K}, \dots, T_{\text{opt},N} = T_0 + N - 1 \text{ K}$ for $218 \text{ K} \leq T_0 \leq 373 - N + 1 \text{ K}$), since we assume that the final outcome of natural selection acting on daisies with randomly mutating optimum temperatures $T_{\text{opt},i}$ is a distribution of $T_{\text{opt},i}$ around the temperature that maximises the growth rate function at the individual level.

Note that the numerical procedure here employed does solve the equations strictly at the steady state. For a fixed value of L and x , we obtain the temperature by solving the steady state Eq. (1) and the result is then used into the β_i parameters that appear in the steady state Eq. (8). Then, we vary the value of N and check if Eq. (8) is satisfied (i.e. we check if the root of Eq. (8) corresponds to the value of x assumed). This procedure is repeated for different values of N . The above is repeated for different values of x . Finally, all the above is repeated for different values of L . In any case, we check that $0 < x_i < 1, x = \sum_{i=1}^N x_i, 0 < x < 1$, and $0 < \beta_i \leq 1$ for $i = 1, 2, \dots, N$.

Figure 2 shows the results found for adaptive daisies with $L = 1$ and $\delta = 2$. The temperature T (triangles), the fractional cover occupied by all species x (closed squares) and the fraction of x occupied by the i -th species ($= x_i/x$) (open squares) are shown for each one of the N values (>1) that provide physically realistic solutions of Eqs. (1), (6) and (7). The solution for $N=1$

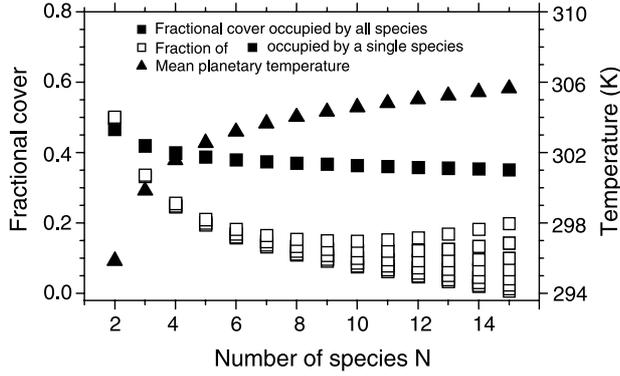


Fig. 2. Fractional cover occupied by all species x (solid squares), fraction of x occupied by a single species ($= x_i/x$) (open squares) and planetary temperature T (triangles) for all types of biodiversity found in an adaptive biota with inter-specific competition. N is the number of species. The case with $N=1$ has been omitted. The solar luminosity L is 1 and the inter-specific competition parameter δ is 2

(single species) would correspond to the point in Fig. 1 with $L=1$ at the boundary line between the sterile planet region and the biota region in the lower right corner (i.e. the case with $T_{\text{opt}}=T$; $x=0.7$). As biodiversity (values of N) increases, the fraction of the planet covered by biota decreases (see Fig. 2), which makes the temperature increase (see Fig. 2). This behaviour arises because, at a given value of solar luminosity, adaptation is optimal for one species only (i.e. the growth rate function β is maximum for one species only). The growth rate of other species does not reach the value that would be obtained in absence of competitors. As a result, the global fractional cover decreases as N increases. In Fig. 2, the maximum number of species in equilibrium is $N_{\text{max}}=15$. We stress that this value of N_{max} would vary by using a discretisation of optimum temperatures different than 1 K. This is the reason why we interpret N_{max} in terms of a biodiversity parameter without paying much attention to its actual number. It is very important to note that in the present analysis, the optimum growth rate temperature is the only parameter that differs among the multiple species. Of course, optimal natural selection would lead that parameter to be the same for all the species, so the distinction between them would vanish. This corresponds to the case with $N=1$.

Following Staley's (2002) work, we have assumed species with equal environmental-altering traits (albedo). Then, different species here

are neither penalised nor benefited depending on the values reached for their environmental-altering traits. This implies that competition among species does not involve any global change on parameters of utmost relevance for the physical environment such as the albedo of the land covered by biota. External factors (e.g. the environment) have the same effect for all of the species. This assumption favours the existence of solutions ranging from a single species to a maximum in biodiversity because species that compete with each other do not substantially modify the physical environment.

Of course, the statement above does not hold in real plant communities. But here we are interested in analysing the consequences of adaptation in different species with the same environmental-altering traits, so evolution does not have a direct effect on extremely sensitive environmental parameters for defining the climate state (e.g. the albedo).

Figure 3 shows the maximum biodiversity N_{max} found with adaptive daisies as a function of the inter-specific competition parameter δ with $L=1$. Fractional cover x and temperature T associated to the N_{max} solution are also plotted. Note that the values of x and T for $\delta=2$ coincide with the $N=15$ case shown in Fig. 2, as it should. An increase in the inter-specific competition allows more species to be in equilibrium (N_{max} increases). However, it also reduces the fractional cover occupied by biota x . Indeed, Eq. (8) predicts a null coverage of biota in the limit of

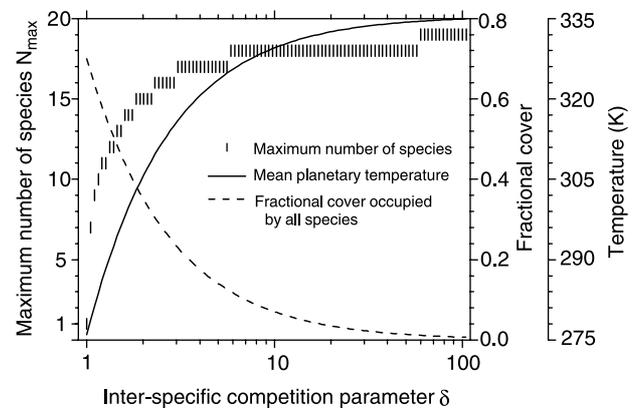


Fig. 3. Maximum number of species N_{max} (vertical marks) found as a function of the inter-specific competition parameter δ for a solar luminosity L equal to 1. Planetary temperature T (solid line) and fractional cover of all biota x (dashed line) at N_{max} are also shown

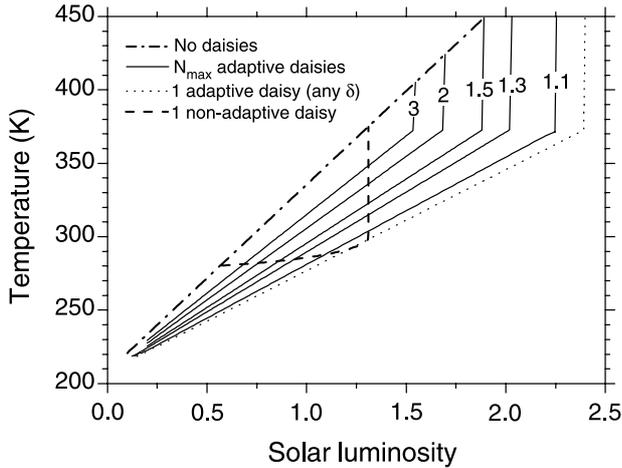


Fig. 4. Planetary temperature T as a function of the solar luminosity L found in a sterile planet (dash-dotted line), in a planet with inter-specific competition and adaptive biota at the maximum biodiversity ($N=N_{\max}$) found (thin solid lines) and at the minimum biodiversity found ($N=1$) (dotted line). Numbers on the thin solid lines indicate the value of the inter-specific competition parameter δ . The solution for a single non-adaptive daisy with optimum temperature equal to 295.5 K is also shown (dashed line)

extremely high values of δ (assuming a finite number of species N). As expected, the decrease in fractional cover x (i.e. in albedo or reflected radiation) implies an increase in temperature T .

Finally, the evolution of the planetary temperature as a function of the solar luminosity is shown in Fig. 4. The thick dash-dotted line corresponds to the solution for a sterile planet, obtained with $x=0$ in Eq. (1). Thin solid lines show the evolution obtained with adaptive daisies for different values of inter-specific competition (the number on the lines indicates the value of the δ parameter used in the simulation) and using the maximum number of species N_{\max} found at each value of solar luminosity L . The dotted line corresponds to the solution obtained with one single daisy for any value of δ (including the $\delta=1$ case). For completeness, the dashed line shows the solution obtained with a single non-adaptive daisy with $T_{\text{opt}}=295.5$ K (as in the original version of Daisyworld).

Solutions for adaptive species lie within the 218 K–373 K region, being the range accepted for the existence of living organisms (Lenton and Lovelock, 2000), which is quite generous as already pointed out. Above 373 K daisies are forced to disappear. For a fixed value of δ , the

value of N_{\max} is almost uniform for the entire range of solar luminosity from which biota grow in the planet. N_{\max} decreases at very high values of solar luminosity. For example, the thin solid line labeled 2 (i.e. the $\delta=2$ case) uses a value of $N_{\max}=15$ from $L=0.22$ to $L=1.63$. Then, N_{\max} decreases to 10 from $L=1.63$ to $L=1.68$, where temperature finally reaches 373 K.

We have found that the fractional cover x for fixed values of δ and N_{\max} is independent of solar luminosity L . This implies that the planetary sensitivity of the evolution with maximum possible biodiversity may be approximated as $\Gamma_x = S[1 - (1-x)A_g - xA_d]/(100B)$. Since $A_d > A_g$, it is obvious that the fraction $\Gamma_x/\Gamma_0 = [1 - (1-x)A_g - xA_d]/(1 - A_g)$ increases as x decreases (i.e. as δ increases; see Fig. 4). In other words, the evolution of the solution with maximum adaptive biodiversity tends to that of the sterile planet as the inter-specific competition increases. For the same level of inter-specific competition, the solution with a minimum number of adaptive biodiversity (i.e. the case of a single species) shows the lowest planetary sensitivity (see Fig. 4). However, the planetary sensitivity for adaptive species (either $N=N_{\max}$ or $N=1$) is substantially higher than that observed with non-adaptive species (dashed line in Fig. 4). Also note that the range of solar luminosity from which adaptive biota grow in the planet is substantially larger than that obtained with non-adaptive biota. In Fig. 4, the temperature increases as the solar luminosity increases for all the results. This implies that $dT/dQ > 0$ so the steady state solutions are stable by following the classical theorem of climatic stability in energy balance climate models (see, e.g. North et al., 1981).

Biodiversity (N_{\max}) increases as the inter-specific competition parameter δ increases in Fig. 4. It means that for higher values of δ there are more species less well adapted to the environmental conditions. This, however, is not the main cause for the reduction of the area covered by biota because for a fixed value of δ , both the temperature and the area coverage do not vary in excess for large values of biodiversity (say $N > 7$). In other words, a similar result to that shown in Fig. 4 would be obtained by fixing the biodiversity to $N=7$ (the value of N_{\max} for the $\delta=1.1$ case) for the $\delta=1.3, 1.5, 2$ and 3 cases.

4. Adding constraints on adaptation

In Fig. 4 we have applied upper and lower bounds to the temperature of living organisms (range between -55°C and 100°C). However, as Lenton and Lovelock (2000) point out, the growth rate function is also constrained in the temperature range suitable for life. Thus, the maximum growth rate at extremely low (or high) temperatures is not expected to be 1 (as assumed in Section 3) but to take a smaller value. This variation in tolerance of extreme temperatures is expressed by introducing a weighting term in Eq. (7), so the growth rate function becomes

$$\beta_i = \left[1 - \frac{(295.5 - T_{\text{opt},i})^2}{c^2} \right] \left[1 - \frac{(T_{\text{opt},i} - T)^2}{\lambda^2} \right], \quad (9)$$

where $c = 77.5 \text{ K}$ (Lovelock and Lenton, 2000). In this constrained case, Eqs. (1) and (8) are still valid.

The behaviour of temperature as a function of the solar luminosity with constrained adaptation and inter-specific competition is shown in Fig. 5 for the same cases analysed in Fig. 4. In general, the behaviour of the constrained case (Fig. 5) is very similar to the unconstrained one (Fig. 4).

The adaptation of a single species ($N = 1$) to the environmental conditions implies $T_{\text{opt}} = T$, so the growth rate function (9) is equivalent to that obtained for a single non-adaptive species (see Section 2) with an optimum temperature equal to 295.5 K and a parameter $\lambda = c = 77.5 \text{ K}$. This case corresponds to the dotted line in Fig. 5. In

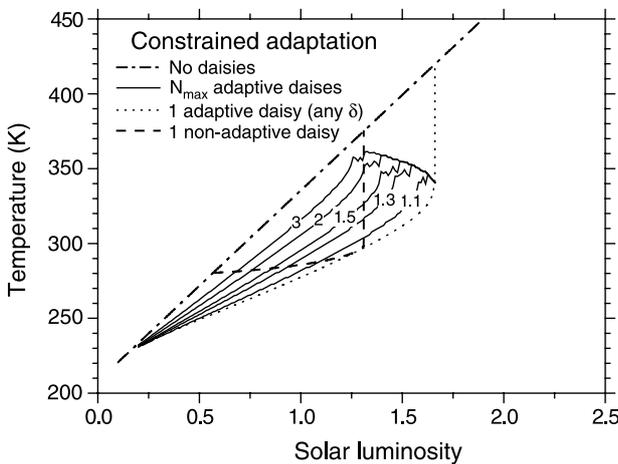


Fig. 5. As in Fig. 4 except for the case with constrained adaptation (see Eq. (9))

comparison, the dashed line shows the solution for a single non-adaptive species with the same optimum temperature (295.5 K) but with a different value of λ ($= 17.5 \text{ K}$). It follows that the planetary sensitivity Γ increases as λ increases. Indeed, a high value of λ enlarges the width of the parabola described by the growth rate function $\beta(T)$, so we may find more temperature values associated to high values of growth rate. This is almost equivalent to assume a single species with unconstrained adaptation. Actually, in the limit of very high values of c in Eq. (9), the growth rate function for adaptive species (i.e. $T_{\text{opt}} = T$) would tend to 1, so both dotted lines in Figs. 4–5 would coincide. We stress that in the analysis of constrained adaptation without inter-specific competition, Lenton and Lovelock (2000) did not find a smaller planetary sensitivity for daisies without adaptation (as here found when comparing the dashed line with the dotted line in Fig. 5) since these authors use daisies with different colour and local temperatures. Thus, that model not only contained adaptation to prevailing conditions (i.e. changes of T_{opt}) but also different ability of biota to alter the environment (i.e. biota with different albedos).

For a fixed value of δ , the evolution at the maximum number of species N_{max} with constrained adaptation is similar to the unconstrained result (see Fig. 4). At high values of solar luminosity, however, the value of N_{max} declines faster than in the unconstrained adaptation case. Since the upper temperature bound $T = 373 \text{ K}$ for $N_{\text{max}} > 1$ is not reached, the thin solid curves in Fig. 5 finally merge with the $N_{\text{max}} = 1$ solution (dotted line) at high values of solar luminosity.

5. Discussion

The result for $\delta = 1$ shown in Fig. 4 (dotted line) is equivalent to the Robertson and Robinson (1998) unconstrained adaptation case with upper and lower bounds for the planetary temperature. In view of the solution, these authors concluded that Darwinian selection does not lead to Gaia. The very same result is also equivalent to the adaptation case described in Staley (2002), who concluded that Darwinian selection does lead to Gaia. The apparent inconsistency of the conclusions reached after analysing the same

mechanism of adaptation disappears when we assume that daisies do not compete for empty land (as in Robertson and Robinson, 1998) but for energy (as in Staley, 2002). Indeed, Staley (2002) substitutes the term within parenthesis in Eq. (3) for the absorbed short-wave energy (l.h.s. term in Eq. (1)). In this case, the population dynamics equation is not only a function of the local temperature of biota T but also on physical environmental magnitudes such as the solar luminosity L . This means that, at the steady state with $T_{\text{opt}} = T$ (adaptation of daisies to the local temperature), the temperature does not vary as a function of solar luminosity (see Staley, 2002). This behaviour differs from that found when using empty space as the raw material for growth (see Fig. 4). Including the effects of inter-specific competition on the energy available to the i -th species when assuming energy as the limiting resource may be worth to explore in further studies dealing with evolution in Daisyworld.

The results here shown refer strictly to steady state conditions. Thus, we assume that the characteristic time scale for the evolution of both physical environment and population dynamics are much shorter than that associated to changes in solar luminosity. This approach may lead to some inconsistencies if the stationary solution at solar luminosity L differs substantially from that at $L + \Delta L$, being ΔL an arbitrarily small increment in solar luminosity. In our simulations, we have checked that for both constrained and unconstrained adaptation cases, the optimum temperatures of the N species ($1 \leq N \leq N_{\text{max}}$) found at $L + \Delta L$ may follow from adaptation of the N' species found at L with an adaptation rate of the order of 1°C per 10 million years and with $\Delta L = 0.01$. For the conversion of luminosity in time we use Caldeira and Kasting's (1992) equation based on the expected evolution of the Sun.

Note that some non-steady state calculations with multiple daisies carried out by several authors (e.g. Lovelock, 1992), assume a time scale for the population dynamics Eq. (5) much larger than that associated to the physical environment but not much shorter than that of the solar luminosity (although see Nevison et al., 1999). Then, the non-steady solution admits more than two species without inter-specific competition.

In the model used here, the assumption of uniform temperatures implies the existence of a very

efficient heat flux flowing from the bare earth region (low albedo, high absorption of solar radiation) to the region with biota (high albedo, low absorption of solar radiation) that homogenises the temperature. Thus, this heat flux cannot be driven by temperature differences between biota and the bare earth region as usually assumed in simple climate models (see, e.g. North et al., 1981). This inconsistency may be removed by using a different temperature for daisies than that for the bare earth. Then, the heat flux between bare earth and biota may be parameterised as in Watson and Lovelock (1983) or in Pujol (2002). In any case, the results for adaptive daisies with inter-specific competition, here not shown, are very similar to those found in previous sections. Adaptation of the optimum temperature does not depend on the non-uniform temperature distribution as long as all species have the same albedo and temperature. It may be also worth exploring in further studies the effect of different heat flux efficiencies in a system composed of adaptive biota with inter-specific competition and different temperature and colour.

Of course, it is very unrealistic to assume the same albedo to all daisy species. However, as in Staley's paper (Staley, 2002), we have focused on the effects of adaptation in non-altering environmental traits. We point out that inter-specific competition associated to different albedos is completely different to the study carried out here. In the present paper, both albedo and temperature are uniform, so altering-environment traits that are key for the stabilisation of the planetary temperature in the classical version of Daisyworld are not accounted for here, where adaptation (i.e. natural selection) changes non-altering – environment traits only. The analysis carried out here also differs from that used by Sugimoto (2002), who studies the effect of Darwinian selection in a Daisyworld seeded with two species only that differ in colour but with equal value of the dimensionless growth rate function β (in contrast with the assumptions here made).

The mechanism adopted here for obtaining biodiversity (i.e. biota with different optimum growth temperature) may be plausible in a spherical version of Daisyworld where the energy per unit area coming from the Sun varies in latitude. In such a scenario, the latitudinal distribution of

the surface temperature in simple energy balance models decreases towards the pole (see, e.g. North et al., 1981). Then, adaptation to the local environment would lead to the biota to achieve optimum growth temperatures as a function of latitude. Here we assume species with different growth rate functions and the results contradict the main conclusion reached by Staley (2002) obtained in a similar model without biodiversity and with energy as the raw material for the biota. Note that the study here shown is the first step only in the analysis on how biodiversity may modify the outcome of adaptive daisymodels. Of course, further studies should be made in order to confirm or deny that Darwinian selection does not rule out the Gaia hypothesis.

Finally, we point out that within the 230 K–300 K range, the linear parameterisation of the outgoing long-wave radiation in terms of the surface temperature T provides a far better agreement than the Stefan-Boltzmann emission ($\propto T^4$) for current Earth's conditions (Marani, 1999). This empirical approximation takes into account the effect of greenhouse gases in the emitted long-wave radiation. Assuming the Stefan-Boltzmann emission instead of the linear parameterisation would not qualitatively modify the results found here. Further studies may assume temperature dependencies on the parameters B and C for explicitly including one of the main positive feedbacks observed in the climate system: the water vapor feedback. In Earth, this feedback arises because of the coexistence of both liquid and gas reservoirs for the main greenhouse gas (water). Note that this condition is very important for the existence of life.

6. Conclusions

We have developed a daisymodel with uniform temperature, adaptive biota (Staley, 2002) and competition between species (Cohen and Rich, 2000). Since inter-specific competition allows stationary solutions with more than two species, we have investigated the consequences of increasing biodiversity on the global mean temperature. Note that, here for the first time, steady state solutions with multiple species ($>$ two) with the same environmental-altering traits are found in a daisymodel with one trophic level.

In order to focus on a single adaptation mechanism to the prevailing environmental conditions, species in the daisymodel developed here differ in their optimum temperatures but not in colour (i.e. albedo). In this model, the best strategy at the individual level for maximising the growth rate is to vary the optimum temperature in order to match the environmental one. At the global scale, this adaptation process (occurred through natural selection acting on daisies with randomly mutating optimum temperatures) reduces the planetary sensitivity (i.e. changes in temperature due to changes in solar luminosity) in comparison with that obtained in a sterile planet. However, the planetary sensitivity with a single non-adaptive species is much smaller than that obtained with adaptive species. In the daisymodel analysed here, the planetary sensitivity tends towards that associated to the sterile planet state as biodiversity and competition between species increase. This effect is also observed 1) by keeping fixed the inter-specific competition parameter and increasing the biodiversity, and 2) by increasing the inter-specific competition parameter and keeping fixed the number of species allowed to grow in the system. We have also checked that using different temperatures for both biotic and abiotic surfaces does not modify the above results.

The main conclusion of the present paper follows from the findings commented above. In a very simple and schematic daisymodel with high biodiversity (more than two species), natural selection does not lead to the Gaia hypothesis. This result contradicts that obtained by Staley (2002) in a daisymodel with a single species and that by Sugimoto (2002) in a daisymodel with only two species that differ in colour but not in the growth rate functions. Note, however, that the results here found are not thought to undermine the Gaia theory. They simply show that adaptation in species with equal environment-altering traits (e.g. albedo) does not seem to be a suitable candidate to provide a strong regulation of the planetary temperature. In order to confirm such a conclusion, a variety of further studies should be carried out in more elaborate and realistic daisymodels. Of particular interest is the analysis of adaptation in biota with multiple species that also differ in environment-altering traits.

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