



Tutorial Modelling of geosphere–biosphere interactions: the effect of percolation-type habitat fragmentation

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Abstract

A considerably extended two-dimensional version of the famous Lovelock–Watson model for geosphere–biosphere interactions (“Daisyworld”) is employed to investigate the impact of habitat fragmentation. The latter is dynamically modelled through the standard percolation process first introduced by solid state theory. It is found that the connectivity of the space accessible for life is crucial for ecological performance. In particular, the self-stabilizing capacity of the biosphere strongly depends on the fragmentation topology. An extremely rich and partially counter-intuitive eco-dynamics is observed when a simple community structure, consisting of plants and herbivores, is introduced. Quite remarkably, high herbivore vitality destroys the stability of the entire biosphere in a way reminiscent of “desertification”. © 1999 Elsevier Science B.V. All rights reserved.

1. Introduction

Life in the Earth system is not simply adapted to fixed or prescribed environmental conditions. The biosphere actually influences and controls, to a considerable extent, the setting for its own evolution. This uncontested insight is echoed by the much-debated “Gaia Hypothesis” (see, e.g., [1]), which speculates about self-stabilizing capabilities of the “planetary super-organism”. Whether the hypothesis is correct or not, the underlying geophysiological approach to the explanation of geosphere–biosphere interactions is most valuable and may provide explanations for some puzzling observations. Long-term sedimentary records indicate, for instance, that there has always existed fluid water on the Earth’s surface [2]. This is a crucial hint to our planet’s strong ability to self-regulate against external and internal driving forces. Although the solar luminosity

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was significantly lower in the past, the dead end of an ice planet has been avoided. A better understanding of this surprisingly resilient character of the coupled geosphere–biosphere system is highly relevant, especially, in view of the unintentional global experiments humankind is presently conducting via modification of the composition of the atmosphere or fragmentation of terrestrial vegetation cover.

A particularly useful ansatz for the investigation of geosphere–biosphere feedbacks is the Lovelock–Watson model (LWM) of “Daisyworld” [3,4]. Despite its toy character, this model sheds much light on possible mechanisms of environment stabilization through evolutionary adaptation of terrestrial vegetation to varying insolation. Even more insights can be gained if the simple LWM is replaced by a 2D cellular automaton (CA) version [5], which takes into account a number of additional physical (e.g., lateral heat flow) and biological (e.g., food-web dynamics, competition and mutation) processes reflecting the interacting elements within the real Earth system.

Within our 2D model the area eligible for vegetation growth is initially a full square normalized to unity, i.e., a simply connected domain. For the sake of realism, however, we also have to take into account that the area available for biospheric adaptation to “Global Change” forces is highly fragmented by civilisatory activities: urban settlements, infrastructures, agriculture, tourism, etc. The implications of habitat fragmentation on biodiversity is at present a much-debated issue.

Our toy planet constitutes an ideal theatre for investigating this question and related ones in some depth; we specifically ask how the species make-up of the biosphere and the resulting self-stabilizing properties depend on landscape heterogeneity. The latter is mimicked here in a well-defined way: we employ the percolation model from solid state physics [6] in order to mimick successive non-trivial reduction of growth space. Thus our paper is organized as follows: In Section 2 we describe in some detail the geophysiological simulation model used by introducing the pertinent elements to be considered one by one. In Section 3, we study the effects of percolation-type habitat fragmentation for different degrees of complexity of the biosphere make-up. The lessons to be learned from our results are reviewed in the short concluding section.

2. Modelling the geosphere–biosphere feedback interactions

2.1. The Lovelock–Watson model of “Daisyworld”

The original LWM is a zero-dimensional caricature of a planet which is illuminated by the sun and which is able to support merely two different types of vegetation cover.

The surface of the “naked” planet, i.e., the planet without vegetation, is characterized by an overall albedo A_0 . The equilibrium temperature T_0 depends on the insolation S and the black-body radiation according to

$$\sigma_B T_0^4 = S(1 - A_0), \quad (1)$$

where σ_B is the Stephan–Boltzmann constant. As mentioned above, the toy biosphere consists of two components only:

- Species 1 with albedo $A_1 > A_0$ (“white daisies”), covering an area a_1 with temperature $T_1 < T_0$;
- Species 2 with albedo $A_2 < A_0$ (“black daisies”), covering an area a_2 with temperature $T_2 > T_0$.

The temperature-dependent growth rate $\beta_T(T_i)$ of species i is a unimodular function with a maximum at $T_{\text{opt}} = 22.5^\circ\text{C}$:

$$\beta_T(T_i) = \begin{cases} \frac{4}{(40-5)^2}(T_i-5)(40-T_i) & 5 < T_i < 40 \\ 0 & \text{else} \end{cases} . \quad (2)$$

The dynamics of our model biosphere is governed by a system of two coupled nonlinear differential equations:

$$\dot{a}_1 = a_1(\beta_T(T_1)x - \gamma) , \quad \dot{a}_2 = a_2(\beta_T(T_2)x - \gamma) . \quad (3)$$

Here γ denotes a constant mortality rate and x , the uncovered area, is trivially given by

$$x = 1 - a_1 - a_2 . \quad (4)$$

This feedback system has been analysed by several authors [7–10] in great detail. One remarkable result is that, in contrast to the uncovered planet, the “bioplanet” is able to keep the global temperature relatively constant when the external “control parameter” S is varied within a rather wide range. This property of self-regulation is referred to as “homeostasis”. As a matter of fact, homeostasis is achieved here by a rather simple mechanism: white (black) daisies are fitter in hot (cold) climates as their comparatively high (low) albedo tends to reduce (increase) the local temperature.

2.2. *Introducing spatial dependence, competition, and mutation into Daisyworld*

In general, the stable coexistence of many different species in Daisyworld can be brought about either by temporal fluctuations or by extending the spatial dimensionality. In this paper, the second approach is used and our planet will be represented by a 2D plane with coordinates x and y [11,5].

The “climate” here coincides with the temperature field $T(x, y, t)$, which is governed by an elementary energy balance equation (see, e.g., [12]):

$$C \frac{\partial T(x, y, t)}{\partial t} = D_T \left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \right) T(x, y, t) - \sigma_B T(x, y, t)^4 + S(1 - A(x, y, t)) , \quad (5)$$

where D_T denotes the diffusion constant and $A(x, y, t)$ represents the spatiotemporal distribution of albedo. The latter reflects the prevailing vegetation pattern.

We consider an extended biosphere consisting of infinitely many different species, which may be conveniently classified by their specific albedos $A \in [0, 1]$. So the variable A serves a twofold purpose, namely (i) to label the “daisies” stored in the genetic pool, and (ii) to express their radiative properties. As a consequence, the vegetation dynamics within our model can be directly represented by the albedo dynamics.

To achieve this we have to translate the vegetation growth rules, which can be set up in the spirit of the LWM, into albedo modification rules. Their dependence on T and Eq. (5) then determine the coevolution of albedo and temperature field, respectively, in the plane. As the analytic solution of this intricate nonlinear dynamics is unfeasible, we will have to resort to numerical computation schemes based on discretization of the system. It is therefore reasonable to employ the CA approach from the outset [13,14]. One major advantage of this approach is the fact that consistent albedo modification rules can be written down immediately.

The CA is constructed as follows: the plane is replaced by a quadratic lattice (x_i, y_j) , where $x_i = i\Delta x$; $y_j = j\Delta y$; $i, j \in \mathbb{N}$, and the basic spatial units Δx , Δy can be chosen arbitrarily. Time proceeds in discrete steps $t_n = n\Delta t$, where $n \in \mathbb{N}$ and Δt is again an optional unit. Thus any systems variable F becomes a function $F(x_i, y_j, t_n)$.

The occurrence of vegetation in a particular cell (x_i, y_j) at time t_n can be indicated by a binary coverage map $c(x_i, y_j, t_n): \mathbb{N}^3 \rightarrow \{0, 1\}$. The albedo dynamics is then determined by the following rules:

(1) $c(x_i, y_j, t_n) = 1$, i.e. the cell is covered by vegetation.

$$\begin{aligned} c(x_i, y_j, t_{n+1}) &= \begin{cases} 1 & \text{with probability } 1 - \gamma \\ 0 & \text{else} \end{cases} ; \\ \Rightarrow A(x_i, y_j, t_{n+1}) &= \begin{cases} A(x_i, y_j, t_n) & \text{if } c(x_i, y_j, t_{n+1}) = 1 \\ A_0 & \text{else} \end{cases} . \end{aligned} \tag{6}$$

(2) $c(x_i, y_j, t_n) = 0$, i.e., the cell is uncovered.

Then choose at random a next-neighbour cell $(x_{\text{NN}}, y_{\text{NN}})$ of (x_i, y_j) and make the following distinction:

(a) $c(x_{\text{NN}}, y_{\text{NN}}, t_n) = 0$

$$\begin{aligned} \Rightarrow c(x_i, y_j, t_{n+1}) &= 0 , \\ A(x_i, y_j, t_{n+1}) &= A_0 . \end{aligned} \tag{7}$$

(b) $c(x_{\text{NN}}, y_{\text{NN}}, t_n) = 1$

$$\begin{aligned} c(x_i, y_j, t_{n+1}) &= \begin{cases} 1 & \text{with probability } \beta \\ 0 & \text{else} \end{cases} ; \\ \Rightarrow A(x_i, y_j, t_{n+1}) &= \begin{cases} f(A(x_{\text{NN}}, y_{\text{NN}}, t_n)) & \text{if } c(x_i, y_j, t_{n+1}) = 1 \\ A_0 & \text{else} \end{cases} . \end{aligned} \tag{8}$$

Thus γ and β denote again mortality and growth rate, respectively. The growth probability β depends only on the temperature of the uncovered cell at site (x_i, y_j) , i.e., $\beta \equiv \beta_T(T(x_i, y_j, t_n))$. The function f in (8) offers the opportunity to incorporate also more sophisticated biological effects: by choosing, for instance, $f(A) = A + R$, where R is a random number distribution with the properties $R \in [-r, r]$, $\langle R \rangle = 0$, it is possible to take mutations of the albedo into account. Here $r \geq 0$ can be interpreted as the mutation rate.

2.3. Introducing herbivores into Daisyworld

In order to reflect fundamental ecosystems dynamics based on trophic interactions as well, we extend the 2D model even further and add herbivores to our toy planet (see also, e.g., [15]). These vegetarian “lattice animals” move on the grid as random walkers. As in reality, the herbivores are capable of reproduction, but the latter capacity depends heavily on their nutritional state.

Formally, the herbivore dynamics can be conveniently described by an occupation map $c_h(x_i, y_j, t_n) : \mathbb{N}^3 \rightarrow \{0, 1\}$, defined on a second lattice layer parallel to the daisy lattice, and a small set of non-deterministic behavioural rules. If the site (x_i, y_j) is occupied by an animal at time t_n , i.e., $c_h(x_i, y_j, t_n) = 1$, then those rules allow for four different events:

Death: The herbivore deceases with a probability γ_h , thus $c_h(x_i, y_j, t_{n+1}) = 0$.

Ingestion: If the herbivore survives and if the cell is covered by a daisy, i.e. $c(x_i, y_j, t_n) = 1$, then the animal consumes the plant. The number of ingestion acts that have been performed by the herbivore considered so far is stored as a state variable N . Thus,

$$N(x_i, y_j, t_{n+1}) = N(x_i, y_j, t_n) + 1 \quad (9)$$

in this case. Evidently, we also have $c(x_i, y_j, t_{n+1}) = 0$ and $A(x_i, y_j, t_{n+1}) = A_0$.

Reproduction: The herbivore in question may give birth to a “lattice child” at a randomly chosen next-neighbour cell with probability

$$\beta = \beta_T(T(x_i, y_j, t_n))\beta_N(N(x_i, y_j, t_n)) . \quad (10)$$

The temperature-dependent factor β_T is chosen similar to the one which governs the growth of daisies, while β_N is assumed to behave like a discrete Heaviside function, i.e.,

$$\beta_N(N) = \begin{cases} 1 & \text{for } N > N_0 \\ 0 & \text{else} \end{cases} . \quad (11)$$

The latter assumption reflects the conception that only “grown-up” lattice animals will be capable of replication. Clearly, the ingestive status of the new-born herbivore is zero.

Move: The herbivore may also walk to a randomly chosen next-neighbour cell if this cell is not already occupied by another herbivore.

As a matter of fact, consistent combinations of all those events may occur according to the probabilistic set-up. Note that the presence of herbivores is not assumed to change the local albedo. So it is only the act of daisy consumption that affects the radiative properties of our virtual environment.

Note that the interaction between plants and animals is realized by mainly two processes, namely (i) temperature-dependent reproduction of herbivores and (ii) ingestion of daisies. Note also that our herbivores are rather dumb as their dietary strategy consists in random walking only.

3. The impacts of fragmentation on ecologic performance

A critical factor affecting real ecosystems is the fragmentation of species habitats. Very few theoretical studies (not to speak about empirical ones) have been performed, however, to reveal the impacts of fragmentation in a rigorous quantitative way. Our extended Daisyworld model allows for such investigations with special emphasis on the modification of habitat geometry. Within the framework of our tutorial model we can expect, in particular, that fragmentation will create “ecological niches” for plants of inferior fitness and obstruct the forage activities of the animals.

Before we describe our specific way of fragmenting the landscape, let us mention that the 2D model without herbivores and homogeneous habitat exhibits an even better self-stabilizing ability than the simple LWM. However if the environmental stress – increasing insolation, for instance – exceeds a certain critical threshold, “life” breaks down on the artificial planet via first-order phase transitions. The latter fact implies the presence of hysteresis effects including bistability. A detailed account of those findings is given in von Bloh [5].

Here we focus on the modifications of geosphere–biosphere dynamics as triggered by restricting the habitable zone within our model world. In order to be specific, we generate landscape heterogeneity by employing the well-known percolation model from solid state physics [6].

The percolation model on a square lattice is formulated in the following way: For a given probability $p \in [0, 1]$, each site will be randomly occupied with probability p . As a consequence, it will remain empty with probability $1 - p$. A connected group of occupied sites is called a “cluster”. The size of the clusters clearly grows with increasing p . “Percolation” is said to set in when the largest cluster extends from one end of the system to the other (“spanning cluster”). In the limit of infinitely large lattices there exists a sharp threshold value $p_c = 0.59273\dots$ for percolation. The spanning cluster associated with this phase transition is a multiple-connected fractal object with a power-law hole-size distribution. Fig. 1 gives an example of such a critical configuration which allows to traverse the entire lattice via next-neighbour steps.

Therefore, we have to distinguish between three qualitatively different regimes determined by the occupation probability:



Fig. 1. Patchwork of occupied sites in the standard percolation model at criticality ($p = p_c = 0.5973\dots$). The fractal spanning cluster is indicated in black.

(1) $0 \leq p \leq 1 - p_c$: the collection of occupied sites does not form any spanning cluster, but the collection of unoccupied sites represents a connected “void space”.

(2) $1 - p_c < p \leq p_c$: neither the occupied nor the void sites form a connected structure.

(3) $p_c < p \leq 1$: the collection of occupied sites does form a connected structure, but the void space is now disconnected.

We introduce civilisatory land-use into our extended Daisyworld by gradually diminishing the potential growth area in the following way: choose a (small) generating probability p_0 . In the first time step, consider all cells within the finite lattice one by one and exclude them from the growth space with probability p_0 . At time t_n , the probability that any specific site has been “civilized” is therefore given by

$$p(t_n) = 1 - (1 - p_0)^n. \quad (12)$$

On the other hand, the statistical fraction of habitable area after n time steps can be calculated by

$$1 - p(t_n) = (1 - p_0)^n. \quad (13)$$

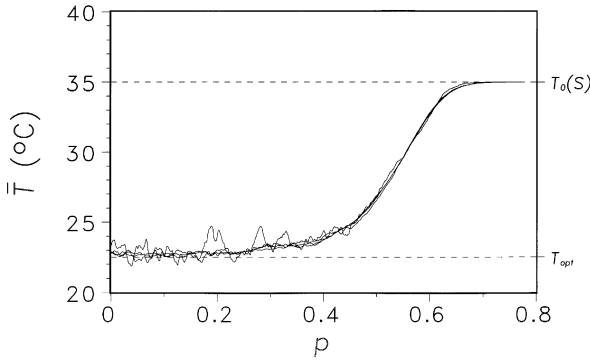


Fig. 2. Convergence of numerical results for p - \bar{T} relationship for increasing lattice size ranging from 200×200 (wiggliest line) to 1600×1600 (smoothest line). S has been fixed to a value that generates a geophysical planetary temperature $T_0(S) = 35^\circ\text{C}$.

Note that our fragmentation scheme is independent of the actual status of the cell under consideration and all physical properties, such as diffusive heat transport remain unaffected.

3.1. Self-stabilization of global temperature without herbivores

First, we test the decay of self-stabilizing power with increasing patchiness in the 2D Daisyworld without animals.

Fig. 2 summarizes our findings regarding the relation between global mean temperature \bar{T} and the percolation parameter $p \equiv p(t_n)$. It can be observed that even the fragmented biosphere is able to stabilize the planetary temperature near the optimal value, unless p exceeds a value of approximately 0.4.

The numerical results are robust. As a matter of fact, Fig. 2 shows for a series of extensive calculations with increasing lattice dimensions that finite-size effects can be neglected. It actually turns out that the above-mentioned threshold value for patchiness has universal character. The adaptive power of Daisyworld clearly breaks down when p approaches the value $\hat{p} := 1 - p_c \approx 0.407$.

The explanation for this phenomenon is simple but illuminating: for $p > \hat{p}$ the growth space has lost its connectivity and is broken up into many isolated domains. Our toy model hence provides us with clear-cut evidence that the ecological performance of a system directly depends on its connectivity! For detailed results concerning, for example, the corresponding change in the species spectrum see again von Bloh [5].

3.2. The role of herbivores in a fragmented landscape

One of the main features of real-world ecological communities is their trophic complexity as defined by the food-web structure [16]. By introducing herbivores into our 2D Daisyworld, we are able to study the most simple non-trivial community case, namely a

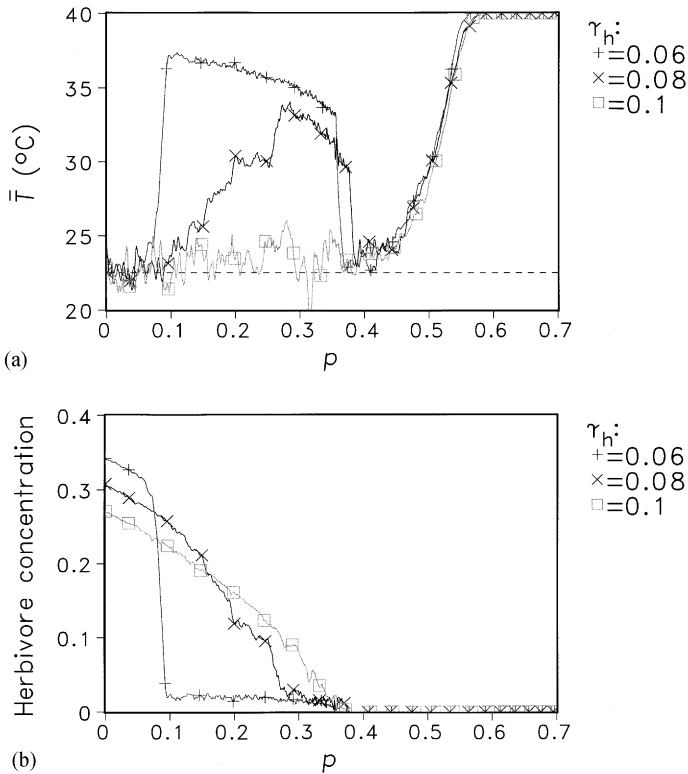


Fig. 3. (a) Dependence of global mean temperature \bar{T} on fragmentation parameter p for distinct herbivore mortality rates γ_h . (b) Dependence of herbivore concentration on p for the same γ_h values as in (a).

classical prey–predator situation. The well-known Lotka–Volterra theory does not apply here, however, as the community strongly interacts with a heterogeneous environment.

The co-dynamics of plants and animals within our model world has been described in Section 2.3 above. If we now “switch on” habitat fragmentation, both daisies and herbivores are affected as more and more cells become inaccessible to growth and grazing, respectively. For the sake of clarity, we keep the insolation S again constant and study exclusively the impacts of denaturalization. Extensive numerical calculations reveal that the crucial parameter is the herbivores’ mortality rate γ_h . This is demonstrated in Fig. 3a and 3b where the relationships between global mean temperature \bar{T} and fragmentation p and between herbivore concentration and p are depicted for different γ_h values.

Four distinct “vitality regimes” can be identified:

(1) $0.15 \lesssim \gamma_h$: The herbivores rapidly die back and the remaining biosphere controls the global temperature until the percolation threshold for the growth space is reached.

(2) $0.07 \lesssim \gamma_h \lesssim 0.15$: The homeostatic power of the co-existing daisy–herbivore community is similar to the one exhibited by the daisy community alone. The concentration of herbivores increases with decreasing mortality γ_h .

(3) $0.05 \lesssim \gamma_h \lesssim 0.07$: In this parameter domain the overall system's behaviour attains a new quality. When the fragmentation degree p grows beyond the approximate value 0.2, an intermediate homeostatic situation emerges, where $T_{\text{opt}} < \bar{T} < T_0$ and plants and animals co-exist at rather low population densities. Even more interesting is the finding that in the moderate fragmentation regime the herbivore concentration is higher for higher values of the mortality parameter! This is in marked contrast to what one would expect and what indeed happens in the homogeneous landscape.

Our interpretation is as follows: In a complex environment, the more vital herbivores turn to “overgraze” their substrate. This behaviour produces additional negative effects by raising the ambient temperature to uncomfortable values.

When the fragmentation approaches the first percolation threshold $1 - p_c$, the herbivores become extinct while the daisies still survive in reduced numbers. Then the system's behaviour is similar to the one of Daisyworld without predators.

(4) $\gamma_h \lesssim 0.05$: Plants and animals die back rapidly with increasing p , and our model world behaves like a desert planet for small values of the fragmentation parameter. Thus the unchecked vitality of the herbivores destroys the ecological balance completely.

Our general finding is that our herbivores can exist in a heterogeneous landscape with albedo feedback only in a rather small regime of the mortality parameter γ_h . While daisies are able to survive in a fragmented growth space even above the first percolation threshold, the “lattice animals” definitely cease to exist there. This reflects an observation encountered again and again in our studies: predators are more vulnerable to habitat fragmentation than their preys as the former depend heavily on mobility.

4. Summary and outlook

We have shown that the fragmentation of species habitat has a significant influence on the homeostatic performance of the biosphere. A unique threshold can be identified, where the regulation of global temperature breaks down and “life” loses control of its own subsistence conditions.

The introduction of herbivores to fragmented Daisyworld generates an extremely rich eco-dynamics. For specific ranges of parameter combinations intermediate homeostatic regimes appear. Remarkably counter-intuitive effects prevail like the reduction of herbivore concentration with increasing vitality. Thus our toy model demonstrates, in a nutshell, the subtleness and vulnerability of community–environment relationships.

Future work on this subject will focus on more realistic rules for animal motion and replication. In particular, the *self-restriction* of herbivores by habitat fragmentation through overgrazing can be simulated (“desertification”). Another interesting option is the simulation of civilizatory habitat fragmentation by more realistic processes for urbanization and infrastructure expansion.

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