

Resolving the anomaly of bare habitable ground in Daisyworld

By ROBIN K. S. HANKIN^{1*} and NEIL MITCHELL², ¹University of Cambridge, 19 Silver Street, Cambridge, CB3 9EP, UK; ²School of Environment, The University of Auckland, Private Bag 92019, Auckland, New Zealand

(Manuscript received 11 November 2009; in final form 16 September 2010)

ABSTRACT

The parable of Daisyworld places biological homeostasis on a non-teleological basis. However, one feature of Daisyworld is that, at equilibrium, the system appears to require habitable but bare ground. The presence of bare ground is an unavoidable consequence of the death rate parameter γ . Here, we simplify Watson and Lovelock's original formulation by removing γ and allowing instead the black and white daisies to infiltrate each others' territory. This device furnishes a model in which the area of bare ground asymptotically approaches zero. The infiltration process is modelled in terms of a parameter that is ecologically interpretable as a quantification of the incumbent advantage enjoyed by the dominant species.

1. Introduction

The parable of Daisyworld (Watson and Lovelock, 1983) outlined a plausible biological feedback mechanism whereby two species of plant (white and black daisies) could regulate the temperature of a planet. Since the original formulation a number of authors have investigated making the model more 'earth-like' and in general increasing the complexity of the interactions between the daisies (Wood et al., 2008, and references therein). However, in all these formulations the original model of Watson and Lovelock is in essence retained, the various refinements being built with this model at its core.

The original model had a number of assumptions and approaches built in to it, which have been carried forward into subsequent analyses. In this paper, we investigate the potential for a simple alteration to the core model that employs fewer assumptions while preserving climatic control.

In the original formulation an arbitrary death rate γ of 0.3 was chosen and has been used by other authors, although Cohen and Rich (2000) found that in their models differences in death rate had a smaller effect than other parameters. The use of a positive death rate also implies that there will always be an area of fertile ground devoid of vegetation. As a result, there are areas of unoccupied, fertile ground, with neutral (or at least intermediate) albedo and thus the classical daisyworld model is

describing a condition in which the land cover switches between the three states of black, white and bare. We were particularly interested in the role of the bare habitable ground (~30% in the original model): on the one hand, bare ground is necessary for either white or black growth and hence homeostasis; but on the other, bare ground is climatically inactive.

We would suggest that once initial colonization of the planet surface had occurred, it is feasible for the whole planet to remain vegetated, through a process such as a cyclical climax (Watt, 1947, 1955), or 'climax microsuccession' (Emborg et al., 2000). In this situation one species replaces the other through invasion or dispersal, as temperature changes.

On an Earth-type ecology, when individual plants die they might leave bare ground—but the globally averaged incidence of bare ground is small. Hubbell (2001), considering general principles applicable to the dynamic modelling of ecologies, states that

'large landscapes are essentially always biotically saturated with individuals. . . no significant amount of space or other limiting resource goes unused for long. Small areas or patches of resource may become unsaturated for short periods of time immediately after disturbances, but at large landscape scales, the surface of the Earth, to a first approximation, is completely and permanently saturated' [his emphasis].

It is thus reasonable to require any model to permit only negligible amounts of bare ground in the steady state. Processes such as desertification are not in scope here, as this violates the central assumption of Daisyworld's habitable zone being 'well watered and laden with nutrients' (Wood et al., 2008).

*Corresponding author.

e-mail: rksh1@cam.ac.uk

DOI: 10.1111/j.1600-0889.2010.00511.x

1.1. Species interaction in Daisyworld

The other perhaps idiosyncratic feature of the original Daisyworld is that the two daisies do not compete directly with one another; their only interaction is via their effect on the planetary temperature. The replacement of one species occurs through the occupancy of ground left vacant by the death of the other species.

Here we re-examine the effects of direct inter-specific competition, at least in the sense that one species directly replaces the other. As conditions change one species can invade the space occupied by the other through superior fitness to the changing conditions.

The fundamental time dependence of Daisyworld is the growth rate of the two species:

$$\dot{\alpha}_w = \alpha_w (x\beta_w - \gamma) \quad (1)$$

$$\dot{\alpha}_b = \alpha_b (x\beta_b - \gamma), \quad (2)$$

where α_w , α_b are the areas covered by white and black daisies, respectively, x the area of bare ground, $\beta_i = 1 - 0.003265 (T_i - T_{\text{opt}})^2$ is the growth rate of the daisies (subscript $i \in \{w, b\}$ denotes the different types of daisy considered); T_i the local temperature of the daisies and γ the death rate. All terminology follows Watson and Lovelock (1983). Here, the two roots of $\beta_i = 0$ are denoted T_{upper} and T_{lower} : these represent the limits outside which neither species of daisy can grow.

Areas are non-dimensionalized with the area of the planet and are thus between 0 and 1 inclusive.

To simplify the system still further, consider a monochromatic Daisyworld in which white daisies are absent. Then

$$\dot{\alpha}_b = \alpha_b [(1 - \alpha_b)\beta_b - \gamma] \quad (3)$$

and the system clearly has a stable stationary state in which $\alpha_b = 1 - \gamma/\beta_b$, implying that there is bare habitable ground¹ of area $\geq \gamma$. Watson and Lovelock, and many subsequent authors, chose $\gamma = 0.3$.

One might argue that a positive γ is relevant to a model based on using the death rate of individuals within a population, but not to a model which, as in this case, tracks changes in growth via area covered. We argue here that a model based on species replacement is simpler to analyse.

A steady state solution of eq. (3) has a net growth rate of zero. The interpretation of Watson and Lovelock (1983) is a non-zero growth rate and a non-zero mortality term, of equal magnitude but opposite sign.

2. Daisyworld with no bare habitable ground

Simply setting $\gamma = 0$ is one solution to the problems discussed above, but is not helpful, since doing so destroys the climate

¹ Watson and Lovelock allow for the possibility that the planet included a certain proportion of infertile ground. We follow standard practice and specify that all ground is fertile; in their terminology $p = 1$.

feedback mechanism of bichromatic Daisyworld. Essentially the system ‘remembers’ the initial conditions, that is, the ordered pair $\{\alpha_w(0), \alpha_b(0)\}$. If the planet becomes fully occupied, that is, $\alpha_w + \alpha_b = 1$, the system remains frozen in a steady state: neither black nor white daisies can grow or die.

To restore the feedback mechanism there are two obvious possibilities: either make $\gamma > 0$, but arbitrarily small; or, leave $\gamma = 0$ and somehow allow a species of daisy to infiltrate area already occupied by different species of daisy and by doing so, exclude any competitor species. However, the process of infiltration thus described is different from colonization of bare ground: the established species possesses an incumbent advantage which may be considerable. From a landscape perspective, plant species are often able to colonize bare ground more easily than they can areas where another species is already established. However, there are many examples of systems in which one dominant species can replace an incumbent, without the need for bare ground.²

Suppose the ratio of colonization rate into bare ground, to the colonization rate into occupied ground is constant: call it Γ .

Considering the general case of an arbitrary number of species, we see that two infiltration processes occur simultaneously: each species infiltrates all the others at its specific growth rate and each species is infiltrated by the others at their specific growth rate. Symbolically:

$$\frac{\dot{\alpha}_i}{\alpha_i} = x\beta_i + \Gamma \left(\beta_i \sum_{j \neq i} \alpha_j - \sum_{j \neq i} \beta_j \alpha_j \right) \quad (4)$$

$$= x\beta_i + \Gamma \left(\beta_i \sum_j \alpha_j - \sum_j \beta_j \alpha_j \right), \quad (5)$$

where Γ is the ratio of ‘infiltration’ into area occupied by the other species, to rate of extension into bare but fertile ground.³ In this case, we have specified $\gamma = 0$ as being the simplest case but investigation of $\gamma > 0$ might be interesting.

If the case of zero unoccupied ground and zero death rate is considered, that is, $x = 0$, $\gamma = 0$, then $\sum \dot{\alpha}_i = 0$ which results in a full planet remaining fully occupied.

In bichromatic Daisyworld, the steady state may be found by observing that a fully occupied planet has only a single degree of freedom; the steady state is then identified by requiring $\dot{\alpha}_w = 0$. This implies that $\beta_b = \beta_w$.

Compare this to the approach of Watson and Lovelock in which the steady state is identified by solving the simultaneous

² Examples drawn from terrestrial ecology include Beech forests (Stewart et al., 1991), in which the filling of canopy gaps is dependent on the differential responses of the species to gap formation.

³ Eqs. (4) and (5) differ from those of Cohen and Rich (2000) and Pujol et al. (2005), in which the infiltration terms for α_i , say, are all proportional to β_i . In contrast, eq. (4) effectively considers infiltration terms to be proportional to the competitor’s rate of growth: We suggest that a given species’s area can be reduced more effectively by a vigorously growing species than a nonvigorously growing species.

equation pair corresponding to ‘white growth equals white death’ and ‘black growth equals black death’, with $\gamma = O(1)$. Then because the death rates of both species are defined to be equal, black growth equals white growth.

We submit that our approach is more intuitive than Watson and Lovelock’s original formulation; if nothing else, we have one fewer free parameter. Observe that the numerical value of Γ is immaterial; to render the steady state reachable it is only required that $\Gamma > 0$.

The system of Cohen and Rich (2000) has some similarities to the one presented here. However, we remove one free parameter, rather than add four, and we retain the desirable behaviour of the free fertile ground area approaching zero as time approaches infinity.

In the general case of polychromatic Daisyworld, steady states are found by considering $\dot{\alpha}_i = 0$ for $i = 1, \dots, n$. These correspond to $\beta_i = \beta$, or all growth rates are identical. Steady states may not exist for such systems and one might expect cyclic behaviour.

The numerical consequences of our reformulation are not immediately obvious, although the biology-climate coupling might be expected to be stronger because all the planet is climatically active. We reiterate our emphasis on conceptual simplification that our approach furnishes.

2.1. Monochrome Daisyworld

It is instructive to consider the case for Daisyworld inhabited solely by black daisies. The steady states in Watson and Lovelock’s formulation are given by the solutions of

$$(1 - \alpha_b) \left(1 - 0.003265 \{ T_{\text{opt}} - [T_e + q'(A_b - A_g)(\alpha_b - 1)] \}^2 \right) = \gamma, \quad (6)$$

where $A_i, i \in \{a, b, g\}$ is the albedo of the daisies or bare ground, T_e is the planetary temperature and q' is a diffusion constant. This is a cubic equation in α_b which, although formally soluble in radicals, has no readily interpretable analytical formula. Compare the approach proposed here in which the equation is simply $\beta_b = 0$. Thus the black daisies’ area increases, warming the planet, until the temperature is sufficiently high to inhibit further growth. It is worth emphasizing the narrative clarity of this process and contrasting it with the more complicated algebra required for eq. (6).

Solving $\beta_b = 0$ is equivalent to solving $T_b = T_{\text{upper}}$ or $T_{\text{upper}} = T_b = T_e + q'(A - A_b)$, where $A = \alpha_b A_b + \alpha_w A_w$ is the planetary albedo. This gives

$$T_{\text{upper}} = T_e + q'(A_g - A_b)(1 - \alpha_b). \quad (7)$$

The overall equation for α_b is therefore

$$T_{\text{upper}} = \left[\frac{SL}{\sigma} (1 - A_g + \alpha_b(A_g - A_b)) \right]^{1/4} + q'(A_g - A_b)(1 - \alpha_b), \quad (8)$$

where $A = \alpha_b A_b + \alpha_w A_w$ is the effective albedo representing a weighted average of A_b and A_g , the ground albedo.

This is a fourth-order polynomial in α_b which, although it has a formal solution in radicals, is best solved numerically in the sense that the analytical solution is difficult to interpret.

Observe the simplicity and compelling narrative implicit in eq. (8). Consider a habitable planet with $\alpha_b \ll 1$. If $L > 1$, the area covered by black daisies increases, heating the planet until $\beta_b = 0$ (i.e. $T_b = T_{\text{upper}}$; the solution to eq. (8)), at which point further growth ceases.

Whether the daisies ‘control’ T_e in this case is moot: the black area increases until the black daisies become too hot to retain a positive growth rate. It might be better to consider this process more in terms of black daisies causing ‘thermal pollution’ which eventually inhibits further growth. Analogous processes occur in monochrome white daisyworld, in which the white daisies cool the planet until their growth is inhibited.

3. Bichromatic Daisyworld

If both types of daisies are present, then the steady state is characterized by $\beta_b = \beta_w$. This implies that T_w and T_b are equidistant from T_{opt} , as the growth curve is symmetrical. The resulting equations are

$$T_e^4 = SL/\sigma \cdot (1 - A) \quad (9)$$

$$T_{w,b} = T_e \pm q'(A - A_{w,b}) \quad (10)$$

$$T_b + T_w = 2T_{\text{opt}} \quad (11)$$

$$\alpha_b + \alpha_w = 1. \quad (12)$$

One interesting consequence is

$$T_e = T_{\text{opt}} - \frac{q'}{2} (A_w - A_b)(\alpha_w - \alpha_b) \quad (13)$$

and the system may be solved by solving the single equation

$$\frac{SL}{\sigma} [(1 - A_w) + \alpha_b (A_w - A_b)] = \left[T_{\text{opt}} - \frac{q'}{2} (A_w - A_b)(1 - 2\alpha_b) \right]^4 \quad (14)$$

(compare eq. 8). This equation is readily solved using numerical methods; the left and right hand sides correspond to the planetary temperature as determined from the overall albedo and the temperature as determined by solving eq. (13).

Figure 1 shows the temperature as a function of solar luminosity L for bichromatic Daisyworld in both Watson and Lovelock’s formulation and that presented here, using their value of $q' = 20$.

Note how $q' = 0$ implies $T_e = T_{\text{opt}}$, which would be interpreted as perfect homeostasis. Another interpretation of $q' = 0$ would be the perfect spatial intermingling of black and white daisies;

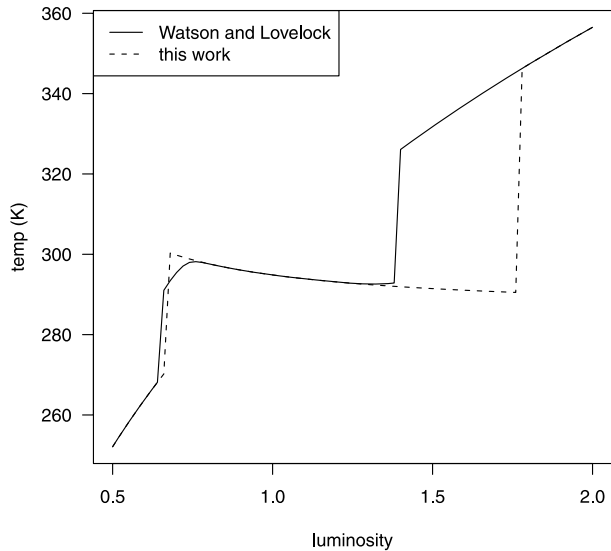


Fig. 1. Temperature versus luminosity for Watson and Lovelock (1983) and the present work. Observe the close agreement, in the biotic regime, between the two formulations; also note the extended region of homeostasis in the present work.

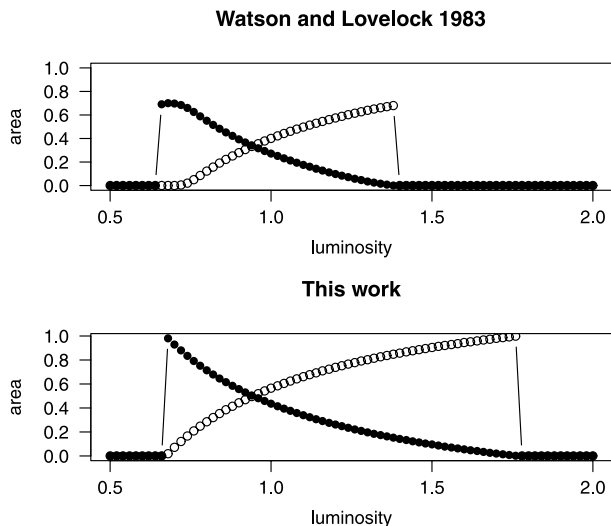


Fig. 2. Areas occupied by white and black daisies (open and closed symbols, respectively) as a function of luminosity according to Watson and Lovelock (1983) (upper figure) and the present work (lower figure).

the spatial aggregation implied by a nonzero value for q' is consistent with a neutral (Hankin, 2007) but not a unified neutral (Hubbell, 2001), ecology.

Figure 2 shows the areas occupied by black and white daisies, again as a function of L . Watson and Lovelock's model predicts

that the bare ground area $x = 1 - \alpha_b - \alpha_w$ is very close to $\gamma = 0.3$ for almost the whole biotic range of L , while in the present work $x = 0$ exactly whenever the daisies are present.

It is straightforward to show that $dT_e/dL < 0$ in the biotic range, which is the range

$$\frac{\sigma T_{\text{lower}}^4}{S(1 - A_b)} \leq L \leq \frac{\sigma T_{\text{upper}}^4}{S(1 - A_w)}. \quad (15)$$

4. Discussion and conclusions

Daisyworld as presented by Watson and Lovelock (1983) included a death rate parameter γ whose value is conventionally taken to be 0.3. A nonzero value for γ yields an equilibrium solution that includes a proportion $\sim 30\%$ of bare, fertile ground which is climatically inactive yet necessary for the model to function.

This paper has shown that one may remove γ from Watson and Lovelock's original Daisyworld and add a species infiltration term Γ . The magnitude of Γ (provided it is positive) does not affect the equilibrium attained, which can be determined by solving a single polynomial equation. This device has the advantage that it reduces the number of free parameters in the model by one, while retaining and extending biologically mediated climatic control.

References

- Cohen, J. E. and Rich, A. D. 2000. Interspecific competition affects temperature stability in Daisyworld. *Tellus* **52B**, 980–984.
- Emborg, J., Christensen, M. and Heilmann-Clausen, J. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.* **126**(2), 173–189.
- Hankin, R. K. S. 2007. Introducing 'untb', an R package for simulating ecological drift under the unified neutral theory of biodiversity. *J. Stat. Softw.* **22**(12).
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press, New Jersey.
- Pujol, T., Fort, J. and Méndez, V. 2005. Consequences of inter-specific competition among multiple adaptive species in Daisyworld. *Theoret. Appl. Climatol.* **81**, 137–147. doi:10.1007/s00704-004-0063-6.
- Stewart, G. H., Rose, A. B. and Veblen, T. T. 1991. Forest development in canopy gaps in old-growth beech (*nothofagus*) forests, New Zealand. *J. Veg. Sci.* **2**, 679–690.
- Watson, A. J. and Lovelock, J. E. 1983. Biological homeostasis of the global environment: the parable of Daisyworld. *Tellus* **35B**, 284–289.
- Watt, A. S. 1947. Pattern and process in the plant community. *J. Ecol.* **35**(1/2), 1–22.
- Watt, A. S. 1955. Bracken versus heather, a study in plant sociology. *J. Ecol.* **43**(2), 490–506.
- Wood, A. J., Ackland, G. J., Dyke, J. G., Williams, H. T. P. and Lenton, T. M. 2008. Daisyworld: a review. *Rev. Geophys.* **46**(RG1001), 1–23.