

Gaia as a complex adaptive system

Timothy M. Lenton* and Marcel van Oijen

Centre for Ecology and Hydrology, Edinburgh Research Station, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

We define the Gaia system of life and its environment on Earth, review the status of the Gaia theory, introduce potentially relevant concepts from complexity theory, then try to apply them to Gaia. We consider whether Gaia is a complex adaptive system (CAS) in terms of its behaviour and suggest that the system is self-organizing but does not reside in a critical state. Gaia has supported abundant life for most of the last 3.8 Gyr. Large perturbations have occasionally suppressed life but the system has always recovered without losing the capacity for large-scale free energy capture and recycling of essential elements. To illustrate how complexity theory can help us understand the emergence of planetary-scale order, we present a simple cellular automata (CA) model of the imaginary planet Daisyworld. This exhibits emergent self-regulation as a consequence of feedback coupling between life and its environment. Local spatial interaction, which was absent from the original model, can destabilize the system by generating bifurcation regimes. Variation and natural selection tend to remove this instability. With mutation in the model system, it exhibits self-organizing adaptive behaviour in its response to forcing. We close by suggesting how artificial life ('Alife') techniques may enable more comprehensive feasibility tests of Gaia.

Keywords: Gaia theory; complexity theory; Earth system; Daisyworld; feedbacks; adaptive change

1. INTRODUCTION

This article focuses on the complex, coupled system of life and its environment on Earth, named 'Gaia' (Lovelock 1972) and defined more rigorously below. There already exists a Gaia theory that attempts to explain the development and functioning of the specific system (Lovelock 1988; Lenton 1998). Aspects of the Gaia theory may also be applicable to other planets with abundant life (Lenton 2002). Our perspective is: what can a general theory of complex systems 'complexity theory' contribute to Gaia theory? We highlight gaps in our current understanding of Gaia, address whether Gaia is a CAS, and consider how complexity theory can help improve our understanding of Gaia.

The Gaia theory replaced the original Gaia hypothesis of atmospheric homeostasis by and for the biota (Lovelock and Margulis 1974) in the mid-1980s. The Gaia theory takes a larger whole system perspective, viewing self-regulation as a key emergent property of the system, with models to demonstrate how such behaviour can arise automatically (Watson & Lovelock 1983; Lovelock 1988). A challenge for Gaia theory is to find principles that explain how regulation can emerge at the global scale from natural selection of environment-altering traits at the individual level (Hamilton & Lenton 1998; Lenton 1998). To what degree the ontogeny (pathway of development) of Gaia is unique or deterministic is a major question (Schwartzman 1999). There is a need to improve our ability to predict what may happen after specific pertur-

bations of the system, including human activities. Furthermore, hypotheses for the effect of life on Earth need to be more rigorously framed and their testability improved (Kleidon 2002; Lenton 2002). Currently, most progress is being made in understanding specific feedback mechanisms using models of fixed structure. To advance Gaia theory, we need to consider the behaviour of many coupled interactions and feedbacks, and the evolution of living components and resulting change at the system level. We also need to test the feasibility of general hypotheses for the emergence of planetary-scale order. These requirements in turn demand new theory and new modelling approaches. Complexity theory may offer both.

It has previously been suggested that both the biosphere (the region in which life exists) and Gaia (the coupled system of life and its environment on Earth) are CASs (Lewin 1993; Levin 1998), in which case Gaia may be the largest in a hierarchy of CASs including cells, organisms and ecosystems (C. G. Langton and S. A. Kauffman, quoted in Lewin (1993)). This view has received relatively little attention from Gaia theorists: we know of only one attempt to test whether Gaia is a complex system (L. F. Klinger, personal communication). If it is, what does this teach us about the system?

We consider which results from complexity theory are relevant to Gaia and how the methods of complexity theory can be applied to advance our understanding of Gaia. First we define the system of interest (§ 2) and review the status of Gaia theory (§ 3), before summarizing relevant concepts from complexity theory (§ 4). We address whether Gaia is a CAS (§ 5), and consider how planetary-scale self-organization can emerge (§ 6). The use of Daisyworld models to explore such emergence is summarized (§ 7) and a simple CA version of Daisyworld is presented, which gives new insights (§ 8). The use of

* Author for correspondence (tlent@ceh.ac.uk).

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'Alife' techniques for assessing the probability of planetary self-organization is discussed (§ 9), and we close by summarizing how complexity theory has already altered our understanding of Gaia (§ 10).

2. GAIA

We define Gaia as the thermodynamically open system at the Earth's surface comprising life (the biota), atmosphere, hydrosphere (ocean, ice, freshwater), dead organic matter, soils, sediments and that part of the lithosphere (crust) that interacts with surface processes (including sedimentary rocks and rocks subject to weathering). The upper boundary of the system is at the top of the atmosphere, with outer space. The inner boundary is harder to define and can be taken to depend on the time-scale of processes under consideration. For time-scales longer than the recycling of the crust (*ca.* 10^8 years) the line may be drawn between the crust and the mantle. For processes that can approach steady state rapidly (in less than 10^3 years) the outer surface of the crust may be considered the boundary of the system. A rigid definition that excludes any component of the crust from Gaia has been suggested (Volk 1998), but we think this is too exclusive. Inclusion of the entire Earth's interior has also been implied (Lovelock 1991), but we think that this is too inclusive. Processes such as volcanism and plate tectonics are ultimately driven by a heat energy source in the Earth's interior, which (like the Sun) is not significantly influenced by surface processes and hence is best considered to be 'outside' the system.

Abundant energy is exchanged across the upper boundary of Gaia (*ca.* 1.75×10^{17} W), but relatively little matter. Only hydrogen atoms can readily escape Earth's gravity (currently *ca.* 2.7×10^8 H atoms $\text{cm}^{-2} \text{s}^{-1}$). Incoming meteoroids supply a small flux of matter to the Earth's surface (more than 10^{11} g yr^{-1}) and atmosphere (as and when they are vaporized) (Isaacs *et al.* 1996). Occasional asteroid (large meteorite) impacts add matter and can also provide sufficient energy to eject meteoroids into space. Matter is exchanged across the lower boundary of Gaia but relatively little energy. Available geothermal energy (*ca.* 3×10^{13} W) is tiny in comparison to solar energy. Exchange fluxes of matter across the lower boundary are significant, but for many elements are orders of magnitude smaller than the internal cycling fluxes (e.g. *ca.* 5×10^{13} mol C yr^{-1} input and output, *ca.* 1.5×10^{17} mol C yr^{-1} cycled within the system).

The energy input to Gaia has been gradually increasing (*ca.* 1% every 10^8 years) as the Sun becomes more luminous with time. Variations in the Earth's orbital parameters also alter the total energy input and its distribution across the Earth's surface on time-scales of 10^3 – 10^5 years. Decay of angular momentum of the Earth–moon system causes the Earth to spin more slowly with time. Occasional asteroid impacts provide massive perturbations of the Earth's surface, releasing large amounts of energy, for example, *ca.* 10^{24} J in the Chicxulub impact at the Cretaceous–Tertiary boundary 65 Myr ago. Thermal decay of the Earth's interior heat source causes a gradual decline in volcanic and tectonic activity including sea-floor spreading rates (volcanic and metamorphic matter input was probably three times greater *ca.* 3 Gyr ago). Occasional catas-

trophic outflow of lava (flood basalt volcanism) occurs. Such events may be triggered by asteroid impact (Rampino 1987), thus providing a possible link between perturbation from above and below Gaia.

We distinguish Gaia from the 'Earth system' (an increasingly popular term), in that the Earth system includes states before the origin of life, whereas Gaia refers to the system with abundant life, and because the Earth system is sometimes taken to include the entire interior of the Earth. We also distinguish Gaia from the 'biosphere' (the region inhabited by living organisms). These are sometimes treated synonymously, but the boundaries of Gaia are almost certainly wider, because the influence of living organisms extends beyond the region they inhabit. The upper boundary of the biosphere is more than 50 km above the Earth's surface in the mesosphere, where viable microscopic fungi and bacteria have been collected by Russian rockets (Imshenetsky *et al.* 1978), whereas the exosphere extends above 500 km. The lower boundary of the biosphere is unknown, but organisms have been found to be thriving at depths of a few kilometres in the Earth's crust. It has been suggested that a 'deep hot biosphere' could survive independently of surface life, but if it could persist at all, this would be a much simpler system running off a relatively tiny amount of free energy.

Gaia has many remarkable physical and chemical properties, especially when contrasted with our neighbouring planets, Mars and Venus. The Earth's atmosphere is in extreme thermodynamic disequilibrium with reactive gases at concentrations many orders of magnitude from those predicted at geochemical and photochemical steady state (Lovelock 1975). Oxygen is extraordinarily abundant at 0.21 atm instead of less than 10^{-12} atm (Kasting 1991). Other reactive gases are at anomalously high concentrations, given abundant oxygen. For example, methane concentration is more than 10^{30} times equilibrium (Lovelock 1975; Sagan *et al.* 1993). The majority of nitrogen should be as NO_3^- dissolved in the ocean, rather than N_2 in the atmosphere (Lewis & Randall 1923; Sillén 1967). By contrast, carbon dioxide makes up a remarkably small fraction of the atmosphere when compared with Mars and Venus. The composition of the Earth's atmosphere shows dynamic stability over periods much longer than the residence time of specific gases (Lovelock & Margulis 1974). For example, the O_2 reservoir with a geologic residence time of *ca.* 3.2 Myr has varied by less than a factor of two over the past 350 Myr (Lenton 2001). Other master variables of Gaia also show evidence of regulation. The Earth's average surface temperature has tended to decline or remain relatively constant over the past *ca.* 4 Gyr despite a *ca.* 30% increase in solar luminosity. Liquid water has been retained at the Earth's surface (in contrast to Mars and Venus). Hydrogen escape to space and consequent water loss has been minimized by the oxidizing state of the atmosphere for the past *ca.* 2.0 Gyr and the existence of a cold trap at the tropopause. Ocean salinity has never reached toxic concentration. pH has remained close to neutral. The chemical composition of Gaia as a whole is such that abundant free energy is available from chemical reaction, most notably from the reaction of O_2 with organic compounds.

Perhaps the most remarkable property of Gaia is the ongoing presence and profusion of life. The Earth's sur-

face has remained habitable for more than 3.85 Gyr (Mojzsis *et al.* 1996). The relatively stable organic carbon content and isotopic composition of the crust indicate that life has been abundant for most of the past 3.8 Gyr (Schidlowski 1988). Life has been invoked to explain many of the Earth's remarkable physical and chemical properties. The abundance of oxygen in the present atmosphere is almost entirely a biological product. Atmospheric oxygen has increased in a stepwise fashion from $pO_2 < 0.002$ atm more than 2.2 Gyr ago, and has been sufficient to support eukaryotes ($pO_2 > 0.01$ atm) for at least the last 2 Gyr (Han & Runnegar 1992). The stability of O_2 over the past 350 Myr has enabled the continuous persistence of large metazoa (requiring $O_2 > ca. 0.15$ atm) and slowly regenerating trees (requiring $O_2 < ca. 0.3$ atm) (Lenton & Watson 2000*b*). The scarcity of carbon dioxide in the atmosphere and consequent cooling of the planet is due to biologically amplified silicate rock weathering, which drives the dominant sink in the long-term carbon cycle (Lovelock & Watson 1982; Schwartzman 1999). Within Gaia there is greatly enhanced cycling of matter, especially of the elements essential to life. For example, phosphorus is cycled an average of 46 times through a terrestrial ecosystem before being lost to the ocean, where it is cycled an average of 280 times before being finally buried in new rocks (Volk 1998). Return of water to the atmosphere is increased approximately three times by the presence of vascular plants on the land surface (Betts 1999; Kleidon 2002). These recycling effects greatly increase global gross primary productivity (Volk 1998; Kleidon 2002).

3. GAIA THEORY

The Gaia theory seeks to explain the remarkable properties of the system just described, especially its far-from-equilibrium ordered state, dynamic stability, habitability, flourishing of life and pattern of change over time (Lovelock 1988; Lenton 1998). From the outset, Gaia has been viewed as a cybernetic (feedback control) system (Lovelock & Margulis 1974). The essential elements of the theory are: (i) life affects its environment: all organisms alter their environment by taking in free energy, and excreting high-entropy waste products in order to maintain a low internal entropy (Schrödinger 1944); (ii) growth (including reproduction): organisms grow and multiply, potentially exponentially; (iii) environment constrains life: for each environmental variable there is a level or range at which growth of a particular organism is maximized; and (iv) natural selection: once a planet contains different types of life (phenotypes) with faithfully replicated, heritable variation (genotypes) growing in an environment of finite resources, natural selection determines that the types of life that leave the most descendants come to dominate their environment.

The overall behaviour of Gaia is governed by a combination of positive and negative feedback. Positive feedback tends to add to change, while negative feedback tends to counteract change. Growth is intrinsically a positive feedback process (the more life there is, the more life it can beget). The growth of life drives life's effects on its environment to become global in scale. The extreme thermodynamic disequilibrium of the Earth's atmosphere

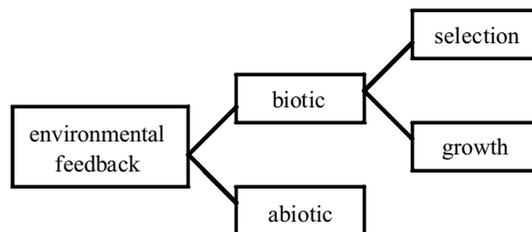


Figure 1. A subdivision of types of environmental feedback.

indicates that this has occurred. The fact that life alters its environment and is also constrained by it means that environmental feedback is inevitable. Environmental feedback arises at the local level (e.g. due to the evolution of environment-altering traits). With growth, environmental feedback has the potential to become global in scale. The types of environmental feedback can be classified in a hierarchy (Lenton 1998).

The first distinction is between abiotic and biotic feedback to the environment (figure 1). The response of life to a particular environmental variable includes habitability bounds for the organisms in question, whereas abiotic responses have no automatic correlation with what is habitable for life. Abiotic responses to a particular environmental variable are typically simple increasing or decreasing functions (figure 2*a,b*). If they also affect the variable in question, then either negative feedback or positive feedback will result. Negative abiotic feedback (figure 2*a*) can stabilize the environment in either a habitable or an uninhabitable state. Positive abiotic feedback (figure 2*b*) can drive the environment into an uninhabitable state, although in many cases it is not sufficiently strong to do so. By contrast, organisms tend to have a peaked growth response to many environmental variables (figure 2*c,d*). If they also affect a particular environmental variable, then the resulting system will have both negative and positive feedback regimes either side of the optimum for growth, and for a range of forcing it will by definition tend to stabilize in a habitable state. For a weak biotic effect on the environment (figure 2*c*) the stable state can be in either the negative or the positive feedback regime. For a strong biotic effect on the environment (figure 2*d*), the system will tend to transit the positive feedback regime and stabilize in the negative feedback regime. For some forcing (e.g. figure 2*d*) multiple solutions can occur such that life maintains the environment in a habitable state when otherwise it would be uninhabitable. If the system is forced beyond the unstable solution in the positive feedback regime, then life will collapse catastrophically.

Biotic environmental feedback can be subdivided (figure 1) into feedback on growth and feedback on selection (Lenton 1998). Non-selective feedback on growth occurs when the effect of a trait on the environment alters the growth rate of the organisms carrying it, but the environmental alteration is a side-effect of the trait that does not hamper its selective advantage. Feedback on selection occurs when the effect of a trait on the environment alters the forces of selection determining its value.

An important example of negative feedback on growth (figure 2*d*) is that resulting from plant-induced amplification of rock weathering. This inadvertently tends to

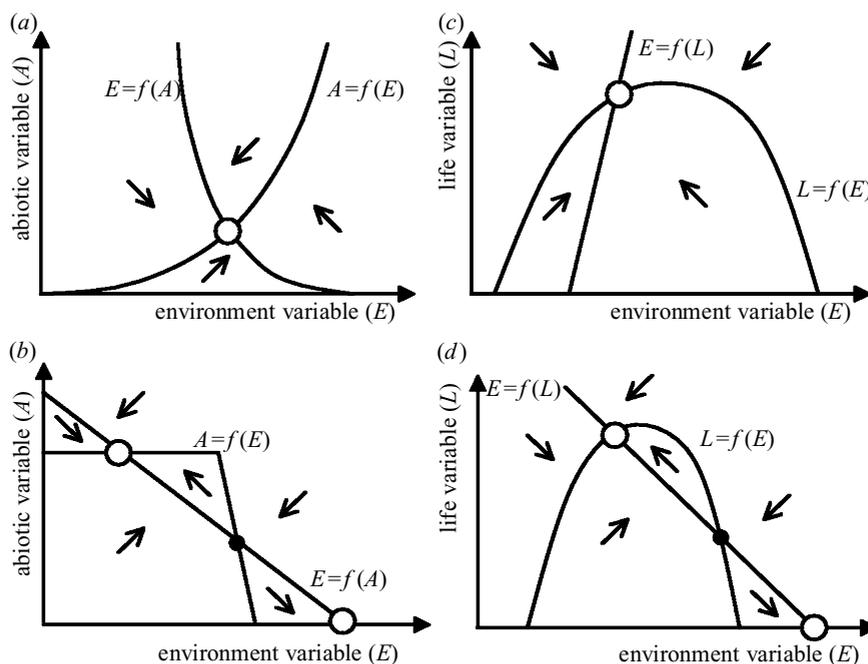


Figure 2. General representations of types of environmental feedback for fixed forcing: (a) abiotic negative feedback; (b) abiotic positive feedback; (c) weak biotic feedback; and (d) strong biotic feedback. Large open circles indicate stable states. Small filled circles indicate unstable states. The arrows indicate the general direction of change for starting states within each regime. The schematic diagrams are loosely based on the following global cases, described in more detail in the text: (a) abiotic silicate weathering rate and temperature; (b) ice cover and temperature; (c) boreal forest cover and temperature; (d) growth rate of rock weathering organisms and temperature.

decrease atmospheric CO_2 and cool the planet. Declining CO_2 and cooling below optimum growth temperature tend to suppress plant growth, closing the feedback loop. Rock weathering traits are probably selected for as a means of acquiring rock-bound nutrients (especially phosphorus), and changes in CO_2 and temperature do not affect this requirement or the resulting selection. (It is more likely that local build-up of phosphorus in soil would do that.) The feedback from changing CO_2 and temperature is very slow, and requires a global spread of the trait over many generations before it affects growth. However, it is key to the long-term regulation of atmospheric CO_2 and temperature, and can thus be beneficial to plant growth in the long term. In particular, it counteracts increasing solar luminosity that could otherwise drive the Earth's surface temperature above optimal levels. Some abiotic negative feedback (figure 2a) would exist in a world without life, but with tectonics and a hydrological cycle (Walker *et al.* 1981). However, rock-weathering organisms greatly strengthen the feedback (Lovelock & Watson 1982; Schwartzman & Volk 1989). They may thus extend their own future persistence on Earth (Lenton & Von Bloh 2001).

An example of positive feedback on growth (figure 2c) is that resulting from the dark, snow-shedding foliage of trees in the boreal forest. By absorbing solar radiation, the trees are warmed (especially relative to snow cover) and their growth is enhanced. This warms their surroundings, thus further enhancing growth (Bonan *et al.* 1992). The positive feedback is constrained in that temperatures in the boreal regions remain below the optimum for growth for much of the year, but they are increased such that

forest is able to persist over large regions that would otherwise be too cold for growth (Betts 1999).

An example of negative feedback on selection is that resulting from nitrogen fixation in the world's oceans, many terrestrial ecosystems, and some freshwater lakes. Nitrogen fixation is an energetically demanding process, which will only be selected for when there is a lack of available nitrogen relative to other potentially growth-limiting nutrients. By fixing nitrogen, the responsible organisms ultimately increase the amount of nitrogen available in their environment for non-nitrogen-fixers. This removes the selective advantage of being a nitrogen fixer and hence the proliferation of nitrogen fixation is self-limited. This mechanism regulates the nitrate content of the world's oceans relative to the phosphate content in a proportion close to organisms' requirements (Redfield 1958; Lenton & Watson 2000a).

An example of positive feedback on selection is that resulting from the ability of sphagnum moss to acidify soil. This environmental change gives the moss a selective advantage relative to other potential invading plants, and encourages succession to a peat bog (Klinger 1991; Hamilton 1996). There are probably other self-limiting (negative) feedbacks on bog growth, given that we do not live in a world dominated by peat bogs (although the authors live in a country dominated by them). Interestingly, examples of positive feedback on selection tend to be more localized than examples of negative feedback on selection.

One of the possible fates for Gaia is for abiotic positive feedback (figure 2b) to take the planet into an uninhabitable or barely habitable state. In the ice-albedo positive

feedback effect, snow and ice form surfaces that are highly reflective (high albedo) to solar radiation, thus cooling their surroundings and encouraging the spread of snow/ice cover. In simple models, a modest reduction in solar input is amplified by this feedback to cause complete ice cover of the Earth (Budyko 1968; Sellers 1969), the so-called 'snowball Earth' (Hoffman *et al.* 1998). Recent simulations suggest that a 'slushball Earth' state, with open water in equatorial oceans may be more realistic and less fatal to life (Hyde *et al.* 2000). If a snowball Earth attractor exists, it should be unstable because CO₂ input from volcanoes can gradually accumulate in the atmosphere until radiative forcing is sufficient to melt continental ice cover.

A key challenge to Gaia theory from evolutionary biologists is to explain how order, especially self-regulation, can arise at the global scale without invoking teleology or selection at the level of the planet (Doolittle 1981; Dawkins 1983). Such criticisms inspired the formulation of the Daisyworld model (Lovelock 1983; Watson & Lovelock 1983), which demonstrates that self-regulation can emerge automatically from competing populations, altering their local environments in different ways (see § 7 and § 8). The idea that evolution within Gaia could have produced organisms that contribute to regulating the planet is still variously criticised as untenable altruism, vulnerable to cheats or demanding large-scale group selection (Hamilton 1995). It is sometimes argued that random variation and natural selection are necessary and sufficient to explain the self-regulation of organisms and candidate super-organisms (e.g. temperature regulated social insect colonies; Ehrlich 1991), in which case, self-regulation of Gaia could not occur. However, regulation can emerge automatically (Saunders 1994; Watson 1999), and hence the mechanisms by which regulation emerges in physiology may have parallels at the planetary scale (Koeslag *et al.* 1997; Saunders *et al.* 1998), even though planetary regulation cannot be refined by selection. We think that with an appreciation of feedback principles, the theories of Gaia and natural selection can be reconciled (Lenton 1998).

Equally, there is a need to extend the original cybernetic view of Gaia to encompass evolution. The continuous generation and selection of different environment-altering traits ensures that the feedback structure of Gaia remains dynamic. Evolution within the biota drives changes in the state, parameters and structure of the system (e.g. the rise of atmospheric oxygen). This in turn facilitates the evolution of new forms of life. It can also alter the set points of regulation, when they are not fixed by thermodynamic, chemical or geophysical constraints (Lenton & Lovelock 2000). Complexity theory may provide a framework for developing Gaia theory by synthesizing principles from cybernetics and evolutionary biology.

4. COMPLEXITY THEORY

Complexity theory is a general theory of complex dynamic systems. The Latin *complexus* comes from the Greek *pleko* meaning to plait or twine. Thus a complex system is literally one consisting of interwoven parts. Complex can also mean difficult to understand or analyse. A broad definition of a complex system is one whose properties are not fully explained by an understanding of

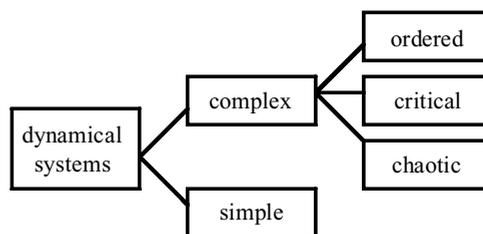


Figure 3. A subdivision of dynamical systems in terms of behaviour.

its component parts (Gallagher & Appenzeller 1999). By contrast, simple systems are ones whose properties are fully explained by the properties of their component parts (e.g. a pendulum). Emergence describes the collective behaviour of complex systems. It can be local or global. Local emergent properties are well studied in physics, where they are often termed 'intensive properties' (e.g. pressure and temperature of an ideal gas). Global emergent properties are the more original focus of complexity theory.

Complexity theory aims to understand the origin of organization. In doing so, it adopts different modelling methodologies to those commonly used to study specific systems. For example, rather than predicting the dynamics of a given organization, rules of interaction between all possible objects are specified, and it is left open which objects appear in a given simulation. An example of this approach is the use of CA. Attempts to simulate 'Alife' communities and ecosystems are also particularly relevant to Gaia.

The relationship between complexity theory and other disciplines can be viewed in terms of a behavioural classification of systems (figure 3). In this case, complex systems are a subset of dynamical systems, and complexity theory is part of dynamic systems theory, which also considers simple systems. Complex systems can be subdivided into ordered systems, critical systems and chaotic systems. Chaos describes unpredictable behaviour emerging from nonlinear equations giving high sensitivity to initial conditions. Order describes a tendency to reside in one state or limit cycle between a limited number of states. Between frozen order and unpredictable chaos, much interest has been focused on a critical regime dubbed 'the edge of chaos'. Complexity theory can be seen as an extension of cybernetics (control theory), which focuses on feedback and feed-forward systems with predictable behaviour. It also encompasses AI and 'Alife' research. By contrast, chaos theory focuses on systems with unpredictable behaviour.

This special issue focuses on the subset of CAS. A 'bottom-up' definition of a CAS has been given (Levin 1998) based on three essential elements: (i) sustained diversity and individuality of components; (ii) localized interaction among those components; and (iii) an autonomous process that selects from among these components, based on the results of local interactions, a subset for replication or enhancement. From these essential elements it is argued (Levin 1998) that the following properties (Holland 1995) emerge: (1) continual adaptation; (2) absence of a global controller; (3) hierarchical organization; (4) generation of

Table 1. Orders of control in complex systems (after Jørgensen & Straskraba 2000).

order	scope for adaptation	example system discussed in text
first	fixed parameters and structure	original Daisyworld model
second	variable parameters, fixed structure	CA Daisyworld
third	variable structure and parameters	'Alife' Guild model
fourth	change of goal functions	Gaia (?)

perpetual novelty; and (5) far-from-equilibrium dynamics. Commonly given examples of CASs are cells, individual organisms and ecosystems.

What is the typical behaviour of a CAS? First, they display 'self-organization', in the sense of emergence of ordered behaviour and structure from many parts with sufficient connections, independent of natural selection (Kauffman 1993). The concept was inspired by the results of mathematical models, which, starting from arbitrary initial conditions and obeying only simple local rules, produced large-scale order. The second law of thermodynamics forbids true self-organization: increasing order is only possible in thermodynamically open systems. Thus self-organization is dissipative, requiring free energy input and producing high-entropy output. CASs may also show 'self-organized criticality' (Bak *et al.* 1987), meaning a tendency to reside in the edge of chaos regime, allowing change without getting locked into frozen order. A power-law distribution of responses is thought to be characteristic of self-organized critical systems, but may occur more widely in nature.

Complex systems can be described in terms of their order of dynamics and control (Jørgensen & Straskraba 2000; table 1). First-order dynamical systems have fixed parameters and structure, and hence can only achieve feedback control. Second-order dynamical systems have variable parameters as well as states, but fixed structure. Third-order systems have variable structure as well as parameters and states. The distinction in fourth-order systems is that changes in states, parameters and structure lead to a change in the goal functions that determine the long-term behaviour of a system (Wilhelm & Brüggemann 2000). How do CASs fit into this classification? The element of replication or enhancement indicates that their structure is variable, allowing third-order control. The generation of continual adaptation suggests that CASs are fourth order with internally generated changes in goal functions.

In what sense are such behaviours adaptive? Adaptation has two common meanings in biology: (i) in evolution: it is a change in the structure or functioning of organisms that makes them better suited to their environment; and (ii) in physiology: it is an alteration in an organism's response to its environment. Evolutionary adaptation (i) is usually thought of as the consequence of natural selection acting on heritable variation. The capacity for physiological adaptation (ii) can be the product of evolutionary adaptation (i). 'Adaptive' is used in complexity theory to describe system development as well as response, and is often applied to systems that are not subject to natural selection as a whole (although their parts may be). Hence, 'adaptive' behaviours described by complexity theorists are not necessarily 'adaptations' in the sense used by evo-

lutionary biologists (i) or physiologists (ii). One way out of this semantic minefield is to consider natural selection as just one (rather than the only) form of selection. Other forms of selection can emerge at levels above that of natural selection acting on heritable variation, e.g. in the process of foraging by social insect colonies utilizing pheromone signals (stigmurgy), or in models of the evolution of altruism, as a consequence of emergent spatial patterns (Paolo 2000). If selection can be broader than just natural selection, then there can be 'adaptive' behaviours that are not necessarily the product of natural selection.

5. IS GAIA A COMPLEX ADAPTIVE SYSTEM?

Gaia is a complex system in that it has many interwoven parts and properties that are not fully explained by an understanding of the parts, for example, the stability of components of the atmosphere. Gaia also fulfils the CAS criteria given previously (Levin 1998), as it contains sustained diversity and individuality of components (e.g. organisms), localized interaction among these components, and at least one autonomous selection process (natural selection). Gaia also possesses non-local interaction of components, because there is global mixing of the atmosphere and oceans. This gives rise to globally mixed variables: atmospheric gases with lifetimes longer than atmospheric mixing (*ca.* 1 yr), and dissolved chemical species in the ocean with lifetimes longer than ocean mixing (*ca.* 1000 yr). There are also non-local interactions in the climate system, described as 'teleconnections'.

If Gaia is a CAS, we can expect it to display characteristic properties and behaviour. Gaia does indeed share generic CAS properties (Holland 1995): far-from-equilibrium dynamics (of life, the atmosphere and aspects of ocean chemistry), generation of perpetual novelty (through evolution), hierarchical organization (e.g. organisms, ecosystems, Gaia), and absence of a global controller. However, non-local interaction simplifies the system and offers the possibility that from its many complex components, Gaia could display emergent simplicity in its behaviour. In what sense might Gaia be *adaptive*? Gaia has not evolved by natural selection at the whole system level, but various types of selection operate within the system. The system can be viewed physiologically, as captured in the term 'geophysiology' (Lovelock 1986), and may respond to forcing in a manner resembling physiological adaptation. There is change at the system level and there may also be developmental trends that enhance life as a whole, e.g. an increase global gross primary productivity with time.

Is Gaia self-organizing? It is often said that Gaia is self-regulating, but what order of control (table 1) is actually

achieved? There are many examples of first-order feedback control (examples in § 3). Gaia also contains evolution, which continually reshapes the system, and thus allows higher levels of system control. The evolution of responses to prevailing environmental conditions and the evolution of environment-altering traits, represent changes in the parameters and structure of the system, allowing for second- and third-order control. For example, the colonization of the land surface by vascular plants altered the climate in a self-beneficial manner (Betts 1999) and led to a reorganization of biogeochemical cycles, including a drop in carbon dioxide (Berner 1998), global cooling, and a rise in oxygen (Lenton 2001). Changes in the Earth's history, such as the switch from anaerobic to aerobic conditions as oxygen rose *ca.* 2 Gyr ago, and the resulting increase in free-energy availability to the biota, could be viewed as fourth-order control: a change in goal function from an anaerobic, 'upside-down' biosphere (Walker 1987), to an aerobic attractor state that allowed the proliferation of new types of life. Thus Gaia may be viewed as self-organizing and more in terms of the levels of control achieved.

Is Gaia in a self-organized critical state? If one contrasts the current state of Gaia with that of Mars or Venus, or the suggested 'snowball Earth' state, Gaia is more complex and less 'frozen' into order (of course Mars is literally frozen as would be the snowball Earth). It has been suggested that the Earth's biota is in a self-organized critical state on the basis that extinction events have a distribution closely approximated by a power law (Kauffman 1993). Proponents of complexity theory propose that the majority of all extinction events are internally generated by the dynamics of coevolution of species. If so, this would indicate criticality of the biota, but not necessarily criticality of Gaia. An alternative hypothesis is that the majority of extinction events are caused by external perturbation. In the case of mass extinctions, there is good evidence for a causative asteroid impact at the Cretaceous–Tertiary boundary, 65 Myr ago (Alvarez *et al.* 1980). Simple models of coevolution (Bak & Sneppen 1993) or of environmental stress (Newman 1997) (without species interaction) as the cause of extinction, both exhibit a power law. Of the two, the environmental stress model has an exponent much closer to actual data. We conclude that although some extinction may result from coevolution, there is not yet a convincing case that the biota is in a critical state. To test whether Gaia is in a critical state, a frequency response analysis of environmental records might be more appropriate. For example, the carbon dioxide and methane records in the Vostok ice core (Petit *et al.* 1999).

6. EMERGENCE OF GAIA

Complexity theory stimulates us to search for a complexity threshold for a planet with life, beyond which the emergence of self-organization (including self-regulation) and adaptive behaviour becomes likely, in other words, a planetary analogue for the emergence of auto-catalytic networks (Kauffman 1993). In coupled open systems of life and environment, does self-organization become vastly more probable beyond a critical 'size' (e.g. number of

organisms)? Also, can we pinpoint a particular time in the Earth's history when Gaia emerged?

Once life arose it must soon have depleted its surroundings of substrates, thus posing a pressing need for recycling. Key biogeochemical transformations of essential elements are present deep in the tree of life among the ancient kingdoms of archaea and bacteria, supporting a view that nutrient recycling evolved early. One further requirement is important for the emergence of planetary scale self-organization: in order to achieve global significance, life must have an abundant source of free energy. The earliest types of photosynthesis used relatively scarce substrates such as H₂S. Once oxygenic photosynthesis emerged using the abundant H₂O as a substrate, then the flux of free energy captured by the biota increased massively (DesMarais 2000). Thus we suggest the genesis of Gaia came with the origin of widespread oxygenic photosynthesis. This occurred at least 2.8 Gyr ago (DesMarais 2000) and possibly as early as 3.8 Gyr ago (Schidlowski 1988).

A remarkable property of Gaia that demands an explanation, is that its abiotic state variables have stayed at levels that support abundant life for most of the last 3.8 Gyr. Early, strong versions of the Gaia hypothesis suggested that all life-forbidding state variable levels are unreachable because there is selection against the processes that would lead there. Selection at the level of the system as a whole seems untenable (Doolittle 1981; Dawkins 1983). However, it may still be the case that life-forbidding state-variable levels are difficult to reach, for at least two reasons: (i) if an organism is driving an environmental variable towards an uninhabitable state, its growth and spread will be suppressed (by negative feedback) such that the system will stabilize within the habitable regime; and (ii) whenever organisms become so abundant that the side-effects of their metabolism become life-threatening on a global scale, different organisms will evolve for which the abundant pollutants and the polluters themselves become resources. If natural selection has enough substrate (genotypic variation) on which to operate, such checks and balances are always likely to evolve and make extreme conditions unreachable. This old idea (originating from Smith 1776) could explain the likelihood of regulation at liveable levels as a side-effect of evolution in sufficiently diverse biota.

Uninhabitable or barely habitable states (with life in refugia) can be reached because of global scale environmental perturbation, e.g. massive asteroid impact (Watson 1999), or extreme external forcing, e.g. future increases in solar luminosity (Lovelock & Whitfield 1982; Lenton & Von Bloh 2001). It is also possible that the evolution of particularly strong biotic effects could 'overshoot' and drive the environment into a barely habitable state, especially if there is a time-delay in self-limiting negative feedback (this is a counter argument to (i) above). Furthermore, variables that cannot function as a resource to any organism may be able to build up to toxic levels (a counter argument to (ii) above). However, useless and dangerous waste products may generally kill off their producers before disrupting the functioning of Gaia as a whole.

Gaia has suffered massive perturbations (asteroid impacts), and 'snowball Earth' states may have occurred

in which life only hung on in refugia. However, abundant life has always reappeared, sometimes remarkably quickly (D'Hondt *et al.* 1998). New types of life appear in the wake of mass extinction, but there is also a system 'memory' carried in the gene pool. This suggests an interesting possibility: if in response to perturbation, a new trait evolves that contributes to recovery, then if it remains in the gene pool and a similar perturbation occurs again, the system may recover faster the second time. In this sense, Gaia may gain from experience.

7. SIMULATING PLANETARY SCALE EMERGENCE WITH DAISYWORLDS

The persistence of life and recovery of Gaia from perturbation suggest that self-regulation occurs. We would like to know how it can emerge and whether it is a chance or a highly probable outcome of life–environment coupling. The feasibility and probability of the emergence of planetary scale 'self-organization' and/or 'adaptive behaviour' can be evaluated using a synthetic approach of mathematical modelling.

The first such attempt to simulate the emergence of planetary scale self-regulation was the Daisyworld model (Watson & Lovelock 1983). In Daisyworld, global temperature regulation emerges automatically from feedback coupling between life and its environment, with selection at the component (individual organism) but not the system (whole planet) level. In Daisyworld, the environment is reduced to one variable: temperature, and life is reduced to two types: black and white daisies inhabiting bare ground. The daisies share the same optimum temperature for growth of 22.5 °C and outer limits to growth of 5 °C and 40 °C. The daisy types affect their environment in opposite ways by virtue of their different reflectivity (albedo). The white daisies reflect more solar radiation than bare ground, whilst the black daisies absorb more. Hence, the local temperature of the daisies differs: black daisies are always warmer and white daisies are always cooler than bare ground. The system is forced by a gradual increase in solar luminosity as has occurred on the Earth.

With only one type of daisy present, there is a range of forcing for which negative feedback occurs and a point at which positive feedback occurs. In the case of black daisies only, when they can establish, their spread is amplified by positive environmental feedback (similar to figure 2c, but the effect of life on the environment is stronger). As luminosity increases, the population of black daisies declines, thus providing negative feedback on temperature. In the case of white daisies only, when they can germinate their spread is immediately suppressed by their cooling effect. As luminosity increases, their population increases, providing negative feedback on temperature. A regime is entered where white daisies maintain the planet in a habitable state when otherwise it would be uninhabitable (figure 2d). Eventually they collapse catastrophically with positive feedback. With both types of daisy present, there is a range of forcing for which global temperature actually decreases as forcing increases. This is an example of 'super-negative' feedback (the sign of response is opposite to that of the forcing (Sardeshmukh 2000)).

The Daisyworld model has been portrayed as a CAS (Lewin 1993), but this deserves closer examination. It

possesses first-order feedback control (table 1) and the regime of super-negative feedback was unexpected from its parts. However, the original model does not explicitly include interacting local components. The system is described by coupled equations and its behaviour can be understood analytically (Saunders 1994; Weber 2001).

If time-delays are introduced into the population and temperature equations of Daisyworld, then apparently chaotic behaviour can be generated (Zeng *et al.* 1990). Varying the time-delay reveals a series of period doublings characteristic of the transition from order to deterministic chaos (De Gregorio *et al.* 1992a,b). There is no real-world justification for the time-delays, and it has been shown that the average of the 'chaotic' solutions is close to the temperature regulation in the original model (Jascourt & Raymond 1992). Introducing an unrealistically large heat capacity to Daisyworld generates limit cycle oscillations of the two daisy populations and temperature (Nevison *et al.* 1999) (i.e. generates the first period doubling). These studies show that the original Daisyworld model resides well into the ordered regime and is not in a critical state.

Subsequent versions of Daisyworld arguably show the emergence of higher-order control (although the final property of temperature regulation is similar in each case). Variants of the model with adaptation of the optimum growth temperature of the daisies (Robertson & Robinson 1998; Lenton & Lovelock 2000) include alteration of parameters, but this is enforced through further parameters. A more fully second-order control system is a Daisyworld with random mutation of daisy albedo (some of the parameters) and subsequent selection (Lenton 1998; Lenton & Lovelock 2001). The structure of this model could be said to change in that new daisy 'species' appear. This suggests there may be some third- and fourth-order control.

8. CA DAISYWORLDS

To fulfil the CAS criteria, models must include local interaction of components. CA provide a tool for this. Hence we have followed the lead of others (Von Bloh *et al.* 1997), and constructed a CA version of Daisyworld to explore the effects of local interaction and the capacity for adaptive system behaviour. The original equations (Watson & Lovelock 1983) are retained where possible. The CA grid and rules are simply used to replace the population equations. We consider a square grid with eight neighbours to each cell, rather than four nearest neighbours (Von Bloh *et al.* 1997). There is no diffusive temperature field, just the original equations for local temperatures of daisies (determined by albedo, global temperature and insulation parameter, q) and global temperature (determined by average albedo of the system and luminosity forcing). Seeding is used to enable populations to establish (but once they are established it has little impact). First we consider the original case of populations of 'black' (albedo $a_B = 0.25$) and 'white' (albedo $a_W = 0.75$) daisies covering bare ground (albedo $a_G = 0.5$). For an empty cell with n_B black neighbours each with growth rate β_B and n_W white neighbours each with growth rate β_W , the following colonization rules apply.

The probability that black will colonize when only they are present is:

$$P(\text{B} | n_{\text{W}} = 0) = 1 - (1 - \beta_{\text{B}})^{n_{\text{B}}} \quad (8.1)$$

The probability that white will colonize when only they are present is:

$$P(\text{W} | n_{\text{B}} = 0) = 1 - (1 - \beta_{\text{W}})^{n_{\text{W}}} \quad (8.2)$$

The probability that the cell remains empty is:

$$P(\text{E}) = (1 - P(\text{B} | n_{\text{W}} = 0))(1 - P(\text{W} | n_{\text{B}} = 0)). \quad (8.3)$$

The probability that black will colonize when both are present is:

$$P(\text{B}) = (1 - P(\text{E})) \frac{P(\text{B} | n_{\text{W}} = 0)}{P(\text{B} | n_{\text{W}} = 0) + P(\text{W} | n_{\text{B}} = 0)}. \quad (8.4)$$

The probability that white will colonize when both are present is:

$$P(\text{W}) = (1 - P(\text{E})) \frac{P(\text{W} | n_{\text{B}} = 0)}{P(\text{B} | n_{\text{W}} = 0) + P(\text{W} | n_{\text{B}} = 0)}. \quad (8.5)$$

The probability of seeding an empty cell is fixed:

$$P(\text{S}) = \eta \quad (\eta = 0.001 \text{ in the results shown}). \quad (8.6)$$

The probability of death at an occupied cell is also fixed:

$$P(\text{D}) = \gamma \quad (\gamma = 0.3 \text{ as in the original model}). \quad (8.7)$$

The 2D CA model has less smooth dynamics than the original zero-dimensional model, in that it can exhibit bifurcations and limit cycling (figure 4). The growth equations are such that for one type alone (figure 4*a,c*), it can reach carrying capacity on the grid even when its local temperature and growth rate are sub-optimal. This is because the presence of many identical neighbours can make colonization of an empty cell highly probable, even when growth rate is suppressed by temperature (equations (8.1) or (8.2)). For black daisies alone (figure 4*a,b*), as forcing is increased, a bifurcation point is reached, where the global temperature is such that the local temperature of black daisies becomes uninhabitable ($\beta_{\text{B}} = 0$ when the temperature of black daisies, $T_{\text{B}} = 40^\circ\text{C}$). This generates partial collapse (*ca.* 30% die-back of the daisies), immediate recovery and resulting oscillations of temperature and population. As forcing is increased further, a second bifurcation point is reached. Then the trajectories combine before the black daisies disappear. For white daisies alone (figure 4*c,d*), there are two period doublings and the beginnings of a third (inset in figure 4*d*) before a return to a single trajectory.

The one daisy-type model illustrates an ‘overshoot’ problem for Gaia: life may develop the capacity to drive an environmental variable into an uninhabitable or barely habitable state if the environmental effect is strong and local interactions that encourage growth outweigh negative feedback on growth from the environment. The model does not include natural selection, in that all the daisies are identical and are always equally fit in terms of growth rate (although in the initial growth phase, clusters form, and cells at the edge of clusters are better able to spread than those within clusters). The model does include a system selection process between bare ground and one daisy type: under a certain range of forcing, daisies are selected over bare ground; outside that range, bare ground will successfully take over from daisies.

When black and white types can both arise, the limit cycle regimes are removed and the solution resembles the original zero-dimensional model (figure 4*e,f*). The two different daisy types have different growth rates and hence fitness, thus adding a crude form of natural selection to the model (although there is no evolution). With this additional selective process the model stays more firmly in the ordered regime. The system is stabilized by at least three effects: (i) if one daisy type reaches an uninhabitable temperature the other may still be able to spread (because their local temperatures differ); (ii) in the mid-range of forcing, a combination of black and white generates a global temperature closer to optimal; and (iii) the presence of one daisy type reduces the area available to the other to expand into.

We have introduced random mutation of albedo to the model, generalizing the colonization equations (8.1)–(8.5) to deal with any albedo type. Mutation is assumed always to occur in the process of colonization of an empty cell (asexual reproduction that always generates mutated offspring). Albedo can mutate within a parameterized width of the parent albedo ($\pm \Delta a$). Within this range, either side of the parent albedo, an offspring albedo is randomly chosen. Limits to mutation are set at $a_{\text{min}} = 0$ and $a_{\text{max}} = 1$.

With mutation and natural selection within the model system (figure 5), its behaviour could be said to be ‘adaptive’ in that it ‘evolves’ to counteract forcing. When the model is seeded with the original ‘black’ daisies ($a_{\text{B}} = 0.25$) and these are allowed to mutate, as forcing increases, progressively paler daisies evolve, cooling the planet and then maintaining the temperature close to constant. Increasing Δa brings the average planetary temperature more rapidly towards the optimum for daisy growth. The tendency for bifurcation (figure 4*a*) is removed by increasing Δa (figure 5), because this tends to generate an early increase in average albedo. In a sensitivity analysis of the stabilizing effect of albedo diversity, $a_{\text{max}} - a_{\text{min}}$ was progressively increased around a central value of $a_{\text{B}} = 0.25$, without any mutation, and this was also found to remove the bifurcations. Albedo mutation extends the range of temperature regulation beyond that in the original model because paler types than the original ‘white’ ones can arise. The latter result has been found in other variants of Daisyworld (Stöcker 1995; Von Bloh *et al.* 1997; Lenton & Lovelock 2001).

A more complex 2D CA version of Daisyworld has previously been formulated with albedo mutation and a continuous temperature field (Von Bloh *et al.* 1997). This system exhibits the remarkable property that under enforced habitat fragmentation using a percolating fractal, the system is able to regulate temperature unimpaired up to a ‘critical’ threshold at which daisy areas become isolated and regulation starts to break down. Once uninhabited land forms a spanning cluster, regulation is completely removed. By contrast, trivial reductions in habitat (e.g. a growing square of ‘concrete’) impair temperature regulation in a linear fashion. In the former case, adjacent daisies can affect the temperature of small, uninhabited areas, but overall temperature regulation depends on competition among daisies across an entire connected space. In other words, the emergent property of global temperature regulation relies on uninhibited local interaction, fitting

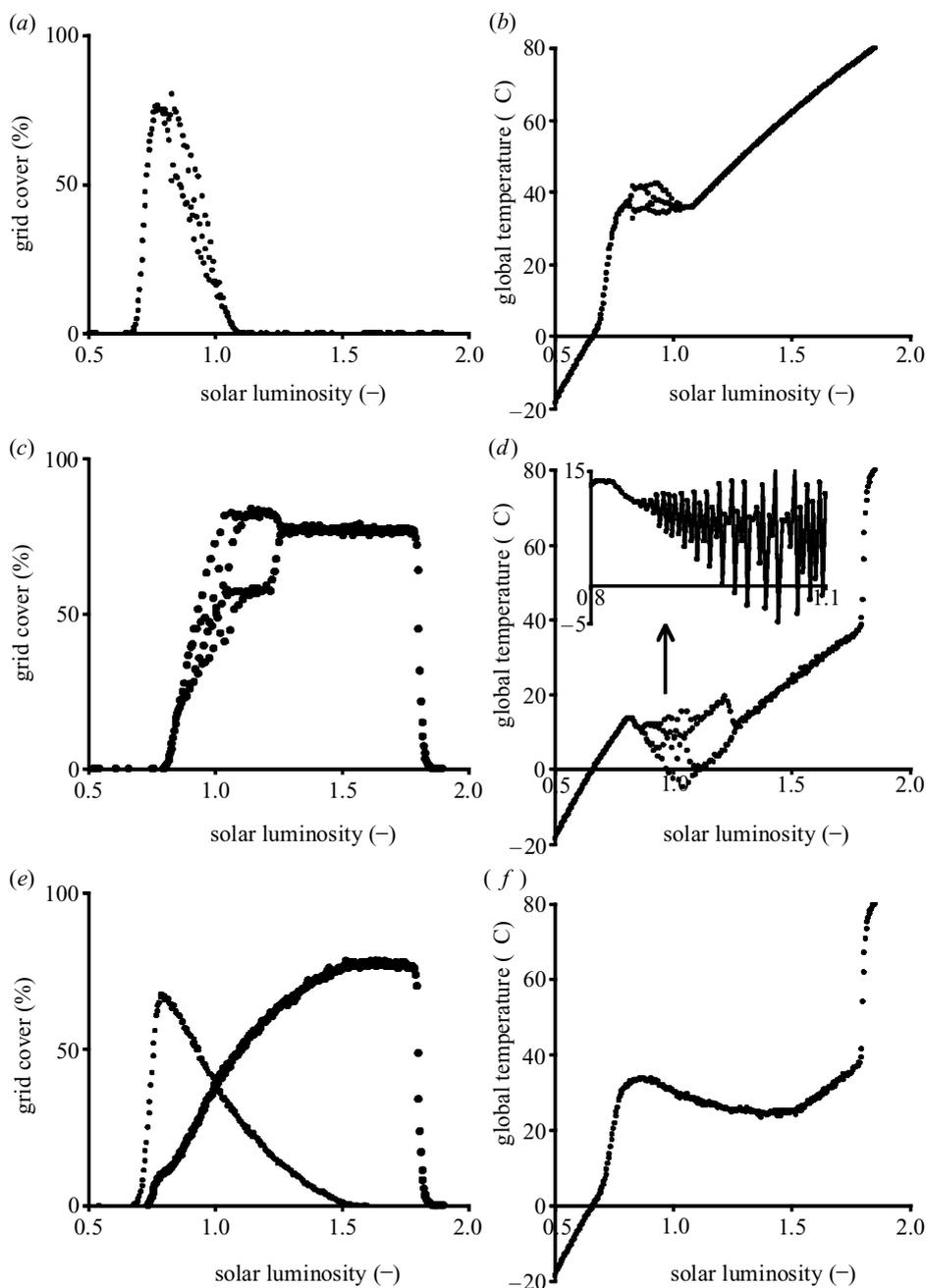


Figure 4. Simulations of fixed albedo populations in a simple CA Daisyworld (64×64 grid). Parameters are as in the original model (Watson & Lovelock 1983) and the CA rules are described in § 8. Solar luminosity (in normalized units) is increased in steps of 0.004, at each of which the model is updated. The left-hand graphs show percentage grid cover by the daisies versus luminosity, and the right-hand graphs show global average temperature ($^{\circ}\text{C}$) versus luminosity. Temperature is a function of luminosity and the albedo, a , and grid cover of daisies and empty cells. (a,b) Seeding with 'black' daisies ($a_{\text{B}} = 0.25$) denoted by filled circles. (c,d) Seeding with 'white' daisies ($a_{\text{W}} = 0.75$) denoted by open circles. (e,f) Seeding with both black and white daisies (albedo of each seed chosen at random). The inset in (d) shows the period doubling in the temperature trajectory with only white daisies.

in nicely with the criteria for a CAS. The system is self-organizing and may arguably be in a critical state near the limit at which daisy areas become disconnected.

9. FEASIBILITY TESTS OF GAIA USING 'ALIFE'

A key criticism of Daisyworld is that it is limited in only considering one predetermined type of interaction between the local and the global, and it is one that will

tend to generate regulation. The daisies affect their environment in the same way at the local and the global scale. Hence, what is selected for at the individual level tends to be beneficial at the global level. With two or more daisy types present, there is negative selective feedback making regulation likely (Lenton 1998).

'Alife' techniques offer a promising way of making unbiased tests of the potential for emergence of planetary scale self-organization. The model environment 'Tierra'

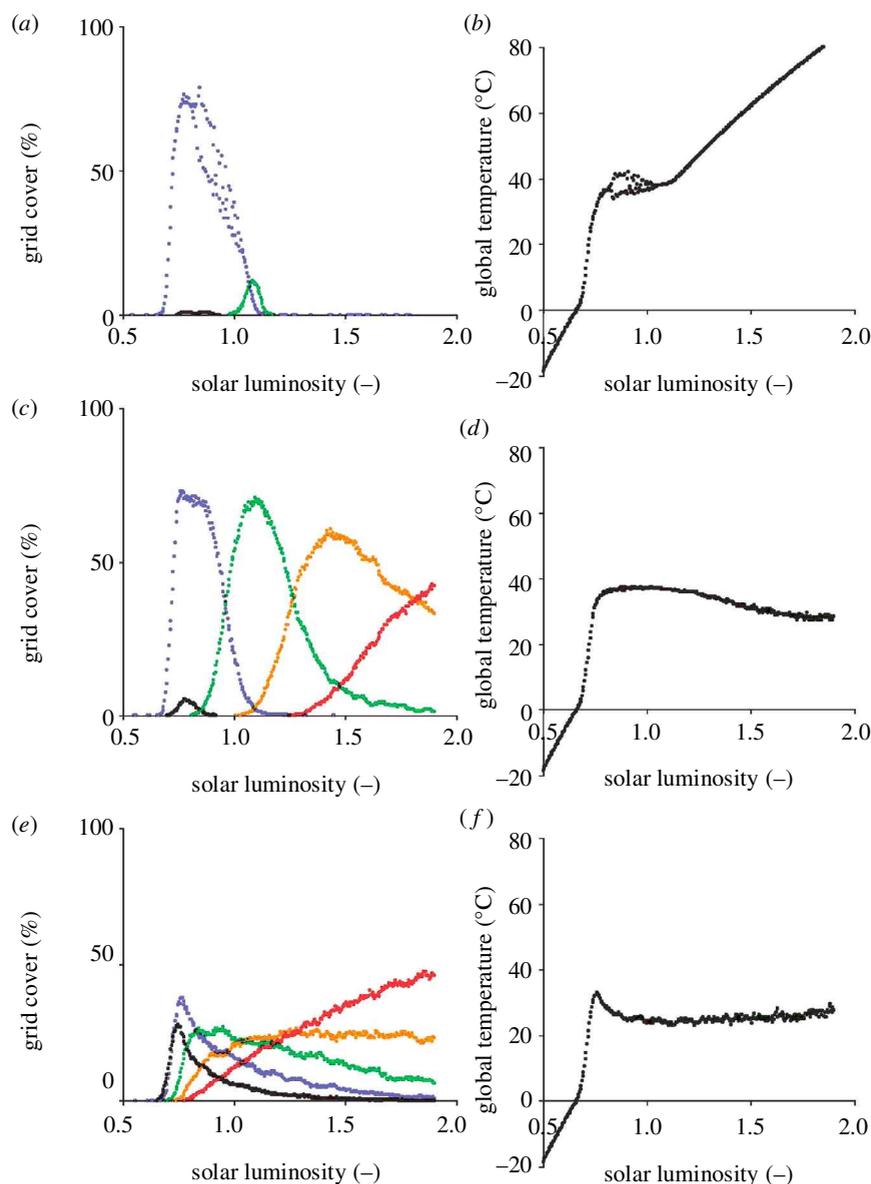


Figure 5. CA Daisyworld simulations with albedo mutation (64×64 grid). In each simulation there is seeding with the original 'black' daisies ($a_B = 0.25$), which fall in the range coloured in blue. The model is updated with each increase in solar luminosity of 0.004 normalized units, and at each update, empty cells can be colonized with offspring cells that differ at most by $\pm \Delta a$ from the albedo of their parent cell. Left- and right-hand graphs show grid cover by daisy populations (%) and global average temperature ($^{\circ}\text{C}$), respectively. The albedo colour scheme in the left-hand graphs is: 0–0.2 black, 0.2–0.4 blue, 0.4–0.6 green, 0.6–0.8 orange, 0.8–1.0 red. The graphs show the effect of increasing mutation range: (a,b) $\Delta a = 0.01$; (c,d) $\Delta a = 0.02$; (e,f) $\Delta a = 0.1$.

(Ray 1991) evolved a community of artificial life-forms that reproduce in different ways, including parasitically. The model 'life-forms' compete for resource (processor time) but they do not produce waste products. Hence their interaction with their environment is not thermodynamically complete in the way that it is for real life-forms, which can only maintain an ordered (low entropy) state by transforming matter as well as energy.

The evolution of matter recycling is addressed using 'Alife' techniques in the Guild model (Downing & Zvirinsky 1999). From one ancestral 'species', a community evolves which is able to recycle a given set of 'chemicals' (which can be thought of as different molecular forms of the same key nutrient element). Such recycling enables greatly enhanced productivity in real ecosystems and Gaia

(Volk 1998). The mechanism of emergence of recycling is quite different from the spontaneous emergence of autocatalytic cycles in systems of very large numbers of chemical reactions (Kauffman 1993). In the Guild model, 'Alife' chances upon closed recycling of a small set of chemicals and this is reinforced by selection. This illustrates part of the mechanism (ii) that we highlighted in § 6.

The main criticisms of the original Guild model are that there is no treatment of energy in the system, and that a deviation of the local environment from the global is assumed that may not be justified for some real world analogues. A 'Guild II' model is being developed (K. Downing, personal communication), that includes free energy and entropy in the abstract chemistry (e.g. it takes free energy to build larger molecules) and makes the local

environment the interior of proto-cells. In this model, despite a relatively small input of free energy in chemical form, recycling and regulation can emerge.

An ideal model world for testing Gaia would contain artificial life-forms that transform 'matter' and 'energy', are 'thermodynamically' constrained, grow and replicate with a heritable genome subject to random mutation, interact with one another, and evolve new ways of altering their environment related to their internal functioning. The environment would contain many 'physical' and 'chemical' variables, some homogeneous (well mixed) and others heterogeneous. The resulting system behaviour would be observable and testable by perturbation.

10. CONCLUSIONS

Many scientists now accept that planetary regulation involving the biota occurs (Longhurst 1998). However, we still have to determine whether Gaia's coming into existence and survival was coincidental or probable, and how fragile or robust the system is at present. We have argued that Gaia is a complex system with self-organizing and adaptive behaviour, but that it does not reside in a critical state. Complexity theory modelling approaches have helped us simulate and understand the emergence of planetary order. 'Alife' techniques can take this further and help in assessing the probability of emergence of planetary regulatory properties. Our attempts to apply complexity theory to Gaia have yielded a broader view of selection than previously encompassed in the Gaia theory (Lenton 1998). Gene-based natural selection is just one type and level of selection operating within Gaia, and it is not a necessary condition for regulation. The existence of different types of selection operating at different levels makes it easier to understand how planetary-scale self-regulation can arise. It also makes it easier to accept that a Gaia-like system may be a probable outcome once there is abundant life on a planet with the capacity for large-scale free energy capture.

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REFERENCES

- Alvarez, L. W., Alvarez, W., Asaro, F. & Michel, H. V. 1980 Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* **208**, 1095–1108.
- Bak, P. & Sneppen, K. 1993 Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* **71**, 4083–4086.
- Bak, P., Tang, C. & Wiesenfeld, K. 1987 Self-organized criticality—an explanation of $1/f$ noise. *Phys. Rev. Lett.* **59**, 381–384.
- Berner, R. A. 1998 The carbon cycle and CO₂ over Phanerozoic time: the role of land plants. *Phil. Trans. R. Soc. Lond. B* **353**, 75–82. (DOI 10.1098/rstb.1998.0192)
- Betts, R. A. 1999 Self-beneficial effects of vegetation on climate in an ocean–atmosphere general circulation model. *Geophys. Res. Lett.* **26**, 1457–1460.
- Bonan, G. B., Pollard, D. & Thompson, S. L. 1992 Effects of boreal forest vegetation on global climate. *Nature* **359**, 716–718.
- Budyko, M. I. 1968 The effect of solar radiation variations on the climate of the Earth. *Tellus* **21**, 611–619.
- Dawkins, R. 1983 *The extended phenotype*. Oxford University Press.
- De Gregorio, S., Pielke, R. A. & Dalu, G. A. 1992a Feedback between a simple biosystem and the temperature of the Earth. *J. Nonlinear Sci.* **2**, 263–292.
- De Gregorio, S., Pielke, R. A. & Dalu, G. A. 1992b A delayed biophysical system for the Earth's climate. *J. Nonlinear Sci.* **2**, 293–318.
- DesMarais, D. J. 2000 When did photosynthesis emerge on Earth? *Science* **289**, 1703–1705.
- D'Hondt, S., Donaghay, P., Zachos, J. C., Luttenberg, D. & Lindinger, M. 1998 Organic carbon fluxes and ecological recovery from the Cretaceous–Tertiary mass extinction. *Science* **282**, 276–279.
- Doolittle, W. F. 1981 Is nature really motherly? *The CoEvolution Q. Spring*, 58–63.
- Downing, K. & Zvirinsky, P. 1999 The simulated evolution of biochemical guilds: reconciling Gaia theory and natural selection. *Artif. Life* **5**, 291–318.
- Ehrlich, P. 1991 Coevolution and its applicability to the Gaia hypothesis. In *Scientists on Gaia* (ed. S. H. Schneider & P. J. Boston), pp. 118–120. London: MIT Press.
- Gallagher, R. & Appenzeller, T. 1999 Beyond reductionism. *Science* **284**, 79.
- Hamilton, W. D. 1995 Ecology in the large: Gaia and Genghis Khan. *J. Appl. Ecol.* **32**, 451–453.
- Hamilton, W. D. 1996 Gaia's benefits. *New Scientist* **151**, 62–63.
- Hamilton, W. D. & Lenton, T. M. 1998 Spora and Gaia: how microbes fly with their clouds. *Ethol. Ecol. Evol.* **10**, 1–16.
- Han, T.-M. & Runnegar, B. 1992 Megascopic eukaryotic algae from the 2.1 billion-year-old Negaunee iron-formation, Michigan. *Science* **257**, 232–235.
- Hoffman, P. F., Kaufman, A. J., Halverson, G. P. & Schrag, D. P. 1998 A Neoproterozoic snowball earth. *Science* **281**, 1342–1346.
- Holland, J. 1995 *Hidden order: how adaptation builds complexity*. Reading, MA: Addison-Wesley.
- Hyde, W. T., Crowley, T. J., Baum, S. K. & Peltier, W. R. 2000 Neoproterozoic 'snowball Earth' simulations with a coupled climate/ice-sheet model. *Nature* **405**, 425–429.
- Imshenetsky, A. A., Lysenko, S. V. & Kazakov, G. A. 1978 Upper boundary of the biosphere. *Appl. Environ. Microbiol.* **35**, 1–5.
- Isaacs, A., Daintith, J. & Martin, E. (eds) 1996 *Concise science dictionary*. Oxford University Press.
- Jascourt, S. D. & Raymond, W. H. 1992 Comments on 'Chaos in daisyworld' by X Zeng *et al.* *Tellus* **44B**, 243–246.
- Jørgensen, S. E. & Straskraba, M. 2000 Ecosystems as cybernetic systems. In *Handbook of ecosystem theories and management* (ed. S. E. Jørgensen & F. Müller), pp. 249–264. London: Lewis Publishers.
- Kasting, J. F. 1991 Box models for the evolution of atmospheric oxygen: an update. *Global and Planetary Change* **97**, 125–131.
- Kauffman, S. A. 1993 *The origins of order: self-organization and selection in evolution*. Oxford University Press.
- Kleidon, A. 2002 Testing the effect of life on Earth's functioning: how Gaian is the Earth system? *Climatic Change* **52**, 383–389.
- Klinger, L. F. 1991 Peatland formation and ice ages: a possible Gaian mechanism related to community succession. In *Scientists on Gaia* (ed. S. H. Schneider & P. J. Boston), pp. 247–255. London: MIT Press.
- Koeslag, J. H., Saunders, P. T. & Wessels, J. A. 1997 Glucose homeostasis with infinite gain: further lessons from the Daisyworld parable? *J. Endocrinol.* **154**, 187–192.
- Lenton, T. M. 1998 Gaia and natural selection. *Nature* **394**, 439–447.

- Lenton, T. M. 2001 The role of land plants, phosphorus weathering and fire in the rise and regulation of atmospheric oxygen. *Global Change Biology* **7**, 613–629.
- Lenton, T. M. 2002 Testing Gaia: the effect of life on Earth's habitability and regulation. *Climatic Change* **52**, 409–422.
- Lenton, T. M. & Lovelock, J. E. 2000 Daisyworld is Darwinian: constraints on adaptation are important for planetary self-regulation. *J. Theor. Biol.* **206**, 109–114.
- Lenton, T. M. & Lovelock, J. E. 2001 Daisyworld revisited: quantifying biological effects on planetary self-regulation. *Tellus* **53B**, 288–305.
- Lenton, T. M. & Von Bloh, W. 2001 Biotic feedback extends the lifespan of the biosphere. *Geophys. Res. Lett.* **28**, 1715–1718.
- Lenton, T. M. & Watson, A. J. 2000a Redfield revisited. 1. Regulation of nitrate, phosphate and oxygen in the ocean. *Global Biogeochemical Cycles* **14**, 225–248.
- Lenton, T. M. & Watson, A. J. 2000b Redfield revisited. 2. What regulates the oxygen content of the atmosphere? *Global Biogeochemical Cycles* **14**, 249–268.
- Levin, S. A. 1998 Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* **1**, 431–436.
- Lewin, R. 1993 *Complexity: life at the edge of chaos*. London: Phoenix.
- Lewis, G. N. & Randall, N. 1923 *Thermodynamics and the free energy of chemical substrates*. New York: McGraw-Hill.
- Longhurst, A. 1998 Too intelligent for our own good. *Nature* **395**, 9.
- Lovelock, J. E. 1972 Gaia as seen through the atmosphere. *Atmos. Environ.* **6**, 579–580.
- Lovelock, J. E. 1975 Thermodynamics and the recognition of alien biospheres. *Proc. R. Soc. Lond.* **189**, 167–181.
- Lovelock, J. E. 1983 Daisyworld—a cybernetic proof of the Gaia hypothesis. *The CoEvolution Q.* **Summer**, 66–72.
- Lovelock, J. E. 1986 Geophysiology: a new look at Earth science. *Bull. Am. Meteorol. Soc.* **67**, 392–397.
- Lovelock, J. E. 1988 *The ages of Gaia—a biography of our living Earth*. The Commonwealth Fund Book Program. New York: W. W. Norton & Co.
- Lovelock, J. E. 1991 *Gaia—the practical science of planetary medicine*. London: Gaia Books.
- Lovelock, J. E. & Margulis, L. M. 1974 Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis. *Tellus* **26**, 2–10.
- Lovelock, J. E. & Watson, A. J. 1982 The regulation of carbon dioxide and climate: Gaia or geochemistry? *Planetary Space Sci.* **30**, 795–802.
- Lovelock, J. E. & Whitfield, M. 1982 Life-span of the biosphere. *Nature* **296**, 561–563.
- Mojzsis, S. J., Arrhenius, G., McKeegan, K. D., Harrison, T. M., Nutman, A. P. & Friend, C. R. L. 1996 Evidence for life on Earth before 3800 million years ago. *Nature* **384**, 55–59.
- Nevison, C., Gupta, V. & Klinger, L. 1999 Self-sustained temperature oscillations on Daisyworld. *Tellus* **51B**, 806–814.
- Newman, M. E. J. 1997 A model of mass extinction. *J. Theor. Biol.* **189**, 235–252.
- Paolo, E. A. D. 2000 Ecological symmetry breaking can favour the evolution of altruism in an action-response game. *J. Theor. Biol.* **203**, 135–152.
- Petit, J. R. (and 18 others) 1999 Climate and atmospheric history of the past 420 000 years from the Vostok ice core, Antarctica. *Nature* **399**, 429–436.
- Rampino, M. R. 1987 Impact cratering and flood basalt volcanism. *Nature* **327**, 468.
- Ray, T. S. 1991 An approach to the synthesis of life. In *Artificial life II* (ed. C. G. Langton, C. Taylor, J. D. Farmer & S. Rasmussen), pp. 371–408. Redwood City, CA: Addison-Wesley.
- Redfield, A. C. 1958 The biological control of chemical factors in the environment. *Am. Sci.* **46**, 205–221.
- Robertson, D. & Robinson, J. 1998 Darwinian Daisyworld. *J. Theor. Biol.* **195**, 129–134.
- Sagan, C., Thompson, W. R., Carlson, R., Gurnett, D. & Hord, C. 1993 A search for life on Earth from the Galileo spacecraft. *Nature* **365**, 715–721.
- Sardeshmukh, P. D. 2000 Coupled systems with super-negative feedbacks. *Geophys. Res. Abstracts* **2**, 421.
- Saunders, P. T. 1994 Evolution without natural selection: further implications of the Daisyworld parable. *J. Theor. Biol.* **166**, 365–373.
- Saunders, P. T., Koelag, J. H. & Wessels, J. A. 1998 Integral rein control in physiology. *J. Theor. Biol.* **194**, 163–173.
- Schidlowski, M. 1988 A 3800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* **333**, 313–318.
- Schrödinger, E. 1944 *What is life?* Cambridge University Press.
- Schwartzman, D. 1999 *Life, temperature and the earth: the self-organizing biosphere*. New York: Columbia University Press.
- Schwartzman, D. W. & Volk, T. 1989 Biotic enhancement of weathering and the habitability of Earth. *Nature* **340**, 457–460.
- Sellers, W. D. 1969 A global climate model based on the energy balance of the Earth-atmosphere system. *J. Appl. Meteorol.* **8**, 386–400.
- Sillén, L. G. 1967 How have sea water and air got their present compositions? *Chemistry in Britain* **3**, 291–297.
- Smith, A. 1776 *An inquiry into the nature and causes of the wealth of nations*. London: W. Strahan & T. Cadell.
- Stöcker, S. 1995 Regarding mutations in Daisyworld models. *J. Theor. Biol.* **175**, 495–501.
- Volk, T. 1998 *Gaia's body—toward a physiology of the Earth*. New York: Copernicus.
- Von Bloh, W., Block, A. & Schellnhuber, H. J. 1997 Self-stabilization of the biosphere under global change: a tutorial geophysiological approach. *Tellus* **49B**, 249–262.
- Walker, J. C. G. 1987 Was the Archaean biosphere upside down? *Nature* **329**, 710–712.
- Walker, J. C. G., Hays, P. B. & Kasting, J. F. 1981 A negative feedback mechanism for the long-term stabilisation of Earth's surface temperature. *J. Geophys. Res.* **86**, 9776–9782.
- Watson, A. J. 1999 Coevolution of the Earth's environment and life: Goldilocks, Gaia and the anthropic principle. In *James Hutton—present and future*, vol. 150 (ed. G. Y. Craig & J. H. Hull), pp. 75–88. London: Geological Society.
- Watson, A. J. & Lovelock, J. E. 1983 Biological homeostasis of the global environment: the parable of Daisyworld. *Tellus* **35B**, 284–289.
- Weber, S. L. 2001 On homeostasis in Daisyworld. *Climatic Change* **48**, 465–485.
- Wilhelm, T. & Brüggemann, R. 2000 Goal functions for the development of natural systems. *Ecol. Model.* **132**, 231–246.
- Zeng, X., Pielke, R. A. & Eykholt, R. 1990 Chaos in Daisyworld. *Tellus* **42B**, 309–318.

GLOSSARY

- 2D: two dimensional
 AI: artificial intelligence
 'Alife': artificial life
 CA: cellular automata
 CAS: complex adaptive system