Review TRENDS in Ecology and Evolution Vol.22 No.11

Do evolution and ecology need the Gaia hypothesis?

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Gaia theory, which describes the life–environment system of the Earth as stable and self-regulating, has remained at the fringes of mainstream biological science owing to its historically inadequate definition and apparent incompatibility with individual-level natural selection. The key issue is whether and why the biosphere might tend towards stability and self-regulation. We review the various ways in which these issues have been addressed by evolutionary and ecological theory, and relate these to 'Gaia theory'. We then ask how this theory extends the perspectives offered by these disciplines, and how it might be tested by novel modelling approaches and laboratory experiments using emergent technologies.

Introduction

The Gaia hypothesis [1] proposes that the biota of the Earth alters its physical environment so as to maintain conditions that are conducive to life itself, despite destabilizing influences (e.g. large meteorite impacts), increasing solar output and internally generated instabilities (e.g. atmospheric oxidation). How could a self-regulating biosphere arise through natural selection acting to maximize the individual fitness of a diverse set of organisms? Because no one organism can regulate all global environmental variables, there is an apparent need for cooperation between distantly related species to obtain global regulation [2]. If such a cooperative endeavour were costly to the individuals involved, it would be susceptible to 'cheats', which could avoid that cost by non-participation. Selection at the level of the biosphere cannot avoid this problem because there is no replicating population of alternative regulating or non-regulating biospheres from which to select [3]. Hence, evolutionary biologists have tended to ignore Gaia theory and the literature on Gaia [4], with some notable exceptions [5,6], ignores much biological theory and, especially, experiment. Here, we define carefully what is meant by 'Gaia' and the properties it must have, describe its relationship to traditional ecology and evolution, and ask whether Gaia theory could be consistent with, and make a useful contribution to, ecology and evolution.

Definitions of Gaia and stability

Concepts such as 'Gaia' and 'stability' have had varied definitions. Kirchner [7] created a 'taxonomy' of the Gaia variants described in the literature (Figure 1; Box 1). Of these, the only plausible and non-trivial form is Homoeostatic Gaia, which states that interactions between life and its environment are generally stabilizing, owing to feedback between biota and abiota. These feedbacks could arise by chance (Lucky Gaia [8]) or through an inherent property of the coevolution of life and its environment (Probable

Glossary

Adaptive feedback: feedback process which is selected at the level of the organism generating the feedback because it enhances the fitness of that organism. Equivalent to modification of the environment in the manner of an extended phenotype.

Byproduct: unselected consequence of a phenotype selected for other reasons, such as environmental modification by wastes secreted by a species. Can subsequently become selected for if two species engage in byproduct reciprocity. The latter is equivalent to syntrophy.

Cycling ratio: biological systems can reuse biologically necessary elements and compounds within the biotic component of the system before their loss to the abiotic component. The ratio of the fluxes through these two pathways is the cycling ratio.

Ecosystem engineering: engineering of an ecosystem caused by transformations of material in the environment of an engineer (e.g. by a beaver dam; allogenic engineering) or by the physical structures of the engineer (e.g. a tree; autogenic engineering).

Goal functions: properties, such as maximization of nutrient cycling, power and exergy, which can be used to define the overall state of an ecosystem at certain stages of its successional development.

Insurance hypothesis: diversity within an ecosystem increases stability because species that are not important to persistence of the system under basal conditions might be better adapted to the altered conditions following perturbation and take over the functions of those required in the base state.

Niche construction: effects of organisms on their environment which generate altered selection pressures on those organisms or other species through feedbacks.

Overyielding effect: diverse systems have increased productivity, possibly because a diverse species set exploits diverse resources more efficiently. The system then tends to a stable state in which nutrients are maximally exploited.

Portfolio effect: diversity enhances stability because the performance of the system under particular conditions is the statistical average of the performances of many individual species, thus avoiding sudden drops in performance if conditions change to disfavour a subset of species.

Rein control: stabilizing control of a particular environmental variable by a pair of feedbacks which individually alter that variable in opposite directions.

Resilience: the ability to recover rapidly to the base state following a severe externally or internally generated environmental perturbation. This definition does not imply a time scale for recovery [10], although we expect that recovery will be rapid on a geological time scale.

Resistance: the ability to stay close to equilibrium in the face of externally or internally generated environmental perturbation.

Robustness: the ability of a biological system to retain its function despite alteration of parts of the system by mutation or environmental perturbation.

Syntrophy: interaction between two spatially adjacent microbial species in which one provides a byproduct to the other in return for another byproduct (chemical or energetic) which makes the metabolic reaction of the first species thermodynamically favourable.

Unselected feedback: feedback onto a particular trait which does not significantly affect the selection of that trait because other selective pressures (e.g. the need to secrete waste) are much stronger.

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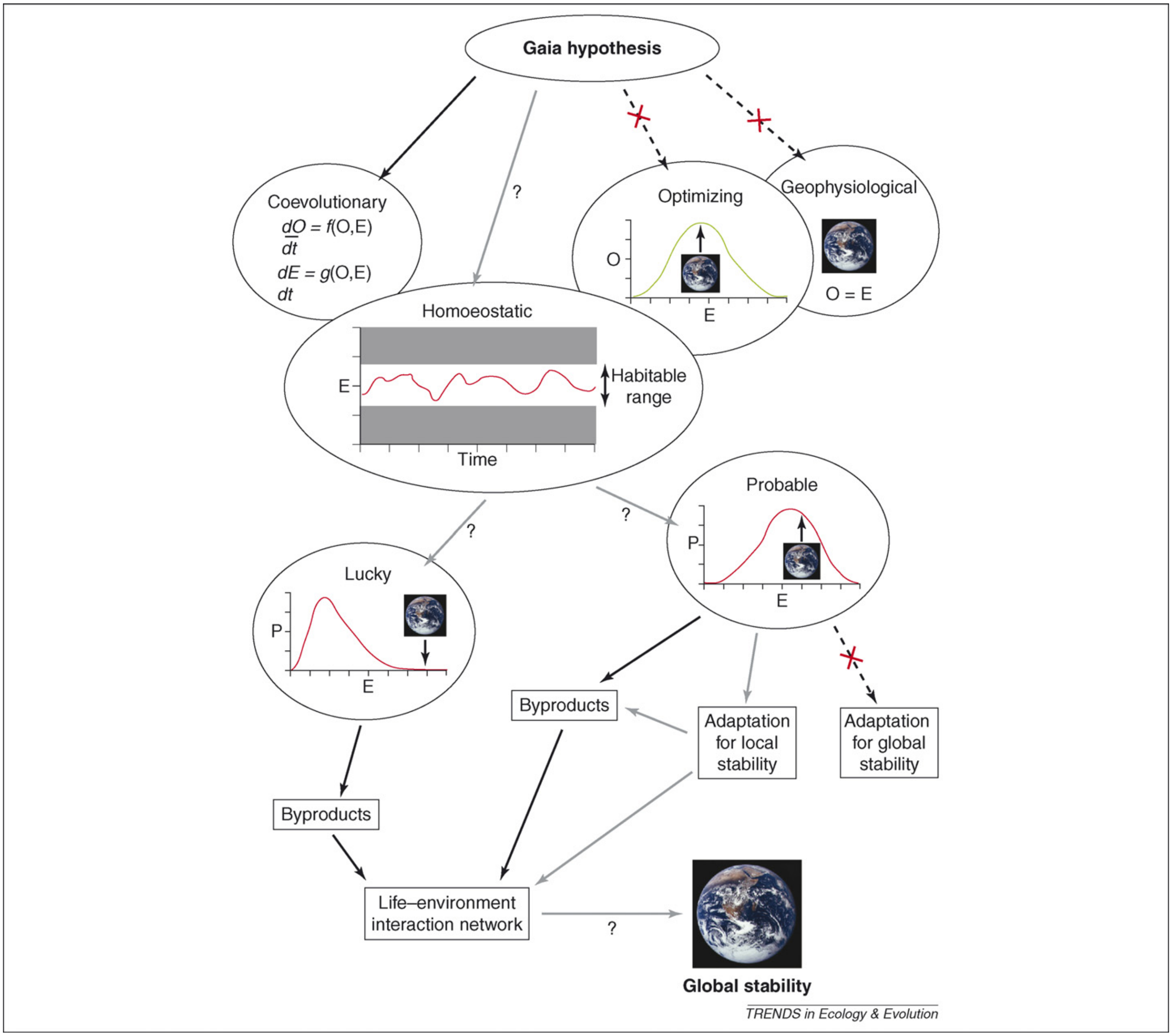

Figure 1. Interrelatedness and plausibility of variants of the Gaia hypothesis. Solid arrow = trivial or well accepted; grey arrow = plausible but unproven; dashed arrow with red cross = implausible. The original Gaia taxonomy divides the hypothesis into coevolutionary, homoeostatic, optimizing and geophysiological variants. Coevolutionary Gaia describes the temporal coupled evolution of life and environment, as described by Lewontin's coupled differential equations [21]. In Optimizing Gaia, the environment of the Earth is supposed to exist in an optimal state for the global biosphere (O is maximized), whereas Geophysiological Gaia equates the whole biosphere to a superorganism. Homoeostatic Gaia, the only plausible and nontrivial variant, describes the restriction of environmental conditions to a habitable range through feedback from the biota. This could occur by luck (Lucky Gaia: Earth is highly improbable) or as a statistically likely outcome (Probable Gaia). In either case, the network of life–environment interactions, largely dependent on the byproduct effects of evolved traits, leads to global stability. However, in the probable case, this might be influenced by adaptation generating local stability; selection for global stability is implausible.

Gaia [9]). Distinguishing these requires us to determine whether generalized life–environment interaction networks tend to stabilize, rather than destabilize, the biosphere (Box 1). A definition of Probable Homoeostatic Gaia would be:

> *'a planet with appropriate starting conditions for life will probably generate a biosphere the lifespan of which will be extended, rather than reduced, by life–environment feedback'.*

We discuss the possible mechanisms involved in more detail later but must first tackle the definition of stability.

'Stability' is a term with many definitions in the ecological literature [10], of which the most useful here are resistance (see Glossary) and resilience to change [11]. Homoeostatic Gaia requires that the biosphere remains within bounds of environmental variables compatible with life [11] (Figure 1). For example, temperature must be within a range enabling water to exist in liquid form, and chemical composition must be compatible with some kind of energy-yielding metabolism. The system should resist externally or internally generated perturbation towards these bounds, and should tend to recover once the perturbation is removed. Life–environment feedback (Table 1) is implicated in resistance to changes in solar output [12,13] and oxygen concentration [14], and in resilience to near-total glaciation by negative feedback onto the causative traits [15,16]. In other cases (e.g. the 300-Myr

Table 1. Examples of life–environment feedbacks over geological time

Geological time division	Years before present	Evolved trait	Environmental response	Feedback on life	Refs
Archean eon[a]	>2.5 Gyr	Methanogenesis	Increased atmospheric $[CH_4]$, increased greenhouse warming	+ve[b] at low temperatures, −ve at high temperatures	[1,13]
Palaeoproterozoic era	2.4–2.2 Gyr	Oxygenic photosynthesis	Increased atmospheric $[O_2]$, decreased atmospheric $[CH_4]$, 'snowball Earth' glaciation	Fewer anaerobic niches (−ve), greater energy to biosphere (+ve), frozen biosphere (−ve)	[17,15,13]
Late Cretaceous period	100 Myr	Efficient rock weathering by angiosperm-deciduous ecosystems	Reduced atmospheric $[CO_2]$, reduced greenhouse warming	+ve at high temperatures, −ve at low temperatures, selection for C_4 photosynthesis (+ve)	[1,5,26]
Archean eon onwards	3.1–0 Gyr	Nitrogen fixation	Increased organic N	Proliferation of nitrifiers (−ve), reduced selection for N_2-fixation (−ve)	[9,75]
Carboniferous period onwards	350–0 Myr	Phosphorous weathering of rocks	Increased productivity, increased burial of organic carbon, increased atmospheric $[O_2]$	Inhibition of C_3 photosynthesis (−ve), increased reactive oxygen species (−ve)	[14]
Holocene epoch (and probably earlier)	10–0 kyr	Boreal forest albedo	Increased temperature of boreal forest regions	Increased forest growth (+ve)	[76]
Anthropocene epoch	200–0 yr	Fossil fuel consumption	Increased $[CO_2]_{atm}$, increased greenhouse warming	CO_2 fertilization, CO_2 drawdown (−ve), increased soil respiration (+ve)	[77,78]

[a] The evolution of methanogenesis during the Archean has been disputed [75].

[b] +ve, positive feedback; −ve, negative feedback.

resistance to atmospheric oxidation following the evolution of oxygenic photosynthesis [17]), the feedbacks are primarily abiotic.

Homoeostatic Gaia implies resistance and resilience over long (Myr) time scales and at global spatial scales, compared with the much smaller spatiotemporal scaling of traditional ecology and evolution (Figure 2). It does not require that individual species and ecosystems persist over such scales. It does, however, parallel the concept of robustness to environmental and mutational change, which is generally applied to biological systems at scales from the genetic code to the body structures of multicellular organisms [18]. The Homoeostatic Gaia hypothesis implies a similar robustness over much larger scales of space and time (Figure 2). The issue of whether such an extrapolation of scale is justified is one of the most important and least resolved surrounding Gaia: although it seems that the diffuse nature of interactions between life and environment over large scales of space and time should make the global system less cohesive [19,20], the Earth system is more cohesive, in that it is essentially closed (unlike ecosystems) and subject to a single input flux (solar energy). We discuss ways in which stability properties might be conferred at the scale of Gaia later.

Characteristics of a 'Gaian' biosphere

For Homoeostatic Gaia to exist, several conditions must be met. The first of these is the existence of feedback between life and the environment, as formalised by the coupled differential equations of Lewontin [21] (Figure 1; see Table 1 for examples of current and previous life–environment feedback). Lenton [5] has separated life–environment feedback into two types: feedback on growth, in which traits selected for their individual fitness benefits have environmental side effects that affect the growth of those individuals and others; and feedback on selection, in which traits affect environmental variables which, in turn, directly affect the selective advantage of those traits. In both cases, the environmental effects are byproducts, not

Box 1. Variants of the Gaia hypothesis

Kirchner [7] organized Gaia definitions that have appeared in the literature in order of increasing departure from traditional thinking: Coevolutionary Gaia, Homoeostatic Gaia, Optimizing Gaia and Geophysiological Gaia. Most of these can be discarded as either trivially true or implausible. Coevolutionary Gaia describes the now well-accepted idea that life affects the development of the planetary environment, which, in turn, affects the future evolution of life [67]. Lewontin [21] recognized this relationship, describing the evolution of life (O) and environment (E) through functions *f* and *g*, by a pair of coupled differential equations (Figure 1). Optimizing Gaia suggests that the effects of life maintain the environment in a state optimal for life itself, so that the fitness of all organisms is somehow maximized (Figure 1). However the 'optimum' conditions for the diverse organisms comprising the biosphere are impossible to define [27], and fitness is not maximized by a single population, let alone an ecosystem. Geophysiological Gaia compares the biosphere with an organism with self-regulating physiology, thus essentially equating life (O) and environment (E). This position is obviously erroneous [27,33].

Homoeostatic Gaia, by contrast, states that feedback interactions between life and its environment are generally stabilizing, and maintain planetary conditions within a range habitable for life over geological time (Figure 1). Of the nontrivial variants of Gaia, this is the least implausible, and is potentially amenable to testing. The stabilizing feedbacks could have arisen by chance in the particular case of the Earth (Lucky Gaia [8]), in which case Earth inhabits the tail of the probability distribution of possible planetary environments (Figure 1). Alternatively, inherent properties of the life–environment coevolutionary process might tend to give rise to stable biospheres (Probable Gaia [9]) – here, the Earth is an 'average' planet (Figure 1). In either case, the unselected byproducts of organismal traits selected for other reasons will determine the resulting life–environment interaction network [23,24]. In Probable Gaia, the nature of the byproducts and the network topology might also be influenced by adaptations for local stability of populations, mutualisms, communities or ecosystems (Figure 1). However, genuine selection for stability of global environmental variables is impossible, owing to the absence of a varying population of biospheres [3]. We therefore define our working hypothesis as a version of Probable Gaia in which adaptation for local stability and/or emergent properties of the interaction network cause global stability to tend to arise; the null hypothesis is Lucky Gaia.

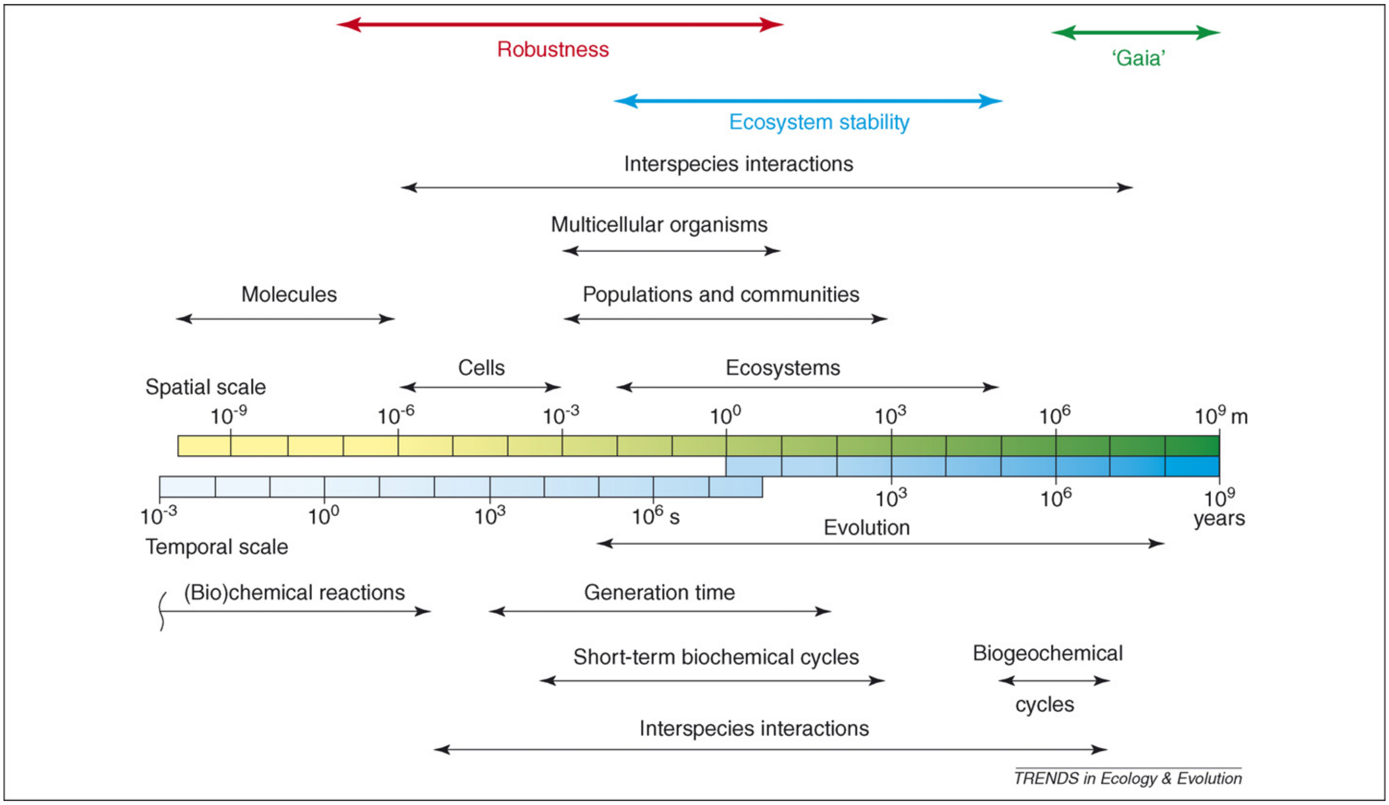

Figure 2. Illustration of the range of spatial and temporal scaling necessary to extrapolate from molecular and cellular processes to the biosphere (Gaian) scale. Space and time are represented on logarithmic scales, with time shown in seconds over short time scales, and years over long time scales for convenience. Ranges shown are designed to cover the possible extremes: for example, the spatial scale of interspecies interactions ranges from μm-scale chemical effects between syntrophic bacteria to planetary-scale interactions through global environmental variables. Approximate ranges covered by the concepts of robustness [18], ecosystem stability [10] and 'Gaia' are indicated at the top of the diagram. The spatiotemporal overlap between different processes suggests ways in which local-scale ecological and evolutionary effects might influence the coevolution of life and environment at Gaian scales of space and time.

adaptations [22]. We can add a third class, adaptive feedback, in which environmental feedback effects are selected for at the individual level (but might also control the environment at the system level). Such traits are equivalent to extended phenotypes [3]. System-level control could conceivably evolve when the system occupies a semi-isolated local environment [7], or when the organisms expressing the selected trait benefit more from it than do the wider biota [9]. Unlike feedbacks from byproducts, true adaptive feedbacks will be susceptible to cheating if they are costly. However, in most real-world examples, the system-level effect is distinct from the effect selected for (Table 1), and the system-level effects should be considered as byproducts of selection [23].

For life–environment feedbacks to control the planetary environment, a global-scale biosphere must arise. This, in turn, requires the recycling of nutrients between different biochemical guilds [24] through the use of waste materials and decaying organic matter. The efficiency of this process is measured as the cycling ratio:

$$\text{Cycling ratio} = \frac{\text{Consumption of element by autotrophs per unit time}}{\text{Flux of element into biosphere per unit time}}$$

Cycling ratios of 10^2–10^3 are observed for many biologically-important elements, indicating that recycling on Earth has evolved to be highly efficient. Nutrient cycling is an unselected feedback effect because the recycled nutrients are byproducts of waste removal or death [24]. A global biosphere requires a large energy source: because pre-existing chemical gradients are unlikely to suffice, the solar energy flux must be tapped by some form of photosynthesis [8,25] for a homoeostatic biosphere to be possible.

The final requirement for Homoeostatic Gaia is less obvious but nevertheless important. Although multicellular organisms (in particular land plants [26]) currently have major effects on the environment of the Earth, for ~85% of its existence, the biosphere has consisted solely of microorganisms, which dominate biogeochemical cycles [27]. This suggests that evolving multicellularity was a difficult, contingency-driven process, owing to the nature of rearrangements in cell organization required [16] and/or to the need to attain a sufficient atmospheric concentration of molecular oxygen [27]. By contrast, the full complement of microbial metabolic diversity probably evolved relatively rapidly [28]. Therefore, we must assume that although life should be inevitable, given appropriate starting conditions, complex multicellularity is not; consequently, a general Homoeostatic Gaia theory must be possible in a biosphere composed entirely of microorganisms. This has important implications for testing such a theory, as described later.

Mechanisms of homoeostasis

Having established the nature of the homeostasis predicted by Gaia, can we envisage mechanisms by which this might occur? One mechanism is a simple feedback on

Box 2. Modelling Gaia: Daisyworld and Guild

Temperature stabilization in Daisyworld

Daisyworld, as originally devised by Watson and Lovelock [30] and subsequently modified and enhanced extensively [55], describes a planet populated by two non-evolving daisy species, black and white, which warm or cool, respectively, their environment owing to their differing albedos. These daisy populations fluctuate and compete to stabilize temperature within their habitable range over a wide range of solar flux through the feedback of temperature on daisy growth [30]. Although the original Daisyworld does not enable the daisies to adapt their preferred growth temperature to existing conditions, such adaptation can still be consistent with regulation, despite some contrary claims [55]. The main weakness of most Daisyworld models is that the only means by which the daisies can affect the global environment (through temperature) is also the sole basis for selection between competing daisy types at the local level [50]. In the real world, some traits with either neutral or detrimental effects on the global environment will be locally beneficial. Therefore, the environmental stability seen in Daisyworld depends on the way in which the model is set up.

Emergent nutrient recycling in Guild

Guild is a second model specifically aimed at testing Gaia theory using an individual-based approach [31]. An initial population of microorganisms is given a suite of environmental chemicals at specified input fluxes, and evolves to metabolize different members of this chemical suite, excreting others as byproducts. All organisms share preferred environmental growth conditions that are unrelated to their preferred metabolic substrate. After several hundred generations, codependency cycles emerge: the waste product of one species becomes the foodstuff of another, and the total biomass expands dramatically [31]. Stable levels of the different chemicals matching the predefined preferences of the organisms are attained, exhibiting resistance or resilience to perturbations in the input fluxes. These properties match the resistance, resilience and recycling properties proposed for Gaia [11]. The main weakness of Guild, as in Daisyworld, is that there is a correspondence between local fitness advantage and global regulation. Separate, locally advantageous traits with coincidental (beneficial or disruptive) effects on the global environment evolve. In addition, the environmental optima of the organisms cannot evolve; such evolving preferences might compromise environmental stability [31].

growth of an environment-altering species. If organism O, which grows as a parabolic function *f* of an environmental parameter E, alters E as a linear function *g* of the abundance of O, the coupled O–E system will stabilize at an intersection point of the functions *f* and *g* in O–E space [11]. However, this system is liable to collapse owing to external perturbations which push its state outside the stable region defined by the intersection points. Greater robustness is achieved by the system dubbed 'rein control' [29], in which two different feedbacks drive a single environmental variable in opposite directions. This phenomenon is typified by the classic 'Gaian' model Daisyworld (Box 2), in which black and white daisies force local (and global) temperature in opposite directions through their differing albedos, which in turn affects how well they grow. Nonetheless, Daisyworld still collapses when external forcing (increasing solar flux) push the system outside its stable range [30]. Daisyworld is also an unrealistic model, principally because its organisms can only enhance their fitness by traits which exert the same effect at local and global levels (Box 2).

The interspecies nutrient recycling networks which exist within the biosphere give the potential for multiple feedbacks on growth at different points in the cycle which together can function to stabilize nutrient levels. Such stabilization is seen in the Guild model (Box 2), which is an individual-based model of microorganisms that can evolve to use chemicals derived from external fluxes or from the waste products and decay of other 'species'. Nutrient recycling emerges automatically in runs of this model, and makes nutrient levels resistant and resilient to external perturbation [31]. However, neither natural nutrient recycling systems nor those simulated in Guild can control non-chemical environmental variables such as temperature, which are important in the Earth system.

Another possibility is that the aggregation of many subsystems which are each stable at the local level will give a stable global system [5]. As noted earlier, genuine adaptive feedbacks might be possible within self-contained local systems (Figure 1). However, the spatial and temporal differences between the stability of such local systems and the biosphere are large (Figure 2), and it is by no means clear that the system formed by a network of stable subsystems will itself be stable [20]. We discuss ways in which local stability might emerge later.

We must also consider the possibility that, even without selection for local stability, properties of the life–environment interaction network that constitutes a biosphere, such as node connectivity and feedback, make it robust to perturbation [32] (Figure 1). Such properties might be describable for ecosystems but harder to assess in the global life–environment network.

Conventional ecology and evolution versus Gaia

Several developing areas of evolutionary and ecological theory and experiment study issues relevant to Homoeostatic Gaia, such as life–environment feedback, interspecies nutrient transfer and local stability. Here, we briefly review these overlaps and assess how they relate to the theoretical literature on Gaia.

Niche construction

Niche construction describes how organisms that use energy and resources, choose habitats, construct artefacts and excrete wastes and detritus modify their environments, in turn affecting the selection pressures that they and/or other species experience [33]. Its proponents prefer an inclusive definition of niche construction that encompasses both feedback from adaptive traits and feedback from unselected byproducts [22]. Niche-constructing processes generate feedbacks which alter natural selection on the niche constructers themselves and/or organisms sharing the same environment, which, for global environmental resources, means most of the biosphere [5]. Models of niche construction demonstrate that environmental feedback can overcome external sources of selection, favouring beneficial environmental modification over unregulated resource consumption [34]. However, such models involve strong feedbacks with the local environment rather than the diffuse global feedback necessitated by Gaia. Niche construction is related to the ecological concept of ecosystem engineering [35]. Engineer species which modify the physical components of their ecosystems are thought to have a generally positive effect on ecosystem stability through feedback, although such feedback will be weak and slow acting if it functions indirectly through other abiotic or biotic components [35].

Social evolution

Social evolution theory demonstrates how shared self-interest can lead to cooperation (e.g. nutrient cycling) between individuals. For instance, two microorganisms, each feeding on waste products of the other, initially exhibit codependency, which can evolve into true cooperation as each increases its waste production to benefit itself indirectly through the other partner [36]. This 'byproduct reciprocity' [37] is equivalent to an unselected feedback process evolving into an adaptive feedback process, and is termed 'syntrophy' by microbial ecologists. A classic example is the interaction between fermenting and methanogenic bacteria, in which waste hydrogen produced by the fermenter is used for methanogenesis, and consumption of the hydrogen by the methanogen makes the fermentation energetically favourable [38]. Although byproduct reciprocity suggests how environmentally stabilizing nutrient cycles could be adaptive, it is susceptible to cheating [36] and has less selective power in multipartner cycles owing to the ineffectiveness of strategies such as punishment [39].

Ecosystem stability

As discussed earlier, one mechanism by which global stability might arise is through interactions between stable communities or ecosystems. There has been much theoretical and experimental work on ecosystem stability, in particular its correlation with species diversity. The latest work suggests that stability in diverse ecosystems is determined by the nonrandom nature of the evolved species interaction network (Box 3). Here, we briefly consider stability in macroscopic and microscopic ecosystems.

Intuitive reasoning that diversity in food webs leads to greater resistance and resilience to environmental perturbation (the insurance hypothesis) is supported by experiments on grasslands placed under drought stress [40]. Plant diversity in experimental prairie plots correlates positively with stability of above-ground plant productivity but not with stability of individual species [41]. Stability results from a combination of statistical averaging of the performance of many individual species (the portfolio effect) and the greater productivity of diverse systems maximizing resource utilization (the overyielding effect). It is important to note that Homoeostatic Gaia requires only the stability of overall ecosystem function, as observed in these experiments, rather than stability of species composition.

Many microbial microcosm ecosystems can maintain a stable function over significant periods of time but significant changes in species composition might underlie this stability. For instance, a methanogenic bioreactor, fed with glucose and maintaining constant pH and methane production over a 600-day period, exhibited sequential replacements and cyclic patterns of substitution within the bacterial community [42]. Replicate bioreactors subjected to perturbation by a glucose pulse showed greater resilience when they processed the substrate through a network of parallel pathways than through serial processing [43,44]. Because parallel processing requires a greater diversity of metabolic activities, these studies suggest how diversity leads to stability at the basic level of nutrient cycling. However, diversity in microbial systems does not necessarily enhance resilience; community structure, equivalent to the interspecies metabolic pathways, might be a better indicator of stability [45]. Therefore, the microbial communities essential to any conceivable Gaia seem to develop stability as a consequence of their distributed metabolic networks, although the theoretical basis for this is poorly understood.

Box 3. Diversity and ecosystem stability

There has been much debate over the relationship between species diversity and ecosystem stability. For diversity itself to arise, ecological opportunity and competitive tradeoffs are required [68]. Ecological opportunity can be provided by the activities of other organisms [69], or by spatial structure in the abiotic environment [57]. Tradeoffs arise when a generalist progenitor evolves better to exploit a specialist niche, concomitantly trading this off against its generalist fitness. Once diversity has been generated, it is generally maintained by negative frequency-dependent selection [68].

Increased stability of more complex ecosystems, through redundancy of interactions and the likely presence of species well suited to altered conditions, seems reasonable and is supported by experiment [63]. However, traditional theoretical approaches suggest that the stability of complex systems will be difficult to achieve [70]. In these models, based on the solution of Lotka-Volterra-type population equations at equilibrium, stability requires particular properties of the community (interspecies interaction) matrix, the probability of which tends rapidly to zero for communities of more than ten organisms [71]. Natural selection [70], possibly acting at intermediate stages in community assembly [72], might be a possible mechanism for tuning these matrix parameters. However, newer models suggest a reconciliation of complexity with stability.

The importance of weak interactions

A breakthrough in the reconciliation of theory with ecological field observations came from the novel modelling strategies of McCann *et al.* [73]. Their model was innovative in enabling the system components to be in dynamic flux rather than at equilibrium, modelling the saturation of growth and consumption at high resource levels, using a range of empirically derived interspecies interaction strengths, and constructing their food webs based on observed patterns rather than randomly, as in the work of May [70]. All of these assumptions are more realistic than those of the original models. The McCann model showed that weak interactions within the food web invariably function to dampen the oscillations caused by strongly interacting resource-consumer dynamics, thereby enhancing the stability of the whole system in response to diversity [73]. More recent work based on modelling of real food webs suggests that the web structure, together with the effects of the biomass pyramid, might be the most important factors in the stabilizing effect of weak interactions [74]. The biomass pyramid causes the sum of total interaction strengths in longer loops to be lower than those in shorter loops, which stabilizes the overall system compared with a random interaction web.

Ecosystem goal functions

An important strand of theoretical ecology concerns whether ecosystems develop in ways that are predictable and stable to perturbation. Theorists have proposed a variety of goal functions towards which ecosystems evolve, such as maximization of total energy flow and nutrient cycling [46], and these functions are related through the feedback network organization of the system [47]. Modelling of ecosystem succession using these principles suggests that it proceeds through stages of growth-to-storage (increasing energy capture), growth-to-throughflow (increasing energy throughput) and growth-to-organization (increasing energy and matter cycling), with some properties maximized throughout [48,49]. These goal functions relate to 'Gaian' properties such as nutrient cycling [24], and maximal exploitation of nutrients and energy [50,51]. Maximization of a function implies local stability, although alternative stable global goals might exist [52]. Moreover, the theory of goal functions has rarely been tested by experiment (e.g. in microcosms).

The importance of spatial structure

Theoretical, modelling and experimental studies all demonstrate the importance of spatial separation and heterogeneity in determining community-level properties. By increasing the cohesiveness of local communities, spatial separation increases the effectiveness of selection at the community level [53]. Models demonstrate that spatial organization can emerge by itself in multispecies systems, and that these systems are more stable than those that lack a spatial dimension owing to the global persistence of communities, despite local extinction [53]. Therefore, destabilizing influences are weeded out at the local level before they can influence the whole system. A spatial, individual-based model of niche construction [54] shows that localized niche construction by two interacting species leads to environmental homeostasis in a manner analogous to rein control in spatially explicit Daisyworlds [55]. Simulation of cooperation versus competition strategies likewise demonstrates that stable interspecific mutualisms emerge more readily and are more stable when the model is run on a two-dimensional grid [56].

Spatial heterogeneity is inevitably provided by any natural environment [25], and in laboratory microcosm experiments facilitates the diversification of microorganisms [57]. Recent work with similar microcosms [58] shows that a structured environment enables the evolution of cooperative interspecies interactions which increase community productivity. Therefore, spatial organization should be regarded as an essential part of explaining cooperative or system-level behaviour in multispecies systems; both cooperation and competition emerge as a result of the juxtaposition of different species combinations [59]. However, it is crucial to realize that in such situations, selection is acting on the local population, and that the global properties that emerge are a side effect of this selection.

Utility and predictions of Homoeostatic Gaia

If many issues raised by the Gaia hypothesis are also considered by conventional evolutionary and ecological science, do we need the hypothesis at all? Importantly, the hypothesis stimulates us to draw together these diverse lines of theory and experiment, appreciate their relatedness and ask whether they can be extended to the spatiotemporal scale of a closed system, the biosphere. Given current concerns about anthropogenic perturbation of the biosphere, all relevant scientific disciplines should contribute to predicting its response. These benefits would apply even if the Gaia hypothesis turns out to be unfalsifiable but that situation would be intellectually unsatisfying.

What, then, are the novel predictions of Gaia? The overall prediction, that most real global biotic systems tend towards long-term stability, obviously cannot be tested. There are, however, some useful secondary predictions:

(i) A coupled life–environment system shows better resistance and resilience than would the abiotic equivalent, and recovers faster from perturbation (has greater elasticity [10]).
(ii) Small-scale biotic systems and those lacking efficient nutrient recycling and photosynthesis are less resistant and resilient than those of large scale and possessing these attributes.
(iii) Life–environment feedbacks should tend to stabilize the system on geological time scales.
(iv) As life and environment coevolve, the biosphere will tend towards greater stability and remain within tighter environmental bounds [11].
(v) The stability of the biosphere should not depend on the presence of particular species or ecosystems, which can only have arisen by chance, and should be possible in a biosphere composed solely of microorganisms.

Testing Homoeostatic Gaia

It is, of course, impossible to perform replicated experiments on a global scale. Therefore, comparison of models with the history of the Earth and its biota is the only option for testing certain predictions of Gaia [11]. Full 'Earth system' models with responsive (but not adaptive) biospheres now exist [60] but are highly simplistic and represent only a handful of plant species. To run an Earth system model on even the shortest time scale relevant to Gaia would require vast increases in computing power and computational efficiency, in addition to a better understanding of how to approximate complex ecosystems in a compact way. Such models, if feasible, could be used to test predictions (i) and (iii) above but would necessarily be restricted to the current (chance) biota of the Earth.

At the other end of the scale are models which describe (simplified) individual organisms, and allow system-level properties to emerge. A recent example is Flask [61], which models microbial evolution in a spatially uniform microcosm. Unlike Guild (Box 2), this model also includes non-nutrient abiotic factors which can be affected by the microorganisms present; the nature of life–environment interactions is not predefined. Flask simulations robustly generate emergent nutrient recycling and stable levels of non-nutrient abiotic factors, which can be disrupted by constraints on adaptation or by 'rebel' organisms that force the environment outside the preferred conditions of the majority for individual gain [61]. This suggests that stability arises by more than just chance but can be disrupted by evolutionary events. Flask-type models could be used to test predictions (ii) (by correlating stability with the level of recycling, abundance of life and use of a single dominant nutrient flux), (iv) and (v).

We have seen how large-scale field experiments can provide information about the stability of sub-Gaian systems on a decadal time scale [41]. However, the numbers of replicates and perturbations applicable to such experiments are limited by their size and duration. Experiments with multicellular organisms are not necessary to test Gaia if the constraint that biospheric stability must be possible with an entirely microbial biosphere is accepted. Microbial microcosms offer great potential for studying ecology and evolution [62]: they evolve rapidly, contain significant diversity in a small volume and can be replicated under different conditions on a short time scale. Modern metagenomic techniques enable correlation of species composition with system-level properties in complex ecosystems [63], and, directed by appropriate theory [64], should enable useful experimental tests of model-based predictions. Future studies should concentrate on self-contained microbial ecosystems and aim to determine their resistance and resilience to imposed environmental changes, the reproducibility of the observed responses, and whether they occur by rearrangements of the interacting species network, through changes in species composition or through adaptation of individual species. Microcosms driven primarily by light energy [65] are the closest analogues to the real biosphere possible in the laboratory. It is impossible to rerun 4 Gyr of evolution in a laboratory experiment but if we accept that all thermodynamically favourable forms of metabolism will arise readily in nature [66] and are present in a microcosm, the results from such experiments will be a useful representation of the biosphere. Microbial microcosms could therefore test predictions (ii), (iv) and (v), in useful comparison with Flask-type simulations. The main weakness of such microcosms is that they do not represent most physical aspects of the Earth system, thus precluding tests of predictions (i) and (iii).

Complementary experiments and simulations therefore provide the best strategy for testing Gaia. The main stumbling block is obtaining convincing proof that the results can be extrapolated to the entire biosphere [19,20] (Figure 2). However, whether science can overcome this obstacle or not, the work necessary to get us to that point should provide fascinating insights into ecology, evolution and the Earth system.

Acknowledgements

The authors acknowledge many helpful discussions with Rosalind Allen, Richard Boyle, John Grace, Kevin Laland, Alan McKane, John Odling-Smee, Stu West, Hywel Williams and Jamie Wood. We are also grateful to Tim Lenton, Dave Wilkinson and two other anonymous referees for helping to improve and clarify earlier versions of this manuscript. A.F. was supported by the School of Geosciences, University of Edinburgh, and the Darwin Trust of Edinburgh, and thanks Simon Allen for an introduction to Gaia theory. N.H.B. was supported by the Royal Society of London and the Natural Environment Research Council (UK).

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