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## Symbiotic physiology promotes homeostasis in Daisyworld

Richard A. Boyle\*, Timothy M. Lenton, Andrew J. Watson

School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

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## ABSTRACT

A connection is hypothesized between the physiological consequences of mutualistic symbiosis and life's average long-term impact on certain highly biologically conserved environmental variables. This hypothesis is developed analytically and with a variant of the Daisyworld model. Biological homeostasis is frequently effective due to co-ordination between opposing physiological "rein" functions, which buffer an organism in response to an external (often environmental) perturbation. It is proposed that during evolutionary history the pooling of different species' physiological functions in mutualistic symbioses increased the range of suboptimal environmental conditions that could be buffered against—a mutual tolerance benefit sometimes sufficient to outweigh the cost of cooperation. A related argument is that for a small number of biologically-crucial physical variables (i) the difference between organism interiors and the life–environment interface is relatively low, and (ii) the biologically optimum level of that variable is relatively highly conserved across different species. For such variables, symbiosis tends to cause (at a cost) an increase in the number of environmental buffering functions per unit of selection, which in turn biases the overall impact of the biota on the state of the variable towards the biological optimum. When a costly but more temperature-tolerant and physiologically versatile symbiosis between one black (warming) and one white (cooling) "daisy" is added to the (otherwise unaltered) Daisyworld parable, four new results emerge: (1) The extension of habitability to a wider luminosity range, (2) resistance to the impact of "cheater" white daisies with cold optima, that derive short-term benefit from environmental destabilisation, (3) the capacity to maintain residual, oscillatory regulation in response to forcings that change more rapidly than allele frequencies and (crucially) (4) "succession"-type dynamics in which the tolerant symbiosis colonises and to an extent makes habitable an otherwise lifeless environment, but is later displaced by free-living genotypes that have higher local fitness once conditions improve. The final result is arguably analogous to lichen colonisation of the Neoproterozoic land surface, followed by the Phanerozoic rise of vascular plants. Caution is necessary in extrapolating from the Daisyworld parable to real ecology/geochemistry, but sufficiently conserved variables may be water potential, macronutrient stoichiometry and (to a lesser extent) the temperature window for metabolic activity.

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## 1. Introduction

The word "homeostasis" means "standing still" (a system resists externally imposed changes) and "similar" (a system remains in a specific equilibrium state), and is a definitive feature of living organisms. James Lovelock's Gaia hypothesis attributes the sustained non-equilibrium composition of Earth's atmosphere "like that of the intake manifold of an internal combustion engine, with oxygen and combustible gases mixed, and very different from the exhausted, carbon dioxide-dominated atmospheres of Mars and Venus" (Lovelock, 1990), to some form of planetary-scale

homeostatic process—resulting from the interaction between life and its physical environment, and leading to a self-perpetuating habitable state that is qualitatively different from comparable lifeless planets (Lovelock, 1965; Lovelock and Margulis, 1974). But because biospheres (even in theory) lack coherent heritable variation, and are not contained in populations whose members interact and differ in survival and fecundity, no holistic property of Earth's (or any) biosphere can be a consequence of natural selection for that property (Dawkins, 1982; Williams, 1992). Despite this implicit conflict with the local, short-term context in which natural selection operates, geochemical evidence supports the idea of a non-equilibrium and somewhat regulated ocean composition (Redfield, 1958; Lenton and Watson, 2000), and CO<sub>2</sub> homeostasis by a negative feedback on the rate of (microbially enhanced) silicate rock weathering (Walker et al., 1981; Schwartzman and Volk, 1989).

\* Corresponding author.

E-mail addresses: [r.boyle@uea.ac.uk](mailto:r.boyle@uea.ac.uk) (R.A. Boyle), [t.lenton@uea.ac.uk](mailto:t.lenton@uea.ac.uk) (T.M. Lenton), [a.watson@uea.ac.uk](mailto:a.watson@uea.ac.uk) (A.J. Watson).

Various theoretical attempts have been made to reconcile the implication that large-scale homeostasis is in some way caused by (or at least intrinsically associated with) life, but not by direct natural selection. It could be the case that biospheres of various degrees of homeostasis and stability occur in the universe, but that the question of the relative probability of their occurrence is subject to a variant of the anthropic principle, in that only long-lived, intrinsically homeostatic biospheres are capable of giving rise to observers who will ask that question (Watson, 2004). Alternatively, physical constraints on adaptation and form might mean that growth of species that destabilise the state of the environment beyond a certain point is simply not possible (Lenton and Lovelock, 2000). However, this would require any negative feedback from the environment to operate over the same timescale as that of the biota, and to have occurred (at least until now) before any tipping point to complete extinction. Evolution may (for an as yet unknown reason) produce a search process for a self-stabilising interaction between species with different preferred conditions but opposite environmental impacts (McDonald-Gibson et al., 2008). Separation of fitness into environmental and non-environmental components may lead to evolutionary constraints in the non-environmental category limiting the spread of mutants that destabilise the environment, eventually causing the biologically optimal state to evolve so as to track to the environmental equilibrium, rather than the other way around (Staley, 2002).

All these theoretical possibilities share the common implicit assumption that natural selection has a predominantly *destructive* impact on large-scale habitability, and that if homeostasis occurs it is because constraints in the Earth system somehow restrict/prevent an inherent disposition for natural selection to favour destabilising species or genotypes. This is a logical inference from the fact that natural selection lacks the capacity to anticipate the future environmental effects of current evolutionary dynamics. However, if Gaia boils down to the idea that the climates of planets with abundant life are (somehow) more homeostatic than those of lifeless planets, then in order to move towards falsifying the hypothesis it is also necessary to determine whether there is anything about life and the evolutionary process that consistently *creates* large-scale homeostasis in the life-environment interaction. The argument put forward here is that on average, over long evolutionary time scales, and with respect to a small number of highly conserved environmental variables, the formation of mutualistic symbioses between different species acts as such a creative influence, because the physiological and ecological consequences of mutualism tends to bias the physical environment towards biologically optimal homeostasis.

## 2. An illustrative example

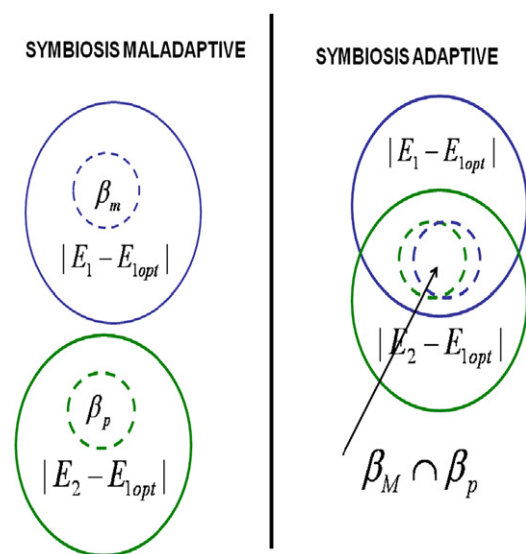
Consider, for argument's sake, the long-term evolutionary dynamics of alleles at a locus in a hypothetical species of fungus, that facultatively forms a lichen symbiosis with a cyanobacterium. The fungus and the cyanobacterium share certain core physiological requirements; a respiratory substrate, an environmental water potential that permits growth, *N*, *P*, *S*, *Ca*, etc. The immediate environment of each species will frequently vary so as to be suboptimal in terms of the supply of one or more of these requirements. The cyanobacterium can fix carbon (and sometimes nitrogen), the fungus is reliant on an external respiratory substrate. The fungus can secrete acids on an inorganic rock substrate so as to obtain *P* and essential metal cations, and form desiccation-resistant spores to survive periods of suboptimum water potential, which the cyanobacterium cannot. This illustrates the (uncontroversial) general principle that mutualistic symbiosis

“evolves most readily between members of different kingdoms, which pool complementary abilities for mutual benefit” (Leigh, 2010). One way of looking at this physiological pooling of abilities is in terms of buffering against environmental conditions that negatively affect reproduction.

Say that the fitness of both species declines with the magnitude of environmental deviation from optimum  $E - E_{opt} = \Delta E = \Delta E_P + \Delta E_M$  (Fig. 1) where  $\Delta E_P$  is that part of environmental deviation from optimum that the photobiont can compensate for but the mycobiont cannot (i.e. not enough respiratory substrate), and  $\Delta E_M$  is the component that the mycobiont can deal with but the photobiont cannot (inorganically extracted macronutrients). Mutualistic interactions create a selection pressure for non-mutualistic cheater mutants that benefit from the other partner but do not reciprocate (e.g. a mycobiont that restricts nutrient supply to its photobiont), potentially making it difficult for symbiosis to evolve. For example, a fungus in an environment with abundant external respiratory substrate will not derive fitness benefit by obtaining these things by forming a lichen symbiosis.

Much existing work on the evolution of symbiosis (e.g. Maynard-Smith and Szathmary, 1995; Frank, 1995, 1997; Van Baalen and Jansen, 2001) focuses on how a given symbiotic interaction may or may not be disrupted by these kind of internal “selfish” influences. However, another aspect of symbiosis is the physiological change that leads to its evolution in the first place, and, in particular, to its subsequent selection. The more mutualistic a given symbiotic allele in one species, the more its presence provides some sort of physiological benefit to the individual of the other species with which it is interacting. Therefore, it is hypothesized that in an environment that is so harsh that the physiological functions of *both* species are necessary for survival and/or reproduction, symbiotic interactions involving cheater alleles will fail and any surviving symbioses will involve mutualist alleles in both species. A relevant environmental condition for coexistence between a costly symbiosis and the free-living species that it evolved from can be derived (Box 1, Eq. (1)) and is of the form:

$$C_M C_P \leq \Delta E_P \Delta E_M (1 - \beta_P)(1 - \beta_M) \tag{1}$$



**Fig. 1.** Deleterious variation in the environment is divided into two categories. Some of those in  $E_1$  can partially be offset by the mycobiont, within the subset  $\beta_m \in (E_1 - E_{1opt})$ , and those in  $E_2$  by the photobiont  $\beta_p \in (E_2 - E_{2opt})$ . The symbiosis is adaptive at the intersection of the regulation regions of each partner  $\beta_m \cap \beta_p$ , which is imposed on the biota by the physical environment.

### Box 1—Symbiosis, physiological flexibility and variable environments

With reference to the hypothetical lichen symbiosis discussed in the text, let the number of individuals in the potential mycobiont (i.e. fungal) population be  $M$  and the number in the cyanobacterial photobiont population be  $P$ . As discussed in the main text, growth of individuals of either species declines with the magnitude of environmental deviation from optimum  $\Delta E = \Delta E_P + \Delta E_M$ , but  $\Delta E_P$  can be rectified by photobiont physiology and  $\Delta E_M$  by mycobiont physiology. Each species contains symbiotic  $s$  and free-living  $f$  individuals. The individual from the other species with which symbiotic individuals interacts may be (theoretically) either a mutualist  $mu$  (from which it gains a physiological contribution  $\beta_p$  that buffers against environmental change) or a cheater  $ch$  (from which it does not). Free living individuals, of course, gain no contribution from the other species. Therefore, the time derivative for the frequency of free-living  $M_f$  and symbiotic  $M_s$  individuals is given by:

$$\frac{dM_f}{dt} = M_f(g_M - d_M - \beta_M \Delta E_M - \Delta E_P) \quad (\text{B1})$$

$$\frac{dM_s}{dt} = M_s \left( g_M - d_M - \beta_M \Delta E_M - \left( \frac{P_{mu}}{P_{mu} + P_{ch}} \right) \beta_p \Delta E_P - C_M \right) \quad (\text{B2})$$

where the per capita growth and death rate for species  $j$  are  $g_j$  and  $d_j$ . Steady state coexistence of symbiotic and free-living individuals independent of the starting frequencies implies that the cost of symbiosis meets  $C_M = \Delta E_P (1 - (P_{mu} / (P_{mu} + P_{ch})) \beta_p)$ , i.e. the cost threshold that can be tolerated increases with the environmental requirement for symbiosis with a photobiont  $\Delta E_P$ , and with the probability of encountering (relative frequency of) a mutualist allele in the photobiont population. For the symbiosis to invade a free-living population, the cost must be less than this. An identical approach for the photobiont population yields  $C_P = \Delta E_M (1 - (M_{mu} / (M_{mu} + M_{mu})) \beta_M)$ . The product of the two cost thresholds in the simplifying case that mutualist alleles have reached fixation in both species gives condition (1) as a requirement for the symbiosis to coexist with and/or outcompete free-living individuals of both other species. Note that the “symbiotic versus free-living” distinction (between different species) is different from the “mutualist versus cheater” (between different alleles at the same locus in a single species) one. In fact, the lack of any a priori justification for any consistent relationship between the two categories is the starting point for most models of the evolution of symbiosis (e.g. Frank, 1995), and the problem of preferential association of altruists with altruists that is part of the wider field of multi-level selection (e.g. Okasha, 2006). The key point for this work is that the tolerable cost of symbiosis is (it is suggested) intrinsically tied to suboptimality in the environment and involves a physiological contribution from the other species. A separate but related issue is that the increase in physiological diversity associated with symbiotic altruism may help the cooperative alleles reach fixation in the first place. Boyle and Lenton (2006) showed that if groups of altruists exhibited sufficient physiological coordination so as to have improved environmental buffering relative to the same number of non-altruist individuals, then altruism could increase from rarity according to  $\gamma |V - V_{opt}| > C$ , (where  $\gamma$  is a buffering factor,  $V$  is an environmental variable of interest, with optimum level  $V_{opt}$ , and  $C$  is the cost of altruism. The reason that groups are hypothesized to have better buffering capacity is that they exhibit the potential for differentiation at the between-individual, as well as the within-individual level, creating a new dimension of phenotypic variation (e.g. it is impossible to form an organ with a single cell). This capacity for within organism diversity and physiological novelty is particularly prevalent in symbioses.

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where the  $0 < \beta < 1$  factors are the extent to which the environmental deviation experienced by the symbiosis is buffered by the mycobiont  $M$  or photobiont  $P$  species (more buffering implies lower  $\beta$ ), and  $C$  is the cost of mutualism for the relevant species. The key point is that other factors being equal, more suboptimal environments and increased buffering of this suboptimality by the other species, permit a higher cost in a mutualistic interaction (Boyle and Lenton, 2006).

The purpose of this paper is not to exhaustively examine the evolutionary trajectories relevant to the origin of symbiosis. Instead the idea here is to explore the implications for the life-environment interaction of the subset of symbioses that are sufficiently mutualistic and physiologically coordinated that a condition of the form of (1) holds. It is proposed that, on average, the increase in the range of external perturbations that can be buffered against creates a physiological versatility in symbioses likely to cause increased tolerance of suboptimal environments compared to the original free-living species. This assumption is supported by a considerable amount of empirical evidence; symbiosis frequently results in an extension of the ecological

range and improved environmental tolerance compared to the ancestral free-living species from which the symbiosis is derived (Box 2). The hypothetical lichen above (or at least variants of it) can colonise any biome on Earth, the ecological ranges of saprotrophic fungi and free-living cyanobacteria are far more restricted (e.g. Honnagar, 1991; Nash, 1996). This sort of improved environmental tolerance by mutualistic symbiosis has certain implications when framed in the exemplar “toy” model used to describe the life-environment interaction, the parable of Daisyworld.

### 3. Symbiotic Daisyworld

Daisyworld (Watson and Lovelock, 1983) is a simple model of an imaginary planet, the temperature of which is influenced by the species that inhabit it. Full equations are given in the appendix, and detailed discussions exist of the model and the derivative studies it has inspired (Wood et al., 2008). Briefly, the temperature of Daisyworld is dictated by the intensity of the

**Box 2**–Symbiosis consistently extends the range of physiological tolerance

A contention in this paper is that those symbiotic interactions that do not descend into mutually exploitative parasitic arms races do so for a reason. This reason is that symbiosis enhances the range of environmental conditions that a given unit of selection is able to tolerate. We strongly argue that this is a consequence of the co-ordinated integration of the physiology of either partner species, a co-ordination that increases the more mutualistic the symbiosis becomes (see text). There are numerous examples in the empirical literature of symbiosis improving environmental tolerance, of which we provide a few:

- *Paramecium bursaria* exhibit improved tolerance of extreme temperatures when they contain symbiotic *Chlorella* algae, perhaps as a biophysical consequence of chemicals produced during algal photosynthesis (Iwatsuki et al., 1998).
- A three way symbiosis between the endophytic fungus *Curvularia protuberata*, containing a virus *Epichloe festucae*, conveys improved thermal tolerance to the tropical grass *Dichantheium lanuginosum* (Marques et al., 2007).
- Various grass species from coastal and geothermal habitats require symbiotic fungi for salt and heat tolerance respectively, as well as increased reproductive success (Rodriguez and Redman, 2008).
- Arbuscular-mycorrhizal symbiosis increases water flow through plant tissues, improving drought tolerance. Other species improve pathogen resistance. Mutualists have more beneficial physiologic effects than pathogenic species (Redman et al., 2001).
- Versatile metabolism derived from various bacterial symbionts is efficient enough to permit (secondary) loss of the digestive and excretory systems of the worm *Olavius algarvensis*. Symbiotic diversity and versatility (theoretically) optimizes host resource supply and metabolism (Woyke et al., 2006).
- Ubiquitous gene exchange permits physiological diversification and acquisition of temporary environment specific functions across the bacterial pan genome (Lapierre and Gogarten, 2009).
- Lichenised fungi occupy a dramatically increased ecological range in comparison to non-lichenised fungi, and in comparison to free living photosynthetic species that may form photobionts (Nash, 1996).
- Sea slugs acquire improved camouflage and reduced dependency on external respiratory substrates by retaining photosynthetic plastids from ingested algae (Rumpho et al., 2000).
- Endosymbiosis with bacteria gave rise to mitochondria and photosynthetic plastids, qualitatively different energy acquisition. A spirochaete origin for protist cilia and eukaryotic flagella is also probable, permitting motility in (respectively) an external and internal sense, hence increasing the range of functions accessible to cell “ecology”. (Summarised in Margulis and Sagan, 1995).
- Water and nutrient absorption by most plants is permitted by the activity of vesicular arbuscular mycorrhizae, and was likely a prerequisite for the colonisation of the land surface (Gerdemann, 1968; Remy et al., 1994).

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solar luminosity flux from a nearby star, which increases linearly over time analogously to Earth's Sun. Any greenhouse effect is ignored for simplicity and the energy balance that arises is dictated by the planetary albedo, which in turn is dictated by the composition of the planet's surface. Daisyworld is inhabited by two species of daisy, white and black, which differ in (only) the nature of their interaction with the environment. The colour difference causes more incoming solar radiation to be reflected from a surface colonised by white daisies than by black (or than by an uncolonised bare rock substrate). This means that the local temperature of white daisies is cooler than the planetary average,

and the abundance of white daisies constitutes a net decreasing influence on planetary temperature (and similarly the local temperature of the black species is warmer and black abundance is an increasing influence).

Temperature homeostasis at a planetary average closer to the (uniform) biological optimum than a lifeless planet can be achieved as a consequence of changes in the relative proportions of the two species, showing how the Gaia hypothesis need not require teleology (Watson and Lovelock, 1983). If the planet deviates from optimum temperature in one direction, the daisy species whose local temperature deviates from optimum in the

opposite direction experiences a higher growth rate, thus increasing in abundance and reining in the temperature deviation (Watson and Lovelock, 1983). Competition for space, combined with the fact that at steady state the local temperature of each species deviates from optimum by the same magnitude but in an opposite direction, creates an integral control system (one in which a feedback will remain active until the “error” in the variable being controlled ceases) between two opposing but complementary “reins” (Saunders, 1994; Harvey, 2004). Such integral rein control systems can achieve strong homeostasis, for example within organisms that use two opposing hormones (rather than one that is present or absent) to control some internal factor, potentially achieving zero steady state error (Saunders et al., 1998, 2000). Regulation in Daisyworld is sensitive to disruption by mutation (Robertson and Robinson, 1998; McDonald-Gibson et al., 2008) cheaters (Keeling, 1991), destructive environmental feedbacks (Watson and Lovelock, 1983), discretization of the albedo trait space (Lovelock, 1992) and the physical constraints on adaptation (Lenton and Lovelock, 2000).

Let us assume that there has evolved on Daisyworld a symbiosis between the black daisy species and the white. Symbiotic individuals experience the cost of altruism relative to free living individuals. Therefore the rate of change of coverage of Daisyworld’s surface by the symbiotic species is given by

$$\frac{d\alpha_s}{dt} = \alpha_s \left( \frac{1}{2} \beta_s x - \gamma - C \right) \quad (2)$$

where  $\alpha_s$  is the fraction currently covered by symbiotic individuals,  $\beta_s$  is the per capita growth rate of the symbiosis,  $x$  is the amount of available bare ground,  $\gamma$  is the death rate and  $C$  is the cost of altruism. The factor of  $\frac{1}{2}$  arises because one symbiotic individual constitutes two free-living individuals—one from each species. (The growth rate of the free-living species (see appendix) has the same form, but there is no cost and no factor of  $\frac{1}{2}$ .) It is assumed that both the black and the white individual in the symbiosis are mutualists, such that each individual has access to the (relevant) physiological capabilities of the individual from the other species, according to the arguments above. The impact of exploitative cheater mutants arising is represented by (an increase in) the free-living species and does not need to be resolved directly. Symbiosis produces increased tolerance of sub-optimal environmental conditions (Box 2), which is expressed in the symbiotic growth function:

$$\beta_s = 1 - (j - k)(T_s - T_{opt})^2 \quad (3)$$

where  $j$  is the sensitivity that (all) daisy species have to temperature,  $T_s$  is the local temperature of symbiotic individuals,  $T_{opt}$  is the (conserved) optimum temperature for growth, and  $k$  is the factor by which symbiotic physiology buffers against suboptimality in local temperature conditions so as to offset their damaging impact on growth. Each free-living species has a growth function of the same form (appendix), but for the relevant local temperature and for  $k=0$ . Buffering of this sort is achieved, as in real symbioses, by a co-ordination of the existing functions of the two free-living daisy species. The local temperature of any daisy species, as in the original model, is dictated by the albedo of that species:

$$T_j^4 = q(A - a_j) + T_e^4 \quad (4)$$

where  $T_j$  is the local temperature experienced by individuals of species  $j$ ,  $A$  is the total planetary albedo,  $a_j$  is that species’ albedo,  $q$  is a heat diffusion parameter and the power of 4 and the degrees Kelvin conversion factor 273 arise from the assumption of a relationship to the planetary effective radiative temperature  $T_e$  according to the Stefan Boltzmann law. The albedo of each species (higher than bare ground for white, lower for black) is a

hard-wired aspect of that species’ physiology. A white daisy has the capacity to cool its locality, a black daisy to warm its locality. If the symbiosis is a physiologically integrated one, it has the capacity to do both, in such a way as to optimize some physiological constraint (the local temperature) shared by both partners. (e.g. to reiterate the analogy above, a mutualistic symbiosis between a fungus and a cyanobacterium can either increase or decrease a shared  $C:P$  constraint by utilising the capabilities of each species according to the environmental conditions, either species alone can only actively move this constraint in one direction because it has access to fewer physiological functions). Therefore, whilst the albedo of the white species is fixed at  $a_w=0.75$ , and that of the black species is  $a_b=0.25$ , the albedo in the vicinity of the symbiosis switches between the two, depending upon which of the two species’ capabilities will move the local temperature of the symbiosis closer to optimum:

$$a_s = (1 - z)a_w + za_b \quad (5)$$

$$z = \frac{1}{2} \left( 1 - \frac{T_s - T_{opt}}{|T_s - T_{opt}|} \right) \quad (6)$$

These equations therefore represent the hypothesized impact of symbiosis on the number of physiological functions and capacity for (internal) homeostasis per unit of selection, and it is important to note that no teleological assumptions are being made about larger scale effects of the symbiosis on habitability. Symbiosis is assumed to improve internal regulation of a highly conserved variable for which the difference between the internal state and that of the life-environment interface is minimal, by using the black or white phenotype in a facultative way. The remaining equations are unmodified from the original Daisyworld model, and are given in the appendix. Having made all these arguments/modifications we are now in a position to state more concisely the hypothesis, relating existing Earth system ideas derived from Daisyworld to the discussion of symbiosis, that this model tests:

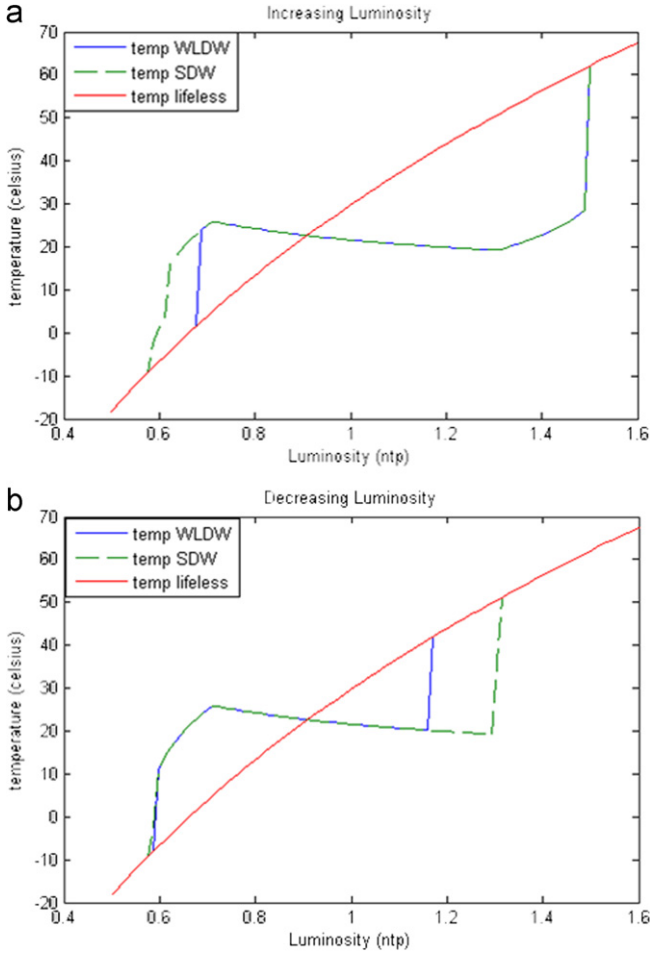
**Hypothesis:** A consistent effect of symbiosis, from a geologic-timescale/Earth system perspective, is to pool together the physiological functions already in the biosphere in a more flexible way, resulting in increased tolerance of suboptimal environments. Consequently, natural selection for such symbiotic tolerance will tend to promote the stable, coordinated coexistence of an increased diversity of physiological functions, including the combinations conducive to homeostasis. On average this will bias towards the biota having a net homeostatic impact on (only) those environmental variables that are sufficiently conserved for the Daisyworld parable to be applicable.

### 3.1. Results

The results are presented in way that emphasizes qualitative differences in behaviour relative to the original model, to examine how symbiosis influences the conceptual parable. A more comprehensive sensitivity analysis and discussion of possible steady states is provided in the appendix.

#### (1) Extension of the luminosity interval that permits habitability

Fig. 2 shows the planetary temperature resulting from progressively increasing (2(a)) and decreasing (2(b)) the luminosity forcing, allowing the model to reach steady state, then using the steady state species frequencies to initialise the model at the subsequent luminosity value—with comparison between the original Daisyworld, symbiotic daisyworld, and a



**Fig. 2.** Steady state temperature (Y-axis) in response to steadily increasing (plot (a)) and decreasing (plot (b)) the intensity of the solar luminosity flux (X-axis, normalised to present), on a lifeless planet (red line), a Watson–Lovelock Daisyworld WLDW (blue line) and a symbiotic Daisyworld SDW (dashed green line). The size of the extra region of luminosity space that the presence of the symbiosis makes habitable can be increased by tuning the tolerance parameter  $k$ , but the qualitative behaviour is not parameter-sensitive—symbiosis leads to an extension of the edge of the habitable zone, before converging on the results of the original model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lifeless planet. The presence of symbiosis allows biological colonisation of the planet from a near zero frequency at an earlier (i.e. further from optimum) luminosity value than would otherwise be the case. As luminosity forcing causes the system to move out of the habitable state, there comes a point at which the impact of the biota on planetary albedo is no longer sufficient for temperature homeostasis, and the system reverts to the lifeless state. When the system is approaching extreme luminosity values from within the habitable region, each run is initialised with relatively high frequencies of the free-living species. This means that the symbiosis does not reach significant frequencies because it cannot stably coexist with the free-living species (see below). As a result, the symbiosis can only extend the side of the habitable region in Daisyworld that is approached from the abiotic state—once a tangible biosphere is established symbiotic physiology makes little difference. This conclusion can be altered by artificially tuning model parameters (to near zero cost  $C$  and near complete tolerance  $k \rightarrow j$ , not shown), but even then habitability is only extended after the free-living

species are entirely extinct. This qualitative difference between the transition from the lifeless to the habitable state and the opposite change reflects, it is argued, a more interesting link between altruism and tolerance, reflected in the second result.

- (2) *Habitability extension requires only transient symbiotic altruism, not its stable fixation*

From the way the model is described above and the arguments about altruism and physiological buffering in Box 1 the intuitive expectation from symbiotic Daisyworld is that if the extra temperature tolerance outweighs the cost of altruism sufficiently, then the symbiosis will grow and habitability will be extended. More formally, the model will revert to Watson–Lovelock Daisyworld if the following relationship does not hold between extra tolerance  $k$ , baseline temperature sensitivity  $j$ , death rate  $\gamma$  and cost of altruism  $C$  (see appendix for derivation):

$$k > 2j(\gamma + C) \tag{7}$$

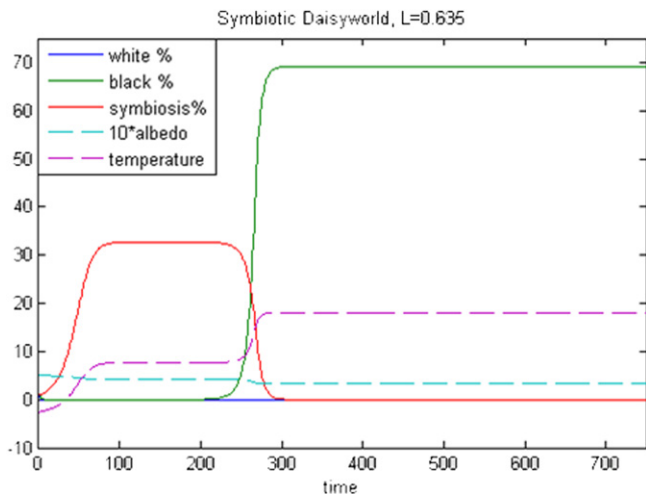
Extrapolating to a clear result from this parameter-sensitive relation alone is difficult—(7) simply gives the condition for the symbiotic species to grow on a planet seeded with the free-living species. It is more useful to compare the life-environment relationship when the symbiosis is the only species on Daisyworld to that when both symbiotic and free-living species are present. If we set the growth equations to steady state and examine the sensitivity of the steady state coverage of the symbiotic species  $\bar{\alpha}_s$  to the extent to which its local temperature  $T_s$  deviates from optimum  $\tau = |T_s - T_{opt}|$  (again with steady state planetary temperature, see appendix) then when the symbiosis is the only species present on Daisyworld, we get:

$$\frac{\partial \bar{\alpha}_s}{\partial \tau \text{ alone}} = \frac{-4(\gamma + C)(j - k)\tau}{(1 - (j - k)\tau^2)^2} < 0 \tag{8}$$

This means that, when the symbiosis is the only species present, the intuitive expectation that the worse the temperature is the lower the steady state frequency will be, holds true. However, when the temperature is at steady state but both other free-living species are present, the algebra is slightly different because we must equate the different growth rates (see appendix), and we end up with a qualitatively different result:

$$\frac{\partial \bar{\alpha}_s}{\partial \tau \text{ coexistence}} = \frac{4C\tau(j + k)}{(j + k)\tau^2 - 1)^2} > 0 \tag{9}$$

The conceptual reason for this difference in sign is that the symbiosis does better *relative* to the free-living species when its tolerance  $k$  justifies the cost, which will happen with larger deviation  $\tau$  from optimum. However, all species experience *net* reduced growth as this deviation increases. The fact that the albedo phenotype of the symbiosis will always move the species' immediate local temperature closer to optimum means that (in the presence of the other two species), an increase in steady state symbiosis frequency is associated with reduced temperature deviation  $\tau$ , creating a contradiction with (9). Because the symbiosis, when it is the sole colonising species, will cause a regime described by (8) to move into one described by (9), this shows that the symbiosis cannot stably coexist with both other daisy species for a non-zero cost  $C$ . Importantly, this also shows that any extension of habitability in this model is not a result of the stable or ubiquitous fixation of altruism. Clearly in nature symbioses do exist with the free-living species that they are derived from, but (9) represents a limiting case in that selfish constraints within the biosphere will, in a constant environment,

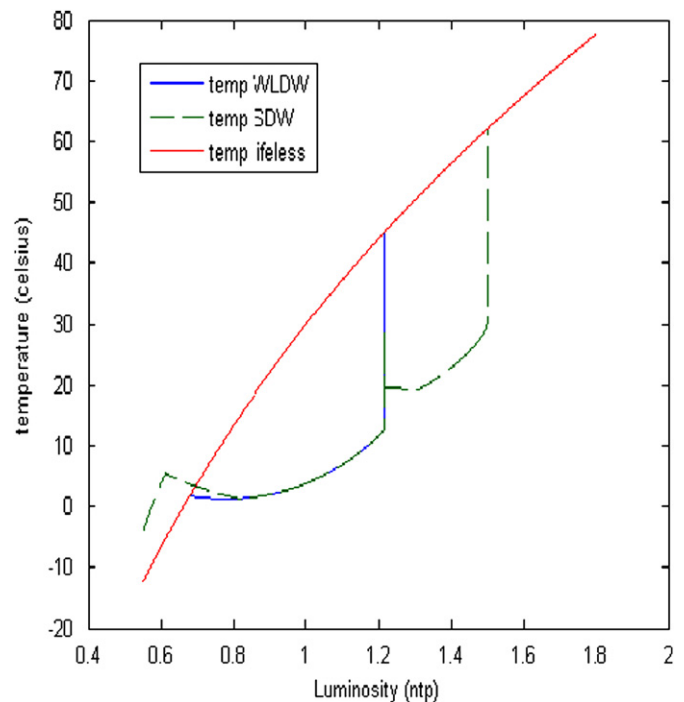


**Fig. 3.** Dynamics of species coverage and climatic properties at the edge of habitability on symbiotic daisyworld; the numerical model run corresponding to the steady state temperature value for  $L=0.625$  for SDW in Fig. 2 a. The planetary temperature (purple) starts off at a value corresponding to the lifeless state. But the extra tolerance of the symbiotic species allows it to grow sufficiently to achieve positive fractional coverage (red line) followed by exponential growth. Because at low luminosity the black species phenotype brings the local state of the symbiosis closer to its optimum, the symbiosis effectively represents, in terms of the climate, a costly but more tolerant black daisy. This causes a partial warming of the planet, and a quasi-steady state at approximately 8 °C. This is sufficient to cause (very gradual) growth of the non-symbiotic black daisy, eventually leading to it growing to tangible fractional coverage (green line). This initiates a positive feedback between the warming of the planet and the frequency of the black species. As the planet warms, the non-symbiotic species gains a progressive selective advantage (see invasibility conditions in main text/appendix), eventually leading to it entirely displacing the symbiotic species and establishing a new steady state of stronger temperature regulation only about 4 °C from the (shared) optimum  $T_{opt}=22.5$ . It is important to note that at this luminosity forcing a Watson–Lovelock Daisyworld without symbiosis remains entirely lifeless. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduce regulation by driving the symbiosis extinct. This is not what happens however, because real environments are not constant.

(3) *Colonisation-succession dynamics analogous to the history of the terrestrial biosphere*

Fig. 3 shows the species dynamics on a symbiotic Daisyworld at a low luminosity value that causes the original model to remain entirely lifeless, and shows how the extension of the width of the habitable interval by symbiotic physiology is the result of two distinct regimes. At luminosity extremes, only the symbiosis survives because the other species cannot tolerate the extreme conditions, and any improvement in habitability relative to the lifeless state results from the low frequency it achieves. However, at luminosity values slightly closer to habitability (like the  $L=0.6235$  in Fig. 3), the initial presence of the symbiosis causes a regime of partial temperature regulation, that leads to exponential increase from minimal initial frequency of the fittest free-living species (at the cold limit shown in the figure, the black species). This triggers a positive feedback between increasing (free-living) species frequencies and albedo changes (reductions) that lead to a relatively stable regulatory regime that would not have been established without the initial presence of the symbiosis. This new regime then results in the decline then extinction of the symbiosis because it cannot compete with the free-living species. The system effectively moves from a steady state regime in the category described by (8) to one in that is described by (9) (the switch happening at a



**Fig. 4.** The introduction of a destructive white daisy species with a colder optimum growth temperature than the rest of the biosphere  $T_{opt,WLDW}=10$  °C drastically narrows the region of luminosity forcing within which habitability can be sustained, but the tolerance of the symbiotic species causes SDW to resist this narrowing to a greater extent than WLDW. The species dynamics in the symbiotic model involve the free-living species being driven extinct as a positive feedback results from increasing frequencies of the white daisy with cold optimum and increasingly low temperatures. However, the combination of tolerance and the flexibility to adopt the black albedo phenotype (because the temperature is lower than optimum), causes the presence of the symbiosis to produce a warming influence that acts as an opposing rein to the destructive species. This resists the mass-extinction caused by the “white daisy that likes it cold” until a more extreme luminosity value.

transient limit in the temperature deviation  $\tau_{displacement} = \sqrt{(2C/x+1)/(j+k)}$ , see appendix). Despite the model incorporating what is a limiting case of altruism so costly as to entirely prevent coexistence, regulation is still established, as a consequence of the link between altruism and physiological tolerance.

(4) *Resistance to the impact of “cheater” white daisies with cold growth optima*

A fundamental criticism of the Gaia hypothesis is the (realistic) prospect of species occurring with a damaging impact on long term habitability but locally high fitness, that (critically) is not checked by any self-limiting negative feedback from the environment until complete loss of habitability. In the language of Daisyworld this problem can be represented by the fact that Watson and Lovelock’s initial model lacked a white daisy species with a cold temperature optimum (or a black with a warm) (Wood et al., 2008). Fig. 4 shows the results of introducing a white daisy species with a colder growth optimum  $T_{opt}=10$  °C. Comparison with Fig. 2 shows how the destabilising positive feedback caused by the cold-preference white daisy (WLC) causes a significant narrowing of the habitable region in both symbiotic Daisyworld and the original model. However, in the symbiotic system, the extra tolerance means that the albedo phenotype of the black daisy can act as an opposing rein to the WLC at more extreme luminosity values, resisting the destabilisation and reducing (although not preventing) the narrowing influence on habitability.

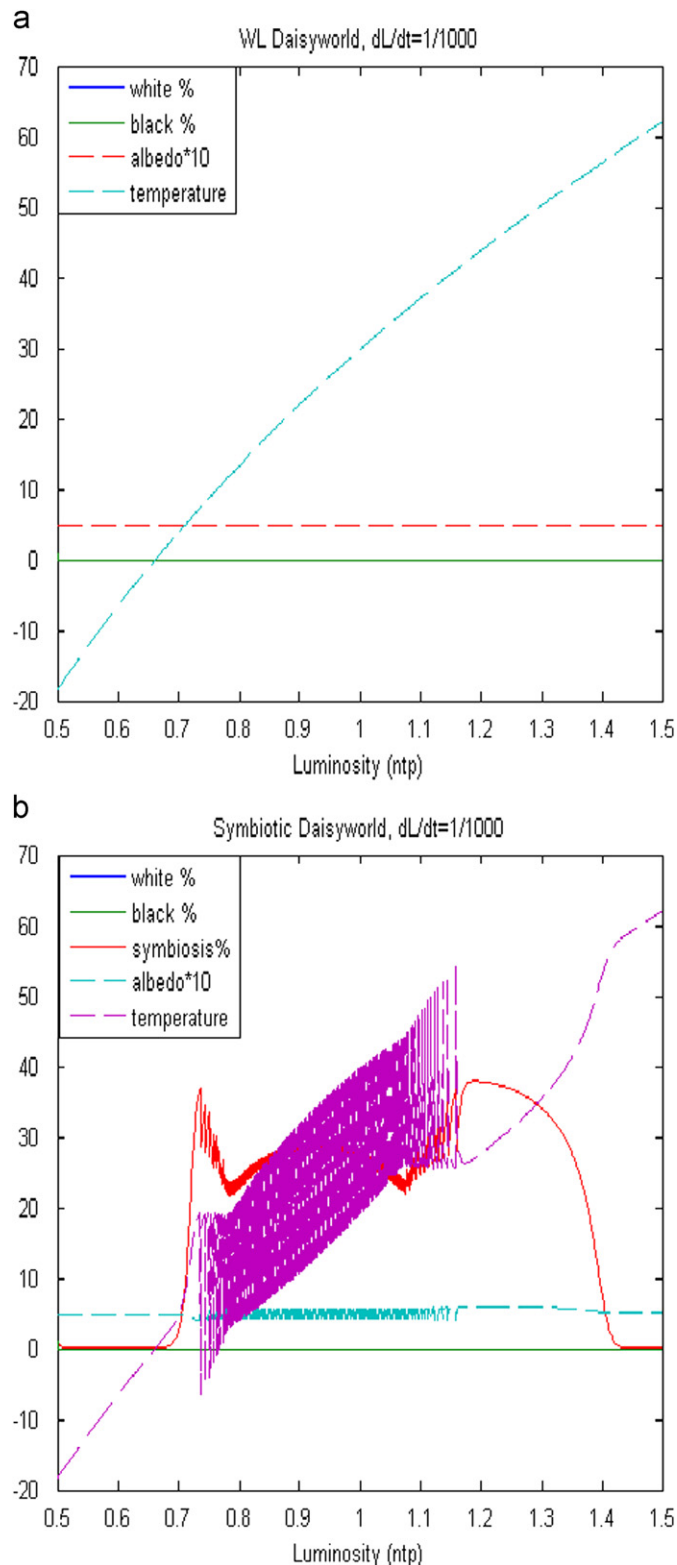
(5) *Residual oscillatory regulation in response to rapid luminosity increases*

Say that for environmental state  $E$  and species abundant  $S$ , if we assume for simplicity that both change over time only as a function of each other, and that  $dE/dt \geq dS/dt$  is sufficient to prevent a destructive tipping point occurring, because species' growth can equilibrate with the environment, then in the simplest case of  $dE/dt = (\partial E/\partial S)(\partial S/\partial t)$ , then for an

environmental variable to permit the species' growth to equilibrate without a positive feedback occurring we need simply:

$$\frac{\partial E}{\partial S_{\text{equilibration}}} \geq 1 \tag{10}$$

It is impossible for evolution to affect this condition, because it refers to the impact/consequences of species growth on the environment, which natural selection cannot anticipate. This makes clear a second fundamental problem with the Gaia hypothesis, that any homeostasis requires the environmental property being regulated to adjust at least as fast as the evolutionary dynamics. If this does not happen, there is the risk of a species with a long-term destabilising impact on habitability experiencing no negative feedback on its own growth until an irreversible positive feedback has been initiated leading to loss of habitability. Symbiotic physiology means that rein control structures capable of resisting this sort of destructive impact may become a function of organism physiology, as well as population level abundance of different species. Therefore if such feedbacks arise they can operate over time scales shorter than those that depend on changing species or genotype abundances. This does not completely rescue the vulnerability of environmental homeostasis to "cheaters" but does create a more rapid homeostatic influence that may resist their effects. Fig. 5 shows the results of increasing solar luminosity continuously during a single numerical run of each of the two Daisyworlds, but doing so at a rate that is too fast to allow the species abundance to equilibrate. This completely breaks regulation in Watson–Lovelock Daisyworld, but in the symbiotic system, the albedo-switching phenotype leads to organism physiology continuously adjusting in response to the rapid environmental change, leading to an oscillating albedo that continuously tracks temperature, and to some extent draws it closer to habitability. The amplitude of these oscillations can be reduced by scaling the switch variable  $z$  by a factor between zero and unity, which might be considered as representing a lag time in the physiological response to the prevailing temperature (see appendix), but this does not qualitatively alter the result. This is not stable regulatory behaviour, but the system remains qualitatively closer to habitability than one in which homeostasis requires population dynamics. Note that this is the only result that explicitly requires the flexibility aspect of the hypothesized symbiosis phenotype, the increased habitability relies on improved tolerance and a single albedo trait value.



4. Discussion

Daisyworld is a metaphor used in order to focus ideas on how life interacts with its physical environment, not a real model of

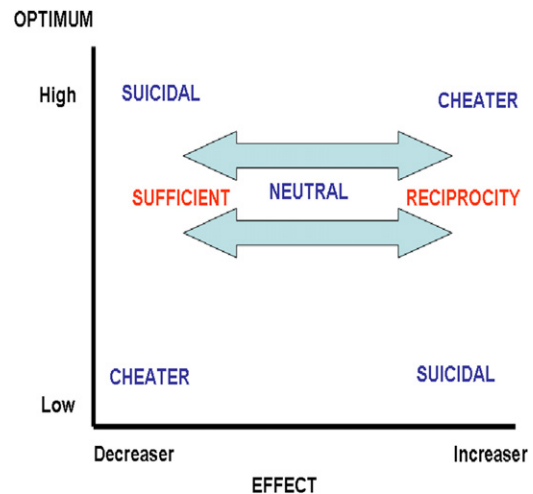
**Fig. 5.** If evolutionary changes cause the integral rein control system capable of regulating daisyworld's temperature to become a property of the physiology of each organism, rather than a population property resulting from the relative proportions of species with different effects, this creates a potential for (some) regulation in response to forcings that change over shorter timescales than the evolutionary dynamics of allele frequencies. Both figures show the result of a single simulation on WLDW in (a) and SDW in (b), in which the luminosity forcing is increased too rapidly for species abundances to come into equilibrium with each particular luminosity value. In the original model this causes a complete failure of regulation and a lifeless planet (b). In the presence of symbiosis equilibration is also not possible and temperature initially tracks a lifeless planet. But subsequently, the combination of temperature tolerance and the flexibility to switch albedo phenotype causes a sustained albedo/temperature oscillation, in which the mean temperature is qualitatively closer to that of a regulated planet than WLDW. Note that this result is the only one of those shown that specifically requires the switching phenotype given by Eqs. (5) & (6), the other results can be achieved with symbiotic tolerance alone, assuming that the phenotype of the symbiosis is black when the planet is too cold and white when it is too warm.

the climate. The results of this work are therefore best viewed as a qualitative comparison between a system with and without the sort of symbiotic physiology discussed. To sum up, improved tolerance (1) extends habitability by (a) allowing the tolerant species themselves to colonise and (b) preparing the environment for less tolerant species via dynamics loosely analogous to an ecological succession, and (2) resists the destructive impact of cheaters. The conclusions hold despite the fact that such tolerance is expressed as a form of altruism so costly as to prevent steady state coexistence with the original species (the limiting case expressing the maximum extent to which internal “selfishness” can disrupt aggregate properties of the biosphere). Improved physiological flexibility may also permit (3) regulation in response to qualitatively more rapid environmental forcings.

As described in the introduction, only a small subset of real physical variables may be represented (even qualitatively) by the parable of Daisyworld. This is because daisies (in this and the original system) move the global temperature in the same direction as the local temperature, and because a species with a local temperature closer to optimum than the global one experience a growth advantage (Wood et al., 2008). This assumption has been characterised as implying that individual daisies experience natural selection for the same properties that cause regulation at the global scale (Kirchner, 2002). To some extent this criticism is valid, and remains valid in terms of the relatively narrow applicability of this work. However, it is argued that in the case of local (i.e. sub-planetary) natural selection for physiological buffering of change in highly conserved environmental variables, critical for all life (as a consequence of physical constraints on adaptation), the correspondence between the fittest phenotypes and those with the most beneficial environmental impact may not be as ad hoc as it sounds. The key constraints is that *the internal state of most species and the state of the life-environment interface are closer to each other than either is to the abiotic state*. In the case of liquid water, carbon:macronutrient stoichiometries, and to some extent temperature, this is feasible, bearing in mind that the fair comparison is between (for example) the water potential of a lichen thallus and a rock weathering interface on Earth, versus that on the surface of Mars.

It is important to emphasize that a distinction exists between a stable equilibrium state and an optimum. The equilibrium planetary average temperature that occurs in Daisyworld may be stable and be qualitatively closer to the biological optimum than a lifeless environment—but will still exhibit some deviation from optimum (as a function of the external forcing and the assumed physical constraints on growth). In contrast, the optimum temperature for daisy growth is a fixed model parameter that represents internal constraints on organism physiology. Rein control in Daisyworld and comparable systems therefore differs from the dynamics of natural selection—which theoretically will tend towards an optimum, at least in contexts in which a constant maximum fitness is attainable (We are grateful to an anonymous reviewer for highlighting the importance of this distinction). Natural selection may act as an (imperfect but effective) optimising influence by changing the abundances of appropriate phenotypes, whose relative fitnesses change in response to the environmental forcing. Physical constraints on adaptation and form limit growth and confine the scope of this optimising influence. The flexible, dynamical control observed in Daisyworld requires the interaction between natural selection and such physical constraints and will lead to equilibration to a state close to optimum, but not a perfectly optimal state.

All of the arguments made about the properties of symbiosis in relation to the free-living constituent species have been probabilistic. The hypothesis tested here is about average physiological properties of symbioses in biospheres in general, over geological



**Fig. 6.** Trait space in the life-environment interaction for the sort of highly conserved physical variable that may be relevant to this work. For a given variable, two traits of a species are relevant, the preferred optimum level (Y-axis, high or low), and the impact that species has (X-axis, increasing or decreasing). In the case of highly conserved physical variables relevant to all life, most physiological functional types that evolution produces will have about the same, intermediate optimum. This is relevant to the formation of symbioses, because it is with respect to highly conserved variables (like water potential, respiratory substrate, macronutrient stoichiometry and temperature) that completely unrelated species are more likely to share an optimum. I.e. it is argued that most mutualistic symbioses form in the middle of the Y-axis. Yet although symbioses are based on common requirements, they are also based on different abilities. The physiological functions of an organism are what dictate its impact on the environment. Because a symbiosis forms between species with qualitatively different physiologies, a symbiosis between two species that occupy the same position on the X-axis is less likely than one between species occupying different positions. Hence, on average, symbiosis is more likely than not to cause fusion of opposing environmental influences with similar preference requirements—that is, to occur between physiological functional types that occupy different positions on the X-axis but roughly the same position on the Y-axis. This biases towards the sufficient (enough reins for each direction the control variable can change in) reciprocity (reins of opposite sign but comparable magnitude) that was simply assumed in the original Daisyworld model, occurring in a single unit of selection. (A species with a low optimum and decreasing effect or high optimum and increasing effect is a “cheater” in that it destabilises the average environmental state in a positive feedback that benefits itself against the common good. A species that always pushes the environmental variable in an opposite direction to its own preference is labelled “suicidal” in that it will self-limit or cause its own extinction.)

timescales and in the case of conserved variables. This is clearly very different to making definitive statements about the life-environment interaction in the case of every symbiosis. What is required is for a variable to be highly conserved across species, for the difference in the state of that variable between organism interiors and the life-environment interface to be minimal in comparison to other variables, and for two different species with similar requirements to form an adaptive, cooperative symbiosis that buffers that state in a stable manner against both increasing and decreasing external forcings (Fig. 6). In order to make clear the probabilistic nature of the requirements, each aspect of the hypothesis is expressed as a specific probability. For a given timepoint, let  $S$  be the number of species in the biosphere, and  $\Delta_{opt}$  the mean, normalised, between-species difference in optimum state for a given physical variable in the abiotic environment. Therefore  $0 < 1/\Delta_{opt} < 1$  is the probability of any two species sharing an optimum for that variable. Let  $0 < |I-E| < 1$  be the mean, normalised difference between organism interior and the exterior life-environment interface with respect to the state of that variable, and  $P_s$  be the probability per species of forming a mutualistic symbiosis, if  $\mu$  is the probability of a physiological function occurring in the biosphere that will

increase the state of that variable, if  $\varphi$  is the probability of a physiological function that will decrease that variable (note that because the direction of the affect is influenced by the climate as well as the biology these two probabilities are not inherently related), then the probability  $\tau$  of physiological symbiosis leading to a self-stabilising feedback that brings the life-environment interface closer towards the biotic optimum for one variable (i.e. of symbiotic Daisyworld representing a real world), at some point in the lifespan  $t$  of the biosphere, is along the lines of:

$$\tau = t \cdot \frac{S\mu\varphi P_s^2}{\Delta_{opt}|I-E|} \quad (11)$$

The kind of conserved variables that may be common to all life is an area of important speculation (e.g. de Duvre, 1994; Kasting, 2010). Most directly relevant to this work is probably macronutrient stoichiometry (e.g. C:N:P)—if the lichen discussed above extracts  $P$  from an inorganic rock substrate it effectively adds that nutrient to a recyclable pool within the biosphere collectively (or at least will do so at death), and causes both lichen biomass and any aqueous solution within the global biogeochemical cycle to be closer to the biologically optimum C:P ratio than the inorganic rock. Another possible example might be the presence of a polar solvent (biochemically-appropriate water potential, or equivalent solvent), and the temperature window for metabolic activity (Schulze-Makuch and Irwin, 2002, 2006; Taylor, 2010). With a sample size of only one biosphere it is not possible to determine whether Eq. (11) appreciably differs from zero, but these factors are potentially measurable, particularly with highly conserved variables and if the sample size of one biosphere is improved upon in the future.

The origin and evolutionary stability of symbiosis is subject to the existing evolutionary problem of altruism. Populations of each partner species will be subdivided into cheater and altruist alleles that, respectively, exploit and provide benefit to the other species. Determining which category of alleles will come to dominate the population is not a simple or a solved problem, and depends on the environmental context. As mentioned above, the Gaia/natural selection problem is also related to altruism, in that parts of the biota that destabilise the environment (like the white daisy that likes it cold, Fig. 4) for the majority bear similarities to cheaters (e.g. Keeling, 1991, outstanding problems summarised in e.g. Boyle and Williamson, 2006; Wood et al., 2008). Therefore the reader might object that trying to solve the Gaia/natural selection problem by invoking symbiosis is an attempt to solve an altruism problem (homeostasis of average environmental habitability) by invoking an altruism problem (between-species cooperation). In some senses this is correct. But the order in which life has solved these problems during Earth history is crucial. The improved tolerance associated with symbiotic altruism can lead to its fixation (at the expense of cheater genotypes within the same species) in suboptimal environments (Boyle and Lenton, 2006). Life consistently does produce symbiosis, indeed the juxtaposition of two interacting but very different systems that promote a mutually-reinforcing optimum state may be the key to phenotypic variation in a more widely applicable sense, up to and including the earliest hereditary systems (e.g. protein-nucleic acid coevolution, Dale, 2006). This paper has argued that over geologic timescales and planetary spatial scales, the repeated fixation of symbiotic altruism fuses the kind of control structure assumed in the initial Daisyworld model into a single unit of selection; biasing certain variables toward the habitable range. Hence, suboptimum environments select for symbiosis, then subsequently symbiosis tends to bias the impact of the biota towards environmental optimisation (Fig. 3). If relevant to real climates, this evolutionary trajectory would provide a mechanism by which natural selection itself could bias the life-environment interaction

towards self-stabilisation, as initially hypothesized by James Lovelock.

## Acknowledgements

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## Appendix A

Original equations from the Daisyworld model can be found in Watson and Lovelock (1983), and the numerous developments upon it are summarised in Wood et al. (2008). Daisyworld's temperature function is analogous to Earth's energy balance with the Sun, radiating in proportion to the fourth power of temperature  $T_e$ :

$$\sigma T_e^4 = SL(1-A) \quad (A1)$$

where  $\sigma = 5.67 \times 10^{-8}$ , influenced by solar energy flux  $S = 9.52.56 \text{ Wm}^{-2}$ , which alters over time according to changes in scaling factor  $0 < L < 1$ . Note that temperature in the model is in Kelvin but optima etc in the text are referred to in Celsius for clarity. Total planetary albedo  $A$  is contributed to by the fractional coverage  $\alpha$  of each daisy species and of bare ground, each of which have different local albedo  $a$ :

$$A = \alpha_g a_g + \alpha_w a_w + \alpha_b a_b \quad (A2)$$

where subscripts "g", "w" and "b" denote bare ground, white and black species, respectively, each with albedo values  $a_g = 0.5$ ,  $a_w = 0.75$ , and  $a_b = 0.25$ . The fraction of Daisyworld's surface that is lifeless  $\alpha_g$  is dictated by the biota:

$$\alpha_g = 1 - \sum_j \alpha_j = x \quad (A3)$$

The amount of available land surface  $x$  appears in the growth equations for the various daisy species:

$$\frac{d\alpha_w}{dt} = \alpha_w(x\beta_w - \gamma) \quad (A4)$$

$$\frac{d\alpha_b}{dt} = \alpha_b(x\beta_b - \gamma) \quad (A5)$$

For death rate  $\gamma = 0.3$ , where the growth rate of the  $j$ th free-living daisy species  $\beta_j$  is dictated by the local temperature of that species  $T_j$  and a universal sensitivity constant  $j = 0.003265$  and optimum growth temperature  $T_{opt} = 295.5 \text{ k}$  ( $22.5^\circ \text{C}$ ):

$$\beta_j = 1 - j(T_j - T_{opt})^2 \quad (A6)$$

As discussed in the main text, growth of the symbiotic species is impaired by a cost  $C = 0.01$  (unless otherwise stated), and each unit change in abundance of a symbiotic individual is equivalent to two free-living individuals:

$$\frac{d\alpha_s}{dt} = \alpha_s \left( \frac{1}{2} x \beta_s - \gamma - C \right) \quad (A7)$$

The reduction in growth rate due to suboptimal local temperature (via the sensitivity constant  $j$ ) if offset, by hypothesis due to the physiological changes associated with the pooling of the functions of the black and white species. This offsetting is expressed by the parameter  $k$ :

$$\beta_s = 1 - (j-k)(T_s - T_{opt})^2 \quad (A8)$$

The default value of  $k$  in the numerical simulations unless otherwise stated  $k=0.8j$ . The implications of variation in the numerical value of the tolerance parameter is encompassed in the analytic result (7) in the main text, and did not alter the qualitative outcome of the simulations. The local temperature of each species ( $T_j$  for the  $j$ th species) had a Stefan Boltzman relationship of the planetary average and the difference between local and planetary albedo:

$$T_j^4 = q(A - a_j) + T_e^4 \tag{A9}$$

where  $q = 2.06 \times 10^9$  is a diffusion constant. The argument in the text is that the symbiosis combines the radiation-absorbing phenotype of the black species with the radiation reflecting phenotype of the white species, and that the physiological flexibility associated with symbiosis creates (at cost  $C$ ) the ability to use either phenotype in a facultative way so as to draw the temperature of the symbiotic organisms (and as a by-product their immediate environment) closer to optimum. This is implemented in a discrete way using the variable  $z$ , which takes the value  $z=1$  when the symbiosis' local temperature is too cold and  $z=0$  when it is too hot:

$$a_s = (1-z)a_w + za_b \tag{A10}$$

$$z = \frac{1}{2} \left( 1 - \frac{T_s - T_{opt}}{|T_s - T_{opt}|} \right) \tag{A11}$$

The causes the albedo-switching phenotype discussed in the main results. The amplitude of the oscillation (of this physiological switching, and its environmental effects, Fig. 5) can be dampened by the introduction of a lag parameter  $0 < \lambda < 1$  dictating the response of albedo to suboptimality in temperature by altering A11 to  $z = \frac{1}{2} (1 - \lambda(T_s - T_{opt}) / (|T_s - T_{opt}|))$ , but this does not qualitatively alter the results.

A.1. Steady state solutions

The edge of the habitable temperature range at which complete extinction of the last remaining free-living species occurs  $\beta_f \leq 0$ . Substituting this into A6 gives the local temperature at this point as  $T_f = T_{opt} \pm 1/\sqrt{j}$ . By hypothesis, the symbiosis will adopt the same albedo phenotype as the last remaining free-living species, because this will be more (locally) homeostatic in terms of its temperature. Therefore putting  $T_s = T_f$ , then substituting into A8 gives  $\beta_s = k/j$ . By A7 and A3, if the symbiotic species is the only species left on Daisyworld and its abundance  $\bar{\alpha}_s$  is at steady state, we infer  $(x/2)k/j - \gamma - C = 0$ ,  $x = 1 - \bar{\alpha}_s$ , therefore a final symbiotic abundance of  $\bar{\alpha}_s = 1 - (2j(\gamma + C)/k)$ . Finally therefore, if the symbiosis is present at a non-zero frequency on a planet on which temperature is too suboptimal to allow survival of the other species, i.e. if symbiosis extends the lifespan of the biosphere, we arrive at Eq. (7) as a constraint on the tolerance parameter  $k$ :

$$k \geq 2j(\gamma + C) \tag{A12}$$

The numerical results showed that the symbiosis never increased from rarity unless this condition was met. What boundary conditions are associated with extinction of the free-living species compared to the symbiosis? From A9 with  $T_j = T_{opt} \pm 1/\sqrt{j}$  and  $A - a_j = a_g(1 - \bar{\alpha}_s) + a_s(\bar{\alpha}_s - 1) = (a_g - a_s)(2j(\gamma + C)/k)$ , we can then solve for the effective radiative temperature of the whole planet at which only the symbiosis is left,  $T_{e(symbionly)}$ :

$$T_{e(symbionly)} = \left( \left( T_{opt} \pm \frac{1}{\sqrt{j}} \right)^4 - q(a_g - a_s) \left( \frac{2j(\gamma + C)}{k} \right) \right) \tag{A13}$$

We can determine the luminosity  $L = \sigma T_e^4 / (S(1 - A))$  with which this temperature is associated using A1 with  $A = a_g(1 - \alpha_s) +$

$a_s \alpha_s = (2j(\gamma + C)/k)(a_g - a_s) + a_s$ , giving an estimate at the threshold luminosity value at which symbiotic physiology may be relevant.

$$L_{(symbionly)} = \frac{\sigma \left( \left( T_{opt} \pm \frac{1}{\sqrt{j}} \right)^4 - q(a_g - a_s) \left( \frac{2j(\gamma + C)}{k} \right) \right)}{S \left( 1 - a_s - \frac{2j(\gamma + C)}{k} (a_g - a_s) \right)} \tag{A14}$$

The same approach for the extinction point of the symbiosis implies, by A8 that it will go extinct at  $T_s = T_{opt} \pm 1/\sqrt{j-k} = T_e$ , therefore a luminosity cut off point at

$$L_{(allexinct)} = \frac{\sigma \left( T_{opt} \pm \frac{1}{\sqrt{j-k}} \right)^4}{S(1 - a_g)} \tag{A15}$$

From which the positive root would be selected for the high luminosity limit (when  $a_s = a_w$ ), and the negative one from the lower limit (when  $a_s = a_b$ ). However, these thresholds cannot, regardless of the symbiosis' albedo phenotype, be related to a unique value for the tolerance  $k$  due to the appearance of the entirely abiotic luminosity term  $S$ . Nonetheless at realistic parameter choices the value  $L_{(allexinct)} < L_{(symbionly)}$  at the lower threshold when  $a_s = a_b$  and  $L_{(allexinct)} > L_{(symbionly)}$  at the upper threshold when  $a_s = a_w$ . The qualitative form of A16 is quite useful. Differentiating  $L_{(symbionly)}$  with respect to tolerance  $k$  gives

$$\frac{\partial L_{(symbionly)}}{\partial k} = \frac{\left( q(1 - a_s) - \left( T_{opt} \pm \frac{1}{\sqrt{j}} \right)^4 \right) 2j\sigma(\gamma + C)(a_g - a_s)}{\left( 1 - a_s - \frac{2j(\gamma + C)}{k} (a_g - a_s) \right)^2 k^2 S} \tag{A16}$$

This matters because, since all parameters are positive and  $q(1 + a_s) - 1/j^2 = 2.06 \times 10^9 \cdot (1.5 \pm 0.25) - 93806.7 \gg 0$ , the sign of  $\partial L_{(symbionly)} / \partial k$  is the same sign as that of  $a_g - a_s$ :

$$\frac{\partial L_{(symbionly)}}{\partial k} = \frac{a_g - a_s}{|a_g - a_s|} \tag{A17}$$

Therefore at the cold luminosity limit, when the symbiosis is black and  $a_g - a_s = 0.25$ , the bigger the value of tolerance  $k$ , the higher the luminosity threshold (the warmer the planet) at which the free-living species goes extinct. Similarly at the hot limit when the symbiosis is white  $a_s - a_g = -0.25$ , this threshold is lower (comparatively cooler) with larger  $k$ . The more tolerant the symbiosis, the easier it will displace free-living species when the system is moving from the habitable region into the non-habitable region. This is consistent with the logical expectation that higher tolerance increases the relative advantage that symbiosis has over non-tolerant species once conditions start to become suboptimal. Similarly, at the low end of overall habitability (i.e. in the absence of free-living species) when Daisyworld is too cold and  $T_s \rightarrow T_e = T_{opt} - 1/\sqrt{j-k}$ , and at the high limit when  $T_s \rightarrow T_e = T_{opt} + 1/\sqrt{j-k}$ , differentiating A15 with respect to  $k$  gives (respectively)

$$\frac{\partial L_{(allexinct)}}{\partial k}_{low} = \frac{-2\sigma \left( T_{opt} - \frac{1}{\sqrt{j-k}} \right)^3}{(j-k)^{3/2} S(1 - a_g)} < 0 \tag{A18}$$

$$\frac{\partial L_{(allexinct)}}{\partial k}_{high} = \frac{2\sigma \left( T_{opt} + \frac{1}{\sqrt{j-k}} \right)^3}{(j-k)^{3/2} S(1 - a_g)} > 0 \tag{A19}$$

These results again formalise a logical expectation—that at the extreme habitability edges, the more tolerant the symbiosis, the

lower the luminosity at which cold drives it extinct and the higher the luminosity at which heat drives it extinct.

### A.2. Steady state species frequencies

Steady state temperature requires the growth rate of the white and black species to be equal  $\beta_w = \beta_b = \gamma/x$ , with the implication that the local temperature of each species deviates from optimum by the same amount in opposite directions,  $1-j(T_w-T_{opt})^2 = 1-j(T_b-T_{opt})^2$ ,  $\therefore \pm(T_w-T_{opt}) = \pm(T_b-T_{opt})$  (Watson and Lovelock, 1983). Symbiosis as modelled here has an identical albedo phenotype to one or other of the free-living species, therefore must have an identical local temperature,  $T_s = T_f$  for one or other  $T_f$ . Solving the model for steady state also involves exploiting the fact that the albedo phenotype of the white  $a_w$  and black  $a_b$  species differ from that of bare ground by the same amount;  $a_g = 0.5$ ,  $a_b = 0.5 - B$ ,  $a_w = 0.5 + B$  (Wood et al., 2008). In this version of Daisyworld A10 therefore implies  $a_s = z(0.5 - B) + (1 - z)(0.5 + B) = B(1 - 2z) + \frac{1}{2}$ . Thus planetary albedo as formulated here, given that  $\alpha_g = 1 - \alpha_s - \alpha_w - \alpha_b$ :

$$A = \frac{1}{2} + B(\alpha_w - \alpha_b + \alpha_s(1 - 2z)) \quad (\text{A20})$$

The linear approximation to the planetary temperature in A1  $T_e = (SL/\sigma)(1 - A)$  does not affect the generality of the results and allows us to write the local temperature of the  $j$ th species as  $T_j = q(A - a_j) + T_e = A(q - SL/\sigma) + SL/\sigma - qa_j$ , hence (with A20) to express the local temperature of each species (white  $T_w$ , black  $T_b$  and symbiotic  $T_s$  in terms of the global species frequencies (using the method of Wood et al., 2008):

$$T_w = ((\alpha_w - \alpha_b) + (1 - 2z)\alpha_s) \left( q - \frac{SL}{\sigma} \right) B + \frac{SL}{2\sigma} - qB \quad (\text{A21})$$

$$T_b = ((\alpha_w - \alpha_b) + (1 - 2z)\alpha_s) \left( q - \frac{SL}{\sigma} \right) B + \frac{SL}{2\sigma} + qB \quad (\text{A22})$$

$$T_s = ((\alpha_w - \alpha_b) + (1 - 2z)\alpha_s) \left( q - \frac{SL}{\sigma} \right) B + \frac{SL}{2\sigma} - q(1 - 2z)B \quad (\text{A23})$$

We can then use the fact that  $T_b + T_w = 2T_{opt}$  to get a first equation constraining the three unknowns by equating the sum of A21 and A22 to  $2T_{opt}$  then solving for the frequency component:

$$(\alpha_w - \alpha_b) + (1 - 2z)\alpha_s = \frac{T_{opt} - \frac{SL}{2\sigma}}{B \left( q - \frac{SL}{\sigma} \right)} = \bar{T}_1 \quad (\text{A24})$$

where  $\bar{T}_1$  denotes the inorganic parameters of the temperature function. Then, substituting this species frequency component A24 back into the temperature Eqs. A21, A22 and A23, we get  $T_w = T_{opt} - qB$ ,  $T_b = T_{opt} + qB$ ,  $T_s = T_{opt} - q(1 - 2z)B$ . These temperature deviations can be substituted into the growth functions A6 and A8 in order to further constrain our three unknowns. By A4 and/or A5 non-zero steady state coexistence of both the two original species requires  $\beta_w = \beta_b = \gamma/x$ , which gives us (by A3):

$$1 - \alpha_w - \alpha_b - \alpha_s = \frac{\gamma}{1 - jq^2B^2} = \bar{G}_F \quad (\text{A25})$$

where  $\bar{G}_F$  denotes the growth constraints on the free-living species. Non-zero steady state for the symbiotic species requires  $\beta_s = (2(\gamma + C))/x$ , so coexistence of all three also gives

$$1 - \alpha_w - \alpha_b - \alpha_s = \frac{2(\gamma + C)}{1 - (j - k)q^2(1 - 2z)^2B^2} = \bar{G}_S \quad (\text{A26})$$

where  $\bar{G}_S$  denotes growth constraints on the symbiosis. Because this implies  $\bar{G}_F = \bar{G}_S$ , we have three unknowns but only two equations, meaning that we cannot solve for unique steady state species frequencies. (This reflects the fact that as a result of the cost of

altruism, the physiological–ecological interaction of the symbiosis is ultimately unsustainable, see below). However, we can solve for the extra tolerance  $k$  that allows the symbiosis to have the same growth rate as the other species, getting  $k = ((1/q^2B^2)(2C/\gamma + 1) + j(4z^2 - 4z - 1 - 2C/\gamma))/(1 - 2z)^2$ . More meaningful is to express the tolerance as a fraction of the initial sensitivity  $j$  by putting  $k = \psi/j$ :

$$\psi = \frac{C^2 \left( \frac{1}{q^2B^2j} - 1 \right) + \left( 4z^2 - 4z + \frac{1}{q^2B^2j} - 1 \right)}{(1 - 2z)^2} \quad (\text{A27})$$

A27 holds when the lag time for the symbiosis' white–black phenotypic switching is any value between  $0 \leq z \leq 1$ . This lag time represents how long the symbiosis takes to switch to the phenotype that will cause its local temperature to move towards optimum. In the main paper we made the simplifying assumption that it was discretized to one or other of these values (A11), because we assumed that it was a hard-wired aspect of mutualistic physiology gained at the cost of symbiotic altruism. In this case A27 reduces to

$$\psi_{discrete} = \left( \frac{C}{\gamma} + 1 \right) \left( \frac{1}{q^2B^2j} - 1 \right) \quad (\text{A28})$$

The wider issue of the relationship between local (biological and evolutionary) and global (climatic) feedback timescales is explored in other Daisyworld work (in progress), not specifically related to symbiotic altruism and involving relaxing this discretization of  $z$ .

### A.3. Symbiosis-free-living coexistence is intrinsically unstable

The assumption of  $T_w - T_{opt} = T_b - T_{opt}$  does not imply enough information to get unique steady state frequencies for all three species, in contrast for the original two species model. This reflects the instability of the symbiotic species in direct competition with the two free-living species when temperature conditions approach habitability. In some cases in nature altruists and cheats can coexist, but our version of Daisyworld contains the limiting case in which altruism is so costly as to always be competitively inferior (at steady state in the habitable zone). Setting the time derivatives A4/A5 and A7 to zero  $\beta_s \frac{1}{2}x - \gamma - C = 0$ ,  $\beta_f x - \gamma$ , eliminating  $\gamma/x$  and substituting in the form of the growth functions:

$$\frac{1}{2}(1 - (j - k)(T_s - T_{opt})^2) - \frac{C}{x} = 1 - j(T_f - T_{opt})^2 \quad (\text{A29})$$

We can define the suboptimality of the environment as  $\tau = |T_s - T_{opt}|$ , the magnitude of the temperature deviation that the symbiosis' locality exhibits from optimum, which will be the same as that for one or other free-living species  $\tau = |T_f - T_{opt}|$  for one or other  $T_f$ . Rearranging A29, substituting for  $x$  and solving for  $\bar{\alpha}_s$ , the steady state frequency of the symbiotic species, we get a steady state constraint relating to this temperature deviation:

$$\bar{\alpha}_s = 1 - \frac{2C}{(j + k)\tau^2 - 1} - \bar{\alpha}_w - \bar{\alpha}_b \quad (\text{A30})$$

We are interested in how this steady state frequency is altered by the deviation that the steady state local temperature of the symbiosis  $\bar{T}_s$  exhibits from optimum. We therefore differentiate A27 with respect to  $\tau$ , emphasising that this is a partial derivative of the steady state condition—as opposed to an actual time derivative in the model. The trickiest part is determining the partial derivative of the free-living species. We can do this by recalling that at steady state the white and black species need to have equal growth rates  $\beta_w = \beta_b = \gamma/x = \beta_f$ . It is at this point that the fact that symbiosis must, if it is to coexist, have the same local temperature as one of the free-living species, becomes of

conceptual importance. As a consequence of this constraint, the partial derivative of the temperature of the free-living species, with respect to the temperature of the symbiosis,  $\partial \bar{T}_f / \partial \bar{T}_s$ , is always equal to 1 for one of the free-living species, and to  $-1$  for the other. This is important when we actually differentiate A30:

$$\begin{aligned} \frac{\partial}{\partial \tau} (\bar{\alpha}_w + \bar{\alpha}_b) &= \frac{\partial \bar{\alpha}_f}{\partial x} \frac{\partial x}{\partial \beta_f} \frac{\partial \beta_f}{\partial \bar{T}_f} \left( \frac{\partial T_w}{\partial \tau} + \frac{\partial T_b}{\partial \tau} \right) \\ &= (-1) \left( -\frac{\gamma}{\beta_f^2} \right) (-2j(T_f - T_{opt})) (1 + (-1)) = 0 \end{aligned} \quad (\text{A31})$$

Note that this assertion is unaffected by the difference in temperature  $T_f$  of either free-living species in the middle bracket. This is because the three species coexistence case implies that  $T_f - T_{opt}$  is the same sign for each  $T_f$  (i.e. black and white). To see this, imagine, that the symbiosis is white, then the relationship between symbiotic temperature and tau will be the same sign as that between the white species and tau, and the opposite sign to that between the black species and tau. However, if the symbiosis is white it uses the white phenotype to improve its temperature, meaning that it must be hotter than  $T_{opt}$  (and so must the free living white species, remembering that we are referring to steady state). If the white species' temperature is hotter than optimum, then so must be the black species' temperature. The same argument means that if the symbiosis is black all three species must be cooler than optimum, so again  $T_f - T_{opt}$  is the same sign for both  $T_f$ , therefore A31 remains true. Consequently the steady state frequency of the symbiosis, if it was to coexist with the free-living species, would always be a positive function of the magnitude of the deviation that its local temperature exhibits from optimum.

$$\frac{\partial \bar{\alpha}_s}{\partial \tau} = \frac{4C\tau(j+k)}{(j+k)\tau^2 - 1} > 0 \quad (\text{A32})$$

This is not just a mathematical idiosyncrasy of the Daisyworld model. The symbiosis as defined here will always cause the temperature of its local environment, and by extension the planet, to move towards its optimum, as all life does at all scales. But the fundamentally short-sighted properties of natural selection mean that when this homeostatic feature comes at a cost, the unit of selection bearing it will only increase in relative frequency when the environment is sufficiently bad for homeostasis to make sense. But *any infinitesimally small increase in the symbiosis' abundance has the by-product of making the environment better, counteracting the selection pressure that lead to the frequency change in the first place.* The symbiosis destabilises any infinitely small increase in its own frequency during the coexistence case, explaining why universal "climatic altruism" can never evolve.

In the alternative case further from the habitable zone in which the symbiosis is the only species on Daisyworld the situation is much more simple. Setting A7 to zero we get steady state symbiosis abundance  $\bar{\alpha}_s = 1 - (2(\gamma + C)) / \beta_s$ , which we can again then take the partial derivative with respect to  $\tau = |T_s - T_{opt}|$ :

$$\frac{\partial \bar{\alpha}_s}{\partial \tau} = \frac{-4(\gamma + C)(j - k)\tau}{(1 - (j - k)\tau^2)^2} < 0 \quad (\text{A33})$$

This is always less than zero because  $k < j$  by definition. Again this is of conceptual importance, because it means that an infinitesimally small positive increase in the steady state frequency of the symbiosis will be able to cause a positive feedback process, by drawing temperature closer to optimum, and giving rise to a greater increase in frequency. This positive feedback allows the symbiosis to colonise the planet with greater efficiency than the free-living species, but can only be sustained when the

symbiosis is the only species on Daisyworld. The switch between a regime described by A33, followed by eventually free-living species growth and a regime described by A32 is the reason for the succession-like behaviour of the model shown in Fig. 3.

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