Interspecific competition affects temperature stability in Daisyworld

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ABSTRACT

The model of Daisyworld showed that nonteleological mechanistic responses of life to the physical environment can stabilize an exogenously perturbed environment. In the model, 2 species of daisies, black and white, stabilize the global temperature of a planet exposed to different levels of insolation. In both species, the response of the growth rate to local temperature is identical, but differences in albedo between the 2 species generate differences in local temperatures. The shifting balance between the daisies keeps the global temperature in a range suitable for life. Watson and Lovelock made the stronger claim that "the model always shows greater stability with daisies than it does without them." We examined this claim by introducing an extra source of competition into the equations that describe the interactions between the daisy species. Depending on the parameters of competition, temperatures can vary more widely with increasing insolation in the presence of daisies than without them. It now seems possible, timely and perhaps necessary, to include an accurate representation of interspecific competition when taking account of vegetational influences on climate.

1. Introduction

It has long been recognized that life influences physical and chemical environments and vice versa, at all scales from the local to the global (Lotka, 1925). Recent empirical and computational studies (Beerling et al., 1998) of Earth's *ménage à trois* — vegetation, climate and atmosphere — support that perspective.

One specific and controversial version of that widely accepted view is the Gaia hypothesis. In its early form (Kump, 1996), the Gaia hypothesis proposed that life affects the physical planet (including the climate and the chemical composition of the atmosphere and ocean) in ways that invariably or usually increase or maintain the suitability of Earth for life (Lovelock, 1988; Lenton, 1998). To demonstrate that planetary "homeostasis by and for the biosphere" could in principle work by mechanisms that entailed no teleology, Watson and Lovelock (1983) proposed a mathematical model called Daisyworld. They analyzed this model numerically. Saunders (1994) analyzed it mathematically.

Watson and Lovelock (1983) made a further strong claim for their "imaginary planet having ... just 2 species of daisy of different colors .... Regardless of the details of the interaction, the effect of the daisies is to stabilize the temperature. ... the model always shows greater stability with daisies than it does without them." Lovelock (1988) later argued further for this claim but with fewer technical details.

Watson (1999, p. 83) articulated a more refined view of the Daisyworld model. He recognized

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that even one species of daisies diminishes changes in temperature in the midrange of insolation. However, life amplifies the temperature effect of small changes in insolation at the extremes where the daisies become just viable or just cease to be viable. "What is the essential difference between the behavior of the system with life and that without it? It is not increased stability, for though this is apparent in some regions, the opposite occurs in others. Rather, it is a change in the character of the system due to the non-linearity that is introduced by the equations governing the population of daisies."

This note describes a further example of the general statement of Watson (1999). We show that if interspecific competition affects daisy growth more than self-inhibition while all other assumptions of the Daisyworld model remain unchanged, then temperatures can vary more widely over some intervals of increasing insolation in the presence of the daisies than without them. The daisies need not stabilize the temperature of Daisyworld. This result suggests that global climatic dynamics may depend on the details of interactions within the biosphere.

This example is one of a growing number of variations on the theme of Daisyworld. Other variations are given by Maddock (1991), Saunders (1994), Harding and Lovelock (1996), Robertson and Robinson (1998) and the references cited by them and above.

2. Daisyworld with interspecific competition

In Daisyworld, a gray planet (with albedo $A_g = 0.5$) is seeded with black daisies (albedo $A_b = 0.25$) and white daisies (albedo $A_w = 0.75$). These 2 species have identical growth responses to local temperature. A sun delivers insolation that is fixed over time but is varied, in comparative statics, from 0.6 to $1.6\times$ the insolation currently reaching earth. For each level of insolation, the Daisyworld model computes the planetary temperature using the Stefan–Boltzmann law for black body radiation and the average planetary albedo. The average albedo is determined by the fraction of planetary area α_b covered by black daisies, the fraction of planetary area α_w covered by white daisies, and the fraction of remaining area of bare gray ground $(P - \alpha_b - \alpha_w)$, where the potential

daisy area P is always taken as 1 (by Watson and Lovelock and here). These areas are determined as the equilibrium of the growth equations of Carter and Prince (1981):

$$\frac{d\alpha_b}{dt} = \alpha_b((P - \alpha_b - \alpha_w)\beta(T_b) - \gamma),$$

$$\frac{d\alpha_w}{dt} = \alpha_w((P - \alpha_b - \alpha_w)\beta(T_w) - \gamma),$$

where γ is the death rate of daisies per unit time, and the growth function $\beta(T)$ (per unit time, per unit area) depends (identically for both species) on the local temperatures T_b, T_w in the areas of the planet covered by black and white daisies, respectively. Saunders (1994, p. 366) emphasizes that the patches of black and white daisies are spatially segregated, but a referee of this note argues that the model need not necessarily be interpreted as assuming spatial segregation because adjacent black and white objects may differ in temperature by several degrees. It would appear that the use of different local temperatures for regions of black and white daisies may require some spatial segregation, rather than random intermixing, of black and white daisies if the temperature differences between the black and white daisies are large enough. The growth function β is assumed to be 0 below $5°C$, to rise in an inverted parabolic U to a value of 1 at $22.5°C$, and to fall to 0 again at and above $40°C$.

To represent interspecific competition we modified the above equations by assuming that

$$\frac{d\alpha_b}{dt} = \alpha_b((P - bb\alpha_b - wb\alpha_w)\beta(T_b) - \gamma_b),$$

$$\frac{d\alpha_w}{dt} = \alpha_w((P - bw\alpha_b - ww\alpha_w)\beta(T_w) - \gamma_w),$$

where bb is the density-dependent inhibitory effect of black daisies on black daisies, wb is the competitive effect of white daisies on black daisies, and so on. In our numerical explorations of the model, we held $bb = ww = 1$ as in the original model and varied only bw and wb. In all other respects, we used exactly the equations and parameter values of Watson and Lovelock (1983), with death rates per unit time $\gamma_b = \gamma_w = 0.3$.

3. Method of analysis

Watson and Lovelock solved their model by numerical iteration of its differential equations until the areas occupied by each species of daisy converged to an apparent steady-state. They compared different equilibria by repeated numerical solutions of the model with different parameters. By contrast, following the analytical approach of Saunders (1994), we assumed a steady-state by setting the right side of the above competition equations equal to 0. We then manipulated the resulting equations symbolically, together with the other equations of Watson and Lovelock, to obtain implicit equations for the state variables at equilibrium. We solved the implicit equations numerically and plotted the results. We carried out the symbolic manipulation, numerical solutions and plotting using Derive (Soft Warehouse, 1997). The reader who wishes the details of how we analyzed the model may obtain a technical description from either author.

4. Results

We first reproduced the prior results of Watson and Lovelock (1983). We omit our reproduction of their Fig. 1 because it has already been reproduced by several others. Although their Fig. 1 did not display a hysteresis at low luminosity, hysteresis does occur when a gradual decrease in luminosity is considered (Maddock, 1991, p. 332; Saunders, 1994, p. 369).

When competition between the black daisies and the white daisies is intense, a small change of insolation can drive a large change in steady-state temperature (Fig. 1). Many additional examples for other values of the competition parameters could also be given. When one of the interspecific competition coefficients retains its original value of 1 and the other interspecific competition coefficient is varied, the transition in temperature is generally less dramatic. The abruptness of the transition can also be modified by changing the parabolic dependence of plant growth on temperature to a Gaussian dependence (Harding and Lovelock, 1996, p. 110), as well as by many other changes in the model. These variations of the model modify the details of the eff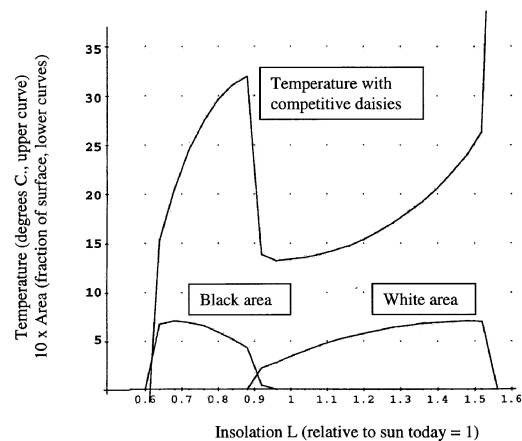ect of interspecific competition but do not change the qualitative conclusion that interspecific competition can amplify the effect on temperature of small changes in insolation.

When competition between daisy species is sufficiently intense, the abrupt temperature transition approximates a jump between the temperature trajectory of a world with black daisies only and the temperature trajectory of a world with white daisies only (T. M. Lenton, personal communication). As long as both kinds of daisies survive, the actual temperature trajectory is intermediate between these 2 extreme trajectories. An abrupt transition induced by interspecific competition does not drive the global temperature out of the range tolerable to life. Even with intense interspecific competition, Daisyworld is habitable over a wider range of insolation with daisies (of 1 species or 2) than it would be without them.

By numerical experimentation (not shown), we found that differences between the death rates of the black and the white daisies had a much smaller effect on the ruggedness of the temperature-insolation profile than did competition between the black and the white daisies.

Fig. 1. Daisyworld temperature (T) as a function of insolation (L), expressed as a multiple of solar insolation, when density-dependent self-inhibition of each daisy species is considerably less than interspecific competition ($bb = ww = 1$, $bw = 2$, $wb = 3$). Between $L = 0.8$ and $L = 1.0$, the effective planetary temperature in the presence of daisies varies far more abruptly than it would in their absence or at lower levels of competition ($bw = wb = 1$). Daisy areas are scaled by $10 \times$ their actual values (which always fall between 0 and 1).

5. Discussion: relevance to earth

The underlying supposition of Watson and Lovelock (1983) is that vegetation can modify global climate. Supporting that view, Hayden (1998) reviews many examples of the ways that vegetation modulates many aspects of climate at all scales, including the global scale. For example, vegetation increases the water vapor in the atmosphere through evapotranspiration. The increased moisture raises the minimum temperature and reduces the maximum temperature. Plants produce non-methane hydrocarbons, about half of which agglomerate as particulate hydrocarbons. At high relative humidities, water vapor condenses on particulate hydrocarbons to form haze and to raise minimum temperatures. The surface roughness of vegetation slows average wind speeds over the interior of England and Scotland by half, compared to wind speeds over the oceans adjacent to the UK. Different plants have different rates of evapotranspiration, produce different hydrocarbons, and have different forms of roughness and responses to wind velocity. Not all plants are interchangeable in their climatic effects.

Plant competition has long been recognized as significant in the composition of biotic communities (Clements et al., 1929; Grace and Tilman, 1990). Mathematical models have been developed to represent plant competition (Pakes and Maller, 1990). Maddock (1991, p. 336) considered interspecific competition in the context of the Daisyworld model, using a mathematical form that is slightly different from that used here, without exploring the extremes of competition considered here and without discussing possible mechanisms.

The interspecific competition modeled here could be produced by a well-known mechanism, allelopathy (Rice, 1984, 1995). Harper (1977, p. 369) wrote: "Some of the depressive effects of a plant upon its neighbours are so striking that an interpretation based on the monopolization of resources has often seemed inadequate. An alternative is obviously that some plants may release into their environment toxic materials that harm or even kill neighbours." Harper (1977) reviewed laboratory experiments that demonstrated the role of allelopathy. More recent studies (Rice, 1984, 1995) document the role of allelopathy in the field and support the assumption made here that a species may inhibit the growth of another species substantially more than it inhibits its own growth.

It seems possible, timely and perhaps necessary, to include an accurate representation of interspecific competition when taking account of vegetational influences on climate. Some general circulation models of the climate now include interaction with dynamic global vegetation models which allow for competition among functional types of vegetation (Foley et al., 1998; T. M. Lenton, personal communication). Such models are clearly a step in the right direction.

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