Emergent patterns in space and time from daisyworld: a simple evolving coupled biosphere–climate model

BY GRAEME J. ACKLAND1,∗ AND A. JAMIE WOOD2,3,4

1 School of Physics and SUPA, University of Edinburgh, Mayfield Road, Edinburgh EH9 3JZ, UK
2 York Centre for Complex Systems Analysis, and 3Department of Biology, University of York, York YO10 5YW, UK
4Department of Mathematics, University of York, York YO10 5DD, UK

We present a simplified model of a coupled planetary geosphere–biosphere, with two evolving species coupled through a single environmental variable. The species do not compete directly, but instead compete through, and can evolve their effect on, this environmental parameter. The model produces an evolutionary arms race, with each species evolving extreme behaviour to counteract the other. The result is an apparently stable balance, with the planet supporting a maximum amount of life, in unusually patterned configurations. However, this balance is achieved by two countering effects and is susceptible to very large correlated fluctuations and extinction events if the balance is disturbed. This arms-race evolution is observed even for very small differences between the species: for a coupled evolving system, the ‘neutral’ theory of identical species is not the limiting case.

Keywords: daisyworld; entropy; feedback; Gaia; logistic

1. Introduction

Understanding the beautiful patchwork of vegetation patterns that satellite photography reveals throughout our planet is a fascinating problem. The major cause is, of course, the difference in climate and geology from one place to another. However, in many places no such external cause exists: patterns are generated spontaneously by the vegetation’s interaction with itself and its interactions with the environment.

As well as spatial patterns, many natural ecosystems are cyclic rather than static. This may be due to random fluctuations or be deterministic, with each vegetation type changing the environment until another type becomes more fit. Such patterns in time may fit into the same theoretical framework as those in space, being caused by short-range (or short-term) advantage at the cost of

*Author for correspondence (gjackland@ed.ac.uk).

One contribution of 17 to a Theme Issue ‘Patterns in our planet: applications of multi-scale non-equilibrium thermodynamics to Earth-system science’. 
long-range disadvantage. One feature of the extinction record is its non-Gaussian
statistics (Newman 1996) hinting at the presence of adapting complex feedbacks
in the ecosystem that promote enhanced stability (Watson & Lovelock 1983;
McCann et al. 1998; Ackland & Gallagher 2004) but also the possibility of
catastrophe as described by Ackland et al. (2003).

Maximum entropy modelling is a powerful method of analysing geographical
patterns of species distribution (Phillips et al. 2006). The general idea of MaxEnt
is that once all the impossible patterns are eliminated, any of the remaining
patterns are equally likely. The entropy is then a count of the number of patterns
that look the same. In order to obtain such patterns, it is necessary to consider
the interplay between vegetation and its environment.

Recent years have seen an explosion in simple computer models that capture
the essence of the biology leading to pattern formation. These typically use the
notion of ‘agent-based modelling’. Each site in space may be occupied by an
agent with various properties representing a plant. Haploid asexual reproduction
and evolution are modelled naturally in this framework by replicating the agent
and all its properties, with the possibility of some mutation. This automatically
preserves linkage disequilibrium.

One-family models of this type are cellular automaton (CA) ‘daisyworlds’.
Inspired by the simple coupled ecosphere–biosphere models of Watson & Lovelock
(1983), these models introduce spatial inhomogeneity and allow the biosphere to
create and maintain its own environmental niche. These agent-based daisyworlds
(von Bloh et al. 1997) give each agent (the daisy) properties of albedo
(colour), temperature-dependent growth rate, mutation rate and death rate. The
parameters determining these agent properties are allowed to evolve by mutation
and natural selection within biologically reasonable values. In addition to the
agents, daisyworlds have a physical environment that depends on the current
nearby daisy cover and the history. The main emergent feature of the daisyworlds
is that the agent properties evolve to regulate the environment in a state that
favours agent reproduction.

A nice feature about daisyworlds is that they finesse the ill-defined biological
concept of ‘fitness’, dealing directly with the well-defined concepts of birthrate
and survival probability.

Although the daisy trait is referred to as ‘albedo’ and the environmental
quantity as ‘temperature’, it is understood that these actually represent a
complicated combination of biological and environmental quantities. These are
folded into single numbers, which, in turn, determine the reproductive success
(‘fitness’) of individuals in their current environment. An excellent example of
how the modelling of real vegetation has utilized the framework of daisyworld
modelling is the work by Baldocchi et al. (2005). These authors replace
temperature by moisture and are able to successfully reproduce the spatial
statistics of desert savanna.

Most daisyworld work in the past has assumed that there is some single ideal
environment in which life in general can flourish. By contrast, here we assume that
two species of plants exist, which grow best in different environments (defined by
local ‘temperature’), and can evolve their trait (‘albedo’) to affect their local
environment. Competition between two such species with different preferred
growing conditions is indirect: they can coexist in the same physical space, but
have to share the same local environment.
In previous CA daisyworlds, there is essentially only one species: any albedo can be obtained from any other by mutation over sufficient generations. Thus, the original daisyworld idea that environmental regulation can be achieved at the ecosystem level was lost: the single species evolved a range of albedos to achieve homeostasis. Here we reintroduce the idea of distinct competing species as well as a variety of traits competing within a species.

We shall test the applicability of ‘maximum life’ (MaxLife), ‘maximum entropy’ (MaxEnt) or ‘maximum entropy production’ (MEP) as principles to describe the behaviour. The model is designed so that these principles are conflicting, or allow more than one plausible definition. So while this single version of the daisyworld cannot prove general applicability, it is valid to conclude that proposed principles which fail to describe its behaviour are inapplicable to evolving systems in general. We will show that there is no evidence for either MaxEnt or MEP, and some constraints on the definitions for MaxLife. We can also test the hypothesis that daisyworld-type models lead to homeostasis despite inhomogeneous pattern formation and fluctuations of the population.

Issues regarding natural selection have a mixed history in the daisyworld system, but we now understand that the unusual frequency-dependent structure of the fitness in the system yields counterintuitive results. This structure induces coexistence between the daisies; interpretation in terms of cooperation and/or conflict is misleading. In the modified model presented here, we are able to explore the interplay between coexistence, competition and cooperation. Finally, we have to ask, are our evolving agents optimizing the environment as envisaged in the Gaia hypothesis of Lovelock & Margulis (1974)?

We may also ask what patterns are formed: are there clumps of typical size? Characteristic sizes of domains are a useful way of predicting pattern formation via Turing instabilities, but it is not clear whether this is a useful tool in the daisyworld system. A modification of this model is the different biomasses of the constituent parts. We make this modification to ask: if plants have different sizes, what should one count for a maximum entropy analysis? And does this lead to one being favoured over the other? Entropy is difficult to define in systems of this type, despite the maximum entropy production principle being increasingly used in climate modelling (Paltridge 1975; Lorenz et al. 2001; Kleidon et al. 2003).

2. Two-dimensional daisyworld: methods

The model is closely related to that used in previous works (von Bloh et al. 1997, 1999; Ackland et al. 2003; Ackland 2004; Wood et al. 2006). The main difference is that we consider two species, which we refer to as trees and daisies, growing independently but sharing a local environment. These species occupy sites on a two-dimensional square grid with periodic boundary conditions. The two species have different fixed preferred growing temperatures and are of different size: individual trees covering four grid squares, an area four times that of the daisies. Each plant has a single trait, the albedo (reflectivity) in the range 0–1, which evolves via natural selection.

We index temperatures and albedos on the periodic grid by longitude $x$ and latitude $y$. The vegetation pattern is then defined by the albedos on the two grids, $A^t(x, y)$ and $A^d(x, y)$. 

Phil. Trans. R. Soc. A (2010)
The temperature field in a unit area changes with $t$ as

$$C \frac{dT}{dt}(x, y, t) = D_T \nabla^2 T(x, y, t) - \sigma_B T_0^3 T(x, y, t) + S_L[1 - A(x, y, t)],$$  \hspace{1em} (2.1)

where $C = 2500$ is a dimensionless heat capacity, $T$ the variable local temperature, $D_T$ the thermal diffusion constant, $\sigma_B$ the Stefan–Boltzmann constant, $S_L$ the current solar insolation and $A$ the albedo field (see below). We also define $L$, an insolation in units normalized to that which gives $T_0 = 295.5$ K on a bare planet, and $D = D_T/C$, a diffusion constant normalized by heat capacity and grid size. As is common, and perhaps unfortunate, practice in the literature, we adopt dimensionless time and spatial length scales but maintain the use of kelvin to describe the temperature field and its thermal radiation.

Square grids with eight neighbouring are used for daisies and trees. Although these grids are distinct, we imagine that they cover the same physical space for purposes of determining the temperature.

The albedo is determined by the plant life growing on the site. In the absence of vegetation, the albedo is $A(x, y, t) = A_g = 0.5$. With vegetation, it is the average of the species growing there:

$$\begin{align*}
\text{no life: } & A(x, y) = 0.5, \\
\text{tree only: } & A(x, y) = A_t(x, y), \\
\text{daisy only: } & A(x, y) = A_d(x, y)
\end{align*}$$  \hspace{1em} (2.2)

and

$$\text{tree and daisy: } A(x, y) = \frac{A_t(x, y) + A_d(x, y)}{2}.$$

At each time step, each site of each lattice is examined.

(i) If occupied, it changes to bare ground with constant probability $\gamma$: the ‘death rate’ that is chosen to be the same for both species.

(ii) If occupied by bare ground, the site is populated with probability $\chi_d(T)$ or $\chi_t(T)$, the ‘growth rates’ for daisies and trees, respectively:

$$\chi_i(T) = 1 - \left( \frac{T_{\text{opt}}^i - T}{17.5} \right)^2.$$

The new daisy or tree has the albedo of a parent, from a randomly chosen neighbouring site, with a random fluctuation (mutation) drawn from a uniform distribution between $\pm \xi_A$. If the randomly chosen site is bare, no growth occurs.

1We use a linearized form of the black body radiation. This makes little qualitative difference, and since temperature is meant to represent a range of environmental variables, the linear expansion is arguably more reasonable, see Wood et al. (2008).
Table 1. The basic simulation parameters used unless otherwise stated in the text. These are in a large part identical to Wood et al. (2006).

<table>
<thead>
<tr>
<th>parameter</th>
<th>symbol</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>fixed parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum number of daisies</td>
<td>$N_d^2$</td>
<td>$256 \times 256$</td>
</tr>
<tr>
<td>maximum number of trees</td>
<td>$N_t^2$</td>
<td>$64 \times 64$</td>
</tr>
<tr>
<td>linear Stefan–Boltzmann constant</td>
<td>$\sigma_{B,T}$</td>
<td>$1.4629 \text{K}^{-1}$</td>
</tr>
<tr>
<td>diffusion constant</td>
<td>$D_T$</td>
<td>$500 \text{K}^{-1}$</td>
</tr>
<tr>
<td>heat capacity</td>
<td>$C$</td>
<td>$2500 \text{K}^{-1}$</td>
</tr>
<tr>
<td>bare ground albedo</td>
<td>$A_g$</td>
<td>$0.5$</td>
</tr>
<tr>
<td>death rate</td>
<td>$\gamma$</td>
<td>$0.02$</td>
</tr>
<tr>
<td>temperature time step</td>
<td>$\Delta t$</td>
<td>$0.25$</td>
</tr>
<tr>
<td>horizontal grid size</td>
<td>$\Delta x$</td>
<td>$1$</td>
</tr>
<tr>
<td>vertical grid size</td>
<td>$\Delta y$</td>
<td>$1$</td>
</tr>
<tr>
<td>width of growth function</td>
<td>$k$</td>
<td>$17.5 \text{K}$</td>
</tr>
<tr>
<td>mean ideal growth temperature</td>
<td>$\tilde{T}_{\text{opt}}$</td>
<td>$295.5 \text{K}$</td>
</tr>
<tr>
<td>geoenvironmental temperature</td>
<td>$\tilde{T}_0$</td>
<td>$295.5 \text{K}$</td>
</tr>
<tr>
<td>solar insolation</td>
<td>$S_L$</td>
<td>$9.17 \times 10^5$</td>
</tr>
<tr>
<td>luminosity</td>
<td>$L$</td>
<td>$1$</td>
</tr>
<tr>
<td>variable parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>difference in ideal growth temperature</td>
<td>$\Delta T_{\text{opt}}$</td>
<td>$0–18 \text{K}$</td>
</tr>
<tr>
<td>rate of mutation of $A_{ij}$</td>
<td>$\xi_A$</td>
<td>$0.05, 0.02, 0.01$</td>
</tr>
<tr>
<td>rate of regenerative reseeding</td>
<td>$\delta$</td>
<td>$10^{-5}, 10^{-5}, 2 \times 10^{-6}, 0$</td>
</tr>
<tr>
<td>daisy/tree albedo</td>
<td>$A_{ij}$</td>
<td>$0–1.0$</td>
</tr>
</tbody>
</table>

(iii) If occupied by bare ground, the site is populated with probability $\delta$: the spontaneous reseeding rate, with a daisy of randomly chosen albedo. In previous work, and in calculations here without regeneration, $\delta = 0$.

Longer lived plants in more favourable conditions have more offspring, so evolution by mutation and natural selection can occur. The parameter values we use for our simulations are shown in table 1.

Two useful concepts arise from the model: the ‘geoenvironment’ is that which would occur on a bare planet with albedo 0.5. The associated temperature is then determined solely by the insolation, and when this matches the preferred growth temperature of the daisies, the geoenvironment can be said to be favourable. At other insolations, there is a particular daisy albedo that adjusts the temperature to its most favourable value for growth, this being the ‘optimal albedo’ for a given geoenvironment. For convenience, we also define $\Delta T_{\text{opt}} = (T_{t_{\text{opt}}} - T_{d_{\text{opt}}})/2$ and $\tilde{T}_{\text{opt}} = (\tilde{T}_{t_{\text{opt}}} + \tilde{T}_{d_{\text{opt}}})/2$.

The extreme cases of zero or infinite diffusion are both pathological, giving no regulation effect. In one case, this is because the environment is not shared, and in the other because there is no niche heredity because the temperature is the same everywhere, and natural selection cannot act on this extended phenotype.
or constructed niche (Odling-Smeel et al. 1996). Picking a parent at random from the whole ensemble, rather than an adjacent site, also leads to system collapse. Long-range dispersal means that although favourable niches are constructed, beneficiaries are unrelated to the constructors.

The daisyworld system has an ‘absorbing state’: once all daisies die out, they cannot return. This provides a problem for stochastic, numerical simulation because die-out can happen by chance in one species or the other. We can avoid this by introducing a very small probability of reseeding the population with an ‘ancient’ seed, which may then grow into a significant population if the situation is favourable. As well as ‘ancient seed’, this may be interpreted as long-range dispersal from outside the explicitly modelled region if the modelled region is regarded as an island or continent. This reseeding approach was also used in the computer calculations by Watson and Lovelock who assumed a small constant population of black and white daisies was always present.

Early daisyworld models attracted criticism on the grounds that they considered only population dynamics, and did not permit evolution to the prevailing conditions. The two-dimensional daisyworlds do permit Darwinian mutation and evolution by natural selection. However, the environment in daisyworld is strongly influenced by the other vegetation present, presenting an ever-changing target for evolution. Furthermore, the ‘heat capacity’ allows environmental change to persist for some time. This means that daisies are able to construct environmental niches and pass them on to their offspring, giving a mechanism for kin selection.

3. Results

(a) Competition and cooperation

The most striking result of the model is the interplay between competition and cooperation. Wood et al. (2006) have shown that daisies in a stable environment will evolve to increase their reproduction rate relative to others (by damaging the other daisies’ environment), while in a harsh environment daisies evolve to increase their absolute reproduction rate (survival in a bare land).

One might guess that the evolved albedos are those that would give maximal growth for each species in the absence of the other. However, as figure 1 shows, the variation is much greater than that. While the temperature remains close to $\bar{T}_{\text{opt}}$, each species can increase its growth probability by adaptations that move the mean temperature towards its $T_{i,\text{opt}}$, but the effect of such adaptations is cancelled by similar adaptations in the other species. Thus, even for small $\Delta T_{\text{opt}}$, each species evolves significantly to maximize its effect in shifting the environment: the neutral model of Kimura (1983), which here applies to $\Delta T_{\text{opt}} = 0$, is not a limiting case.

This balance harks back to Watson & Lovelock (1983): the system as a whole has greater stability against stochastic fluctuation than its constituent parts. In more recent years, this stability has been explained in terms of the cybernetic theory of rein control (Harvey 2004; reviewed in Wood et al. 2008), which proposes that the differing colours of daisies act as opposing reins to control...
the global temperature. However, the apparent stability becomes increasingly vulnerable as the reins ‘pull harder’. If one population is reduced by a stochastic imbalance in the birth/death process, the other is left maladapted to the changed environment. Normally, it adapts to the change, making the fluctuations in the mean albedo much smaller than those for individual species. However, for large fluctuations, there is a positive feedback that gives rise to large, coupled die-backs.

These large coupled feedbacks lead to near-extinction events, but they do not usually lead to complete extinction. The recovery mechanism is that the two species become isolated spatially from one another, which uncouples their growth and allows local recovery as in the single-species CA daisyworld.

(b) Patterning by competitive exclusion

For small $\Delta T^{opt}$, when the ideal growth temperatures are similar, the daisies and trees coexist and occupy most of the available space; however, when very different environmental conditions are preferred, it may be that the optimal temperature for growth of one type is such that the other type cannot survive. Now, if fluctuations lead to one type dying out in a given region, the surviving type will rapidly evolve to regulate temperature at their $T^{opt}$, excluding reseeding.
Figure 2. Plot of three time series of the mean planetary temperature as the difference between the optimal temperatures is increased. The $x$-axis shows simulation time in units of turnover, i.e. when, on average, the whole daisy population is replaced. Dark grey lines are the optimal temperature of daisies, light grey lines are optimal for trees, and black lines are the mean planetary temperature. This simulation has no reseeding, and the mutation rate is 0.05. (a) $\Delta T_{\text{opt}} = 4.0$, (b) $\Delta T_{\text{opt}} = 8.0$, and (c) $\Delta T_{\text{opt}} = 12.0$; other parameters are as in table 1. For low $\Delta T_{\text{opt}}$, temperature regulation is good, and there are no dramatic die-backs. Note that the temperature tracks a slightly higher value than optimal, an effect induced by the spatial grid variation between trees and daisies, confirmed by reversing the optimal temperature assignment. This means that the trees are marginally more successful than the daisies perhaps as their effective environmental impact turnover is faster. The graph in (b) has a series of near-extinction events followed by collapse onto the single-species (tree) daisyworld. For $\Delta T_{\text{opt}} = 12.0$, daisies become extinct immediately leading to single-species regulation prior to collapse onto the competitive region.

of the other type. Extensive simulation results in the literature indicate that two-dimensional daisyworlds of this type can regulate the planetary temperature to that optimal for growth even when the geoenvironment would be uninhabitable. This leads to two simple regimes in our models—firstly, where the daisies and trees together regulate the temperature and, secondly, where one species is extinct and the other may regulate the planet. In the absence of spontaneous reseeding, the single-species state is an absorbing state: once reached the system remains there forever.

Ultimately one or other of the species is stochastically eliminated and a stable population level of a single type resumes regulation. The probability of an extinction event increases with $\Delta T_{\text{opt}}$ and with the time since the previous extinction (as the competition increases). We also find that for the two-species coexistence, near-extinction events are commonplace. Near-extinction events lead to oscillations in global temperature (figure 2)—these are smoother than the population variations, implying that the environmental change is caused by the population crash, rather than vice versa.

To our knowledge, the system does not have a representation as a dynamical system where this sequence of die-back and recovery could be explicitly verified. Simple analysis, using the methodology of Wood & Coe (2007), indicates two-species stability, but this is erroneous as it explicitly does not take account of the local competition between the differing species types or of the differing spatial resolutions. This null result does at least indicate that the local competitiveness between the species, combined with the inherent stochasticity, is the origin of the instabilities that occur.

Near-extinction events lead to a situation where the species exist in distinct regions, creating their own microclimate that excludes the other (figure 3).
Boom and bust in daisyworld

Figure 3. Figure showing patterns adopted by daisies and trees in the same region of space sharing the same temperature. (a) The daisyfield and (b) the trees. Vegetation shown in shades of grey representing albedo, red represents absence of that vegetation type. A number of features are visible. The daisies are confined to a small number of regions, and have evolved a pale albedo to adapt to geoenvironment hotter than their ideal. The trees have much darker albedo in general, but this is particularly so in the areas where they cohabit with the daisies. The difference in $T_{\text{opt}}$ is large, 20 K, so cohabitation is difficult, and each species flourishes where the other is absent. Albedo is correlated in space, illustrating that a mutation remains somewhat localized. (c) The associated temperature distribution (blue, cool; red, hot) shows that each species exists in an area of favourable temperature of its own making. The geoenvironment for this pattern is uniform everywhere, being exactly intermediate between the two $T_{\text{opt}}$ values; periodic boundary conditions eliminate edge effects.

(c) Fluctuations in time

Wood et al. (2006) have shown that allowing daisies to mutate their optimal temperature leads to persistent boom-and-bust oscillations. By contrast, genetic evolution of $T_{i_{\text{opt}}}$ is not allowed here, although the system can adjust $T$ through population dynamics. Like Wood et al. (2006), we find a regime in which the temperature oscillates smoothly but aperiodically in time (figure 2).

The variation of albedo in time gives some indication of the driver for this (figure 1). The albedo variation has an asymmetric wave structure: when the planet is fully vegetated, there is a fitness benefit to any mutation that drags the local temperature towards $T_{\text{opt}}$, thus the albedos of each species move to more and more extreme values, without affecting the averages. This extreme competition leaves both species maladapted to the geoenvironment and vulnerable to the collapse of the other.

Figure 1 also shows the variation in each population with time. Two strong feedbacks combine to enhance the die-back effects. First, as explained above, die-back of one species changes the environment to which the other has evolved. Second, the formation of a small desert region creates a boundary where there are fewer daisies and therefore less ability to regulate the system. As a consequence, boundaries between desert and vegetation are less favourable for growth than within the vegetation region: once formed deserts tend to expand.

It is notable that the oscillations do not have a fixed period. Rather, the environment becomes increasingly competitive and vulnerable to collapse, but the collapse itself is triggered stochastically. Throughout each cycle there are minor collapses that do not become global. The size of the collapse seems to

*Phil. Trans. R. Soc. A* (2010)
be independent of the time since the previous one. It is possible for the highly competitive state to persist at a quasi-equilibrium with mean albedos around $0.5 \pm 0.35$ without further albedo evolution. This is the steady state reached for low $\Delta T_{\text{opt}}$ where stochastically induced die-backs occur, with a lower frequency.

\[(d)\ \text{Effect of latitude}\]

The simple model assumes that the geoenvironment is constant. We also examine the situation where the geoenvironment varies as solar insolation varies with latitude. We do this in a simple ad hoc manner: the planet is assumed to have parabolic curvature, equal area at all latitudes, with an equator to pole ratio of incident radiation of 2.4. With the average insolation maintained at unity, this leads to a normalized latitude-dependent solar radiation given by

\[
S(y) = 0.517 + 2.896 \times y(1 - y), \tag{3.1}
\]

where $y = 0, 1$ are the poles, and the equator is at $y = 1/2$.

With this configuration, the polar regions receive insufficient radiation to support any daisy or tree population, so that life is confined to a band around the equator, for all $\Delta T_{\text{opt}}$ considered. Life in this band is able to regulate the temperature to support itself, despite the average planetary temperature dropping markedly owing to the polar deserts.

The results are shown in figures 4 and 5. As one might expect, each species does better in the latitude where the geoenvironment is more favourable; however, in addition to the species range, we see that the mean-albedo trait varies with

\[
G. J. Ackland and A. J. Wood

Figure 4. Plot of (a) albedo and (b) temperature as a function of latitude (black). Three different systems are shown on the same plot, with a mutation rate of $m = 0.02$ and differing $\Delta T_{\text{opt}}$: solid line, $\Delta T_{\text{opt}} = 1.0$; dashed line, $\Delta T_{\text{opt}} = 5.0$; dashed-dotted line, $\Delta T_{\text{opt}} = 9.0$ (which is common to both plots). The dark grey central line is the ideal temperature and the light grey lines indicate the preferred temperatures of the different species as $\Delta T_{\text{opt}}$ is increased (the hatching of the light grey lines matches the hatching of the black lines). For low values of the difference parameter, the warm-loving species wins out as it prefers that area of space that is more habitable and so the system is regulated to its temperature. As the gap increases, the equator is maintained at a hotter temperature, thereby increasing the area of land that on average has a hotter optimal temperature. Finally, when the gap increases still further, there exists nowhere on the planet that can be sustained at the optimal temperature of the warm-loving species and it goes extinct, to be replaced by the cold species that resumes regulating the planet at the lower optimal temperature. See text for explanation.
latitude (towards optimal) and, more strikingly, varies sharply where competition with the other species exists, owing to overlap of species range. The sharpest feature in the albedo is its very low value between the temperate and polar regions: here only dark plants can survive.

The details of the composition of the planetary life are, however, more intriguing. In the curved system, stochastic extinction events are suppressed owing to the presence of latitudes where one or other species is preferred, providing effective refugia. This leads to a dynamic and varied state at intermediate $\Delta T^{\text{opt}}$ that still maintains the planet at the mean of the optimal temperatures but at a dynamic equilibrium with significant regions of single-species occupation, and associated temperature fluctuations. Figure 4b shows longitudinally averaged cross sections of the planet to display the temperature of the system as a function of latitude. These plots show the time average of a complex series of configurations that the planet adopts as the similarities between the optimal temperatures of the two species converge. Figure 4 should be compared with figure 5: the averages shown in the former are over relatively stable configurations with continuous coverage for both low and high values of $\Delta T$ (figure 5a,e). For intermediate values, however, the average is composed of a bewildering array of differing configurations that are highly dynamic in nature (figure 5b–d).

(e) Maximum life

The probability of regrowth at a site is given by $\chi_d(T) + \chi_t(T)$. At temperatures $\Delta T^{\text{opt}} > 12.37$, this probability has a local minimum at $T = 295.5\,\text{K}$. We might expect that the behaviour of the system will change here.

Ackland (2004) proposed that daisyworlds exhibit ‘maximum life’. This claims that when more than one state exists, the one actually observed will be that which has the largest number of living sites. Life in the context of the CA is any agent that replicates itself: here the daisies and trees. The relevant states here are coexistence, extinction of one type or the other, and all dead. These are the same states as in Watson & Lovelock (1983) where the stable state at any temperature is always the one with the maximum total number of daisies.

There are two possible definitions of the amount of life here: either the number of individuals or the area covered, i.e. individual trees count as four times the daisies. Ackland (2004) proposed that the second is the appropriate measure of life defined by the coupling to the rest of the system: this hypothesis is tested in this model, alongside competing hypotheses that the maximization occurs on total number of individuals, the entropy (see below) or none of these.

In figure 6, we see the total amount of life plotted as a function of $\Delta T^{\text{opt}}$ assuming that trees count as four daisies. For small $\Delta T^{\text{opt}}$, coexistence is favoured (total amount of life is greater than 1, at high $\Delta T^{\text{opt}}$). Once the total amount of life supportable by the coexistence falls below 1, MaxLife predicts that the system will switch to a single species with albedo adjusted to perfect regulation. This is borne out in figure 6. The same graph can be plotted for the other proposed

$^2$Strictly, $e^{-\gamma}$, as the finite death rate precludes the single-species population reaching 1, even if temperature is perfectly regulated.
Figure 5. The patterns that emerge for differing values of $\Delta T_{\text{opt}}$ in the curved system without regeneration. The model has an insolation that varies according to equation (3.1) and all other parameters are as given by table 1. Each panel shows the daisy field, the tree field and the temperature field. In the former two, the grey scale indicates albedo and red indicates a patch of bare ground. The temperature is shown using a false colour map (white, blue, green, red, black in order of coldest to hottest, green is the optimal temperature, and pure red and pure blue are 17.5° above and below the optimal, respectively). (a,e) The stable configurations for low and high values of $\Delta T_{\text{opt}}$ ($\Delta T_{\text{opt}} = 1$ and $\Delta T_{\text{opt}} = 9$, respectively) with simulation snapshots. (b–d) Three differing configurations of the system for intermediate values of $\Delta T_{\text{opt}}$. It is striking that these snapshots are dominated by dynamic boundaries between the two differing types, as has been observed before in systems where the growth curve does not have a single maxima.
maximization quantities: in each case, the switch from single- to two-species stability is accompanied by a discontinuity in the entropy or entropy production. Thus, the alternative hypotheses are falsified.

It is important to note that this CA is not time-reversible: there is no true ‘equilibrium’ state, only steady states. For a finite simulation system, special care must be taken of the absorbing dead state, from which the system cannot escape.

Thus, reseeding is allowed, but at such a low level that the average populations of the steady states are unaffected. Its major effect is to allow the system to recover from the dead state. In principle, reseeding allows the system to escape from a tree-only state to coexistence or daisy only. The latter transition is very rare, but one atypical dramatic counterexample is depicted in figure 7. Here at some time a fluctuation is sufficient to tip the entire system from the tree-only to the daisy-only stable state. The change in the vegetation type induces a change in the global temperature, despite the geoenvironment remaining unchanged. The fluctuations in the populations at other times give some indication of how rare this event actually is: to induce a transition, the spike in light grey or black needs to fill the entire space.

This complete change in environment involves the stochastic extinction of a 2500-strong population. Normal population statistics would suggest such an event is 50 standard deviations from the expected fluctuation (i.e. $\sqrt{2500}$): an inconceivably small probability. Yet, the event occurs without any external trigger or forcing—it is entirely self-generated by the coupled ecosystem. Although our model is simplified, this illustrates the danger of applying standard statistical methods to a strongly coupled system.

Phil. Trans. R. Soc. A (2010)
(f) Varying insolation

For most simulations, we chose the insolation to give a geoenvironmental temperature of 295.5—exactly midway between the two species. We also investigated cases where the geoenvironment favoured one or other species. This is a fairly stiff test for maximum life hypothesis—if correct, it implies that despite the imbalance of the geoenvironment, the albedos should adjust the actual environment back to the mid-point between the two $T^{\text{opt}}$ values.

Figure 8a shows that the MaxLife prediction holds: the albedos are not equally displaced from the mean, rather the daisies adopt a more extreme value, bringing additional cooling to compensate for the increased insolation. Figure 8b shows that even as the $\Delta T^{\text{opt}}_i$ varies, the temperature is maintained at the value that gives maximum life: 295.5.

Interestingly, for high $\Delta T^{\text{opt}}_i$, where the trees can grow in the geoenvironment, not only do trees become established, but they cool the system sufficiently to allow the daisies also to establish. However, we are now outside the stable coexistence regime, so one or other species becomes extinct. In some cases, despite the geoenvironment favouring the tree-only state, switching between the daisy-only and tree-only state is observed.

Further still, if the daisies are given a faster growth rate, then the daisy-only solution is ultimately found, despite it being unsustainable in the geoenvironment. Here the trees act as a pioneer species, cooling the planet to their own benefit, which allows the daisies to become established. The more productive daisies then lower the temperature further, driving the trees to extinction.

(g) Patterns and emergence

An important purpose of agent-based modelling is to identify larger scale emergent objects that have real world relevance. Deserts and species boundaries are two such concepts.
Figure 8. (a) Figure showing mean albedo of daisies (black) and trees (dark grey) with $\Delta T_i^{\text{opt}} = 1.0$ and luminosity $1.1$ (geoenvironment $325$ K). Neither species can grow in this geoenvironment, but starting a simulation with a populated grid allows homeostasis to stabilize the system, and no die-backs are observed in this simulation. For intermediate values of $\Delta T_i^{\text{opt}}$, the system cannot recover from die-back fluctuations. (b) Temperature versus $\Delta T_i^{\text{opt}}$ (symbols, right axis) at luminosity $1.05$ (geoenvironment $310.3$ K): the system temperature is essentially unchanged even when the $T_i^{\text{opt}}$ approaches the geoenvironment and the $T_i^{\text{opt}}$ moves away from it. Also shown (lines, left axis) is the fractional population of trees (grey) and daisies (black). The small increase in temperature (small compared with the increase in either geoenvironment or $T_i^{\text{opt}}$) can be attributed to the increased amount of bare ground (albedo 0.5). At higher $\Delta T_i^{\text{opt}}$, desert formation becomes significant and the amount of bare ground increases sharply (cf. figure 6) and the averaged temperature moves towards the geoenvironmental $T = 310.3$ K.

Most of the behaviour can be understood from properties of the individual daisies; however, the system also generates emergent patterning (figure 5). These patterns evolve slowly in time, with desert regions advancing and retreating in an apparently non-systematic way. The boundary between a vegetated and desert region has its own dynamics. Owing to the temperature-stabilizing feedback, both regions are stable. The interface has a temperature gradient, which means that regions of high curvature are unfavourable. So, although the motion of the boundary is purely random, smooth interfaces are favoured over fractal ones.

Boundaries between two single-species regions also have a temperature gradient, which means that again both sides are stable. There are two regimes: for low $\Delta T_i^{\text{opt}}$ the species coexist and interfacial advance occurs through survival in the environment regulated by the other. For higher $\Delta T_i^{\text{opt}}$, the change in temperature may be so extreme that an unpopulated region exists between the two. Now the advance depends on how well the species can tolerate ‘extreme’ temperatures.

(h) Constraints on maximum entropy

With hundreds of independent sites we expect that the patterns observed should satisfy the maximum entropy principle once all other constraints are satisfied. Identifying these constraints is not straightforward.

For the biodiversity, the entropy of the pattern is conventionally defined by

$$\int_0^1 p(A) \ln p(A) \, dA,$$

*Phil. Trans. R. Soc. A* (2010)
where \( p(A) \) is the probability that the albedo of a randomly chosen site is \( A \). This is subject to the constraints of normalization

\[
\int p(A) dA = 1
\]

and other relevant constraints.

One such constraint appears to be that the amount of life is maximized (Ackland 2004). For reasonable insolations, von Bloh et al. (1997) show that this occurs when the mean albedo is that which would regulate the temperature to \( T_{\text{opt}} \). Ackland et al. (2003) find this also applies on a curved planet where the geoenvironment varies with latitude.

Even once the constraints are identified, the conventional entropy distribution is not quite correct: it ignores local correlations in albedo. As reproduction occurs locally, the probability of finding two similar albedos nearby is higher than a random distribution according to what \( p(A) \) would predict. To apply maximum entropy, these correlations must be removed, and then the MaxEnt distribution is exponential. In practice, the distribution does tend to exponential in the limit of high diffusion and long-range seeding. By contrast, at low diffusion, it is peaked around the optimal: this comes from optimizing the temperature locally as well as globally.

Applying the maximum entropy argument subject only to these constraints in the present case, we would expect to see the average albedo of each daisy type being the same as the overall average. Figure 1 shows that this is clearly not the case. In fact, far from cooperating to regulate the temperature, the two plant types appear to be competing strongly via their albedos. The lighter daisies have a cooling effect, while the darker trees are warming. Clearly, natural selection introduces a further constraint on maximum entropy through competition.

The maximum entropy analysis can only be applied once three additional criteria have been considered: the evolution to optimal mean albedo, the effect of diffusion and the evolution of each species independently to maximal fitness. Unfortunately, we are unable to obtain an analytic form for the latter two constraints, so it remains unclear whether the observed patterns do follow maximum entropy, or whether yet another constraint exists.

The related idea of maximum entropy production can be tested to the temperature diffusion. In that case, the thermodynamic entropy production from heat transferred from a hotter region to a cooler one is defined by

\[
\dot{S} = \sum_{i,j} D_T \frac{T_i - T_j}{2T_i},
\]

where the sum runs over the neighbours \( j \) of all sites \( i \). In the present model, we were unable to find any maximizing behaviour associated with this quantity.

4. Conclusions

We have shown that complex behaviours, which have counterparts in the real world, emerge from a simple model without the necessity of invoking complex explanations.
The daisyworld model shows that even a very simple ecological model with two species leads to spontaneous formation of patterns on an otherwise homogeneous background. Although geological and hydrological inhomogeneities play the largest role in patterning the planet, competing vegetation is capable of self-generating complex patterns. Among the emergent feature are deserts, local regions with environments shaped by one species to the exclusion of others and boundary regions in which populations can expand or contract.

When the geoenvironment varies, we see evolution acts to mitigate its effect and regulate the environment. Thus, regions that receive less solar heating are not especially cooler: rather they are home to darker plants.

If one imagines trying to detect environmental variation (heating), it is best seen not as its direct effect (temperature) but rather by the effect on evolution (dark plants). As heating is easily measured directly, the example of temperature is not the best one here—but one can imagine other geoenvironmental features that are best detected by the type of plant life found there.

The model shows that tight coupling of evolving life to the environment can stabilize that environment. This is characterized by periods of apparent stasis, during which evolution drives ever-more competitive behaviour in the agents. These periods of equilibria are punctuated by crashes in which rapid die-back occurs.

In a well-regulated situation, the main driving force for evolution is obtaining a competitive advantage: fitness depends more on other populations than on the static geoenvironment. After a crash, islands exhibiting cooperative, regulated behaviour can grow to recolonize the planet: fitness depends on adaptation to the geoenvironment. In a curved planet, the varying geoenvironment provides refugia in which such cooperative behaviour is preserved: these are typically harsh environments in which only one species survives. These effects have been played out more recently in microbial microcosms with limited spatial connectedness but shared environments (Williams & Lenton 2007, 2008).

Patterns in time series are even more pronounced. The model has four distinct states: all-dead, daisies-only, trees-only and both vegetation types. Provided some regeneration is allowed to ensure that all states are accessible, the ‘maximum life’ heuristic enables us to determine which of these states will be observed, i.e. both vegetation types at low $\Delta T_{\text{opt}}$ and one type only at high $\Delta T_{\text{opt}}$.

Even in the lower $\Delta T_{\text{opt}}$ state very large non-Gaussian fluctuations occur, bringing the systems close to the dead state. Such near-extinctions appear to be possible at all $\Delta T_{\text{opt}}$, but they are stochastically induced and therefore rarer in the low $\Delta T_{\text{opt}}$ regime. Unless regeneration is allowed, the very long-term behaviour in a finite system will be extinction.

Evolutionary dynamics introduces some constraints to the system, but these are not quantifiable. So, although the model exhibits a wide range of albedos and continually changing instantaneous patterns, we are unable to directly apply a maximum entropy or maximum entropy production as in Dewar (2003).

In this article, we have argued that understanding the indirect interactions between differing species, through the medium of an abiotic variable, can lead to insights into pattern formation in the real world. These effects are not often included in ecological models and in some situations they may be crucial. It is worth reflecting on the philosophical inception of daisyworld.
as a mathematical parable to illustrate the Gaia hypothesis (Lovelock 1972; Lovelock & Margulis 1974), which itself was conceived as a possible detection method for extraterrestrial life (Lovelock 1965, 1975). This concept has never been more relevant, and it is perhaps in the understanding of patterns on other planets that modelling of this type may have the greatest future role.

References


Lovelock, J. E. 1965 A physical basis for life detection experiments. Nature 207, 568–570. (doi:10.1038/207568a0)

Lovelock, J. E. 1972 Gaia as seen through the atmosphere. Atmos. Environ. 6, 579–580. (doi:10.1016/0004-6981(72)90076-5)


Phil. Trans. R. Soc. A (2010)


