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## Thinking of Biology

# Gaia and evolutionary biology

**T**he Gaia concept has achieved some prominence in the discourse of earth-system science. Although the notion that the biota, atmosphere, oceans, and soils make up a single self-regulating system of global scale is still controversial, articles by the originators of the idea are regularly cited by scientists exploring the role of life in creating the climate and chemistry of Earth.

Independent British scientist James Lovelock and American biologist Lynn Margulis (now at the University of Massachusetts, Amherst) gave birth to the Gaia hypothesis 18 years ago (Lovelock and Margulis 1974, Margulis and Lovelock 1974). Since then, a second generation of researchers, ourselves among them, has been inspired to look for new connections between life and the global environment: Do sulfur compounds released by marine plankton promote cloudiness and thereby cool the earth (Charlson et al. 1987)? Did the proliferation of carbonate-shelled foraminifera and coccolithophorids during the last several hundred million years prompt an increase in CO<sub>2</sub> emissions from subduction zones (Volk 1989)? Might the self-catalyzed expansions and retractions of bogs and peatlands account, in part, for the ebb and flow of ice ages (Klinger 1991)? Could Precambrian mats of bacteria on an otherwise barren land surface have cooled the earth at least 35°C by enhancing rock weathering during the eons before plants evolved (Schwartzman and Volk 1989)? Lovelock (1990, 1991) summarizes the concepts in earth-system science triggered by the Gaia idea.

What impact, however, has Gaia had in the purely biological realm?

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by **Connie Barlow**  
and **Tyler Volk**

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### Although many biologists have been hostile to the Gaia concept, the debate may lead to fruitful inquiry

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How do biologists respond to the claim that the biosphere is a self-regulating system, that it displays a coherence—indeed, an identity—deserving of recognition in the hierarchy of life?

This article examines the reasons why many biologists, in contrast to earth-system scientists, have been cool (or downright hostile) to the Gaia concept as initially formulated by Lovelock and Margulis. Subsequent reworkings of the idea by the originators and by other scientists are also regarded, especially by evolutionary biologists, as seriously flawed, but the debate itself may be leading to fruitful areas of inquiry. Although many writings in evolutionary biology could be brought to bear on the Gaia debate, only those works that expressly examine—pro or con—the biosphere in an evolutionary framework are considered here.

### A taxonomy of Gaia concepts

James W. Kirchner, a philosopher and physicist in the Energy and Resources Group at the University of California, Berkeley, compiled the first “taxonomy of Gaia hypotheses” (Kirchner 1989, 1991). Our own review of the literature yields a list with a half dozen distinct versions of Gaia. All of them present a global-scale system that exhibits one key feature of living systems: self-regulation.

In each version, Gaia is framed as a composite system of the biota, oceans,

atmosphere, and soils that has not merely changed conditions on Earth but has outright controlled the chemical and thermal regime to keep the planet livable or more livable than it otherwise would have been. In Lovelock’s most poetic phrasing, “The atmosphere is not merely a biological product, but more probably a biological construction: not living, but like a cat’s fur, a bird’s feathers, or the paper of a wasp’s nest, an extension of a living system designed to maintain a chosen environment” (Lovelock 1979). Where the interpretations differ is in the degree of global-scale regulation thought to be indicated in the geologic record and in earth processes today.

The degree of self-regulation posited in the original formulation of Gaia (Lovelock and Margulis 1974, Margulis and Lovelock 1974) was complete (homeostasis). Not only did the biota create an atmosphere with a composition, acidity, redox potential, and temperature history differing greatly from that of other terrestrial planets (Mars and Venus), it has actively maintained these conditions with a stability akin to the self-regulating physiologies of living organisms.

The architects of Gaia pointed to astrophysical evidence that the sun has increased in luminosity 25% or more since sediments with the now-oldest evidence of fossilized life were deposited in an aqueous environment. Yet, if no modulating changes had been made in the atmosphere along the way, that aqueous environment should have given way to a world today in which only thermophilic bacteria could survive. On the other hand, the same atmosphere that produces a global average temperature today of 15°C would translate into a frozen planet back at the origin of life.

Researchers working on this “faint

young sun" problem (Newman and Rood 1977) agree that the atmosphere must in fact have changed and that a decrease in greenhouse gases through time offset the sun's increasing strength. But what caused this fortuitous shift in atmospheric composition? Are living organisms simply lucky that abiotic and biotic processes happened to work out just so? Or did the planet in some way self-regulate? According to Lovelock and Margulis, evidence of long-term thermal homeostasis grounds one of the most compelling arguments in favor of Gaia.

Critics of Gaia, however, culled from the geological record events that in other ways seemed to belie the notion of global homeostasis. Notably, if Gaia exists, why did the atmosphere become aerobic after many hundreds of millions of years in which bacterial life had prospered in an oxygen-free atmosphere (Schneider 1986)?

In 1990, Lovelock offered a revision to accommodate upsets in homeostasis occasionally evidenced in geologic history. Gaia was no longer purely homeostatic, but "punctuated homeostatic." Upsets do happen; Gaia is not all-powerful. But after disturbances, the planet once again settles into relative stability, albeit sometimes at an altogether new chemical or thermal state.

At about the same time, Margulis set forth her own revision of Gaian self-regulation. In her view, Gaia, "like the physiology of an embryo, is more homeorrhetic than fixed-from-the-outside setpoints" (Margulis 1990). This repackaging of Gaia within a more developmental context would make the accumulation of global oxygen no more inimical to the continuity of a global system than does metamorphosis into a butterfly signify the demise of the organism that was once a caterpillar. In his recent book, Lovelock (1991) equates homeorrhesis with punctuated homeostasis.

We have proffered a version of Gaia that moves even further away from the initial homeostatic formulation (Barlow and Volk 1990; presaged by Botkin 1982). For us, the merit of the Gaia concept should not hang on geologic evidence of protracted stability or lasting directional change in global chemistry and climate. The simple fact that life has persisted for more than three billion years in itself

demands some sort of causal explanation, be it Gaia or an alternative thesis.

Consider the long-term stress of a 25% increase in the luminosity of the sun during the tenure of life and the episodic, but dramatic, stresses of colossal extraterrestrial impacts (Rampino 1991) that may make rain as toxic as battery acid and wreak havoc with global temperatures. Consider, too, the need for a global system—unlike any organism or even ecosystem—to recycle completely all its essential materials. At today's scale of biological activity, for example, the entire volume of carbon in the atmosphere is removed and replenished by a combination of biotic and abiotic processes in approximately a decade. All in all, the persistence of life in geologic time seems to us sufficiently provocative to invite a search for underlying processes.

Vilmos Csányi, an ethologist at the University of Budapest, has added a twist to our reworking of Gaia.<sup>1</sup> Csányi notes that whereas life in one form or another has indeed persisted, biospheric regulation—and therefore Gaia—might be an emergent property that comes and goes. Internally triggered imbalances (e.g., the switch to an oxygen-rich atmosphere when photosynthetic bacteria discovered a way to extract otherwise-scarce hydrogen from water) or externally generated catastrophes (e.g., the meteor impact that is thought to have taken out the dinosaurs) might destroy global processes of self-regulation and stability. It is only when material cycles re-emerge and climate has once again stabilized that this intermittent form of Gaia may be deemed to exist.

Finally, rounding out the taxonomy to include the weakest possible version of Gaia, we note that the word *Gaia* might be dispensed with entirely, in favor of such relational terms as *more gaian* or *less gaian*. Eras of relative stability in which the biota clearly played a role would be more gaian, whereas unstable episodes in Earth history would be less gaian. The terminology might be handy; more appealingly, it would be free of presumption that an entity Gaia exists.

A key ontological question thus

emerges from an effort to construct a taxonomy of Gaia concepts: Does Gaia merit status as an individual? Or should the global earth system be treated as the aggregate of distinct living and nonliving systems that happen to profoundly affect one another?

Evolutionary biologists and philosophers of science, in debating whether species are bona fide individuals, use a definition of individual that also accords with common sense. An individual is "a spatiotemporally localized cohesive and continuous entity" (Hull 1992). Is Gaia an individual in this sense? Might the debate about species individuality be revisited in a new context to clean up the ontological confusions about Gaia?

David Hull, a philosopher of science at Northwestern University, frames the issue this way: "How much of Gaia's individuality is due merely to isolation and how much to internal interdependence?"<sup>2</sup> In other words, does there appear to be something interesting at the global scale simply because the earth is constrained by the happenstance of an empty stretch of space surrounding it? Or is there something cohesive about the cycling of materials and the transformation of energy on the earth's surface that suggests interdependencies among the biota, atmosphere, oceans, and soils reminiscent of the interdependencies found among the tissues and organs of a living organism, among the cells that constitute organs, and among the organelles that make up a cell?

By calling for an examination of Gaia's alleged internal interdependence, Hull is pointing to the need to move beyond debates about evidence for and degree of global self-regulation. Scientists also need to devote attention to matters of process. If biospheric self-regulation (to a greater or lesser extent) is real or possibly real, how does it come about? Herein lies the problem that has made the Gaia concept, thus far, especially unattractive to evolutionary biologists.

### The problem of the population of one

The key biological objection to the Gaia concept is built from two parts.

<sup>1</sup>V. Csányi, 1991, personal communication. University of Budapest, Budapest, Hungary.

<sup>2</sup>D. Hull, 1991, personal communication. Northwestern University, Evanston, IL.

First, there is an awareness that everything known to be self-regulating in the universe is either alive or, like a central heating system with a thermostat, built by something that is alive, (Wright 1991). Indeed, self-regulation implies a self.

Self-regulation is not, therefore, a label to be used lightly. Earth, for example, remains in a fairly uniform orbit around the sun, but it does so for reasons explained by physics; Earth is not tweaking its movements to keep on course. Thus, the contention of Gaia proponents that the global system as a whole is doing precisely this sort of tweaking to keep its climate and chemistry stable (or livable), albeit unconsciously, infers that the surface of Earth comprises a living system.

By attributing self-regulation to the biosphere, Gaia proponents have made the biosphere an individual within the hierarchy of life, whether or not they affix the word *living* to their definitions. Recognizing this problem, Lovelock (1991) suggested the word *quasi-living* as a category "for Gaia and for ecosystems, beehives, and other systems that contain organisms and exhibit self-regulation" (p. 31).

Second, every living thing here on Earth (and, we suspect, anywhere else) owes its existence, at least in part, to a historic process of variation and natural selection. All manner of startling complexities, as well as powers of self-regulation, have arisen in this way. According to this logic, if a self-regulating system of global scale has come into being, it must owe its existence to a historic process of variation and selection. Natural selection, however, can only take place within a population of living things. And there is only one biosphere.

For these two reasons, Gaia has met with a chilly reception within evolutionary biology. "How does a species of one evolve? There's nothing for natural selection to select among," protests W. Ford Doolittle, a molecular biologist at Dalhousie University, in his critique of Gaia (Doolittle 1981).

As a lone system, the putative Gaia cannot possibly evolve by variation and natural selection the way organisms do. Gaia has no ancestors that might have given birth to a variety of kin, so that those with the best mutations for coping with an increasingly

luminous sun might thrive, while those with detrimental mutations would fall. And there is surely no way for competition to mean anything at a gaian scale (at least at this time), even if planets elsewhere in the galaxy do support life. Fundamentally, a lineage represented by a lone biosphere cannot afford to make lethal mistakes.

Mutation and selection are, of course, proceeding apace at lower levels in the hierarchy of life. But natural selection at the organismic, population, and perhaps even species levels cannot in a darwinian way account for global coherence. Consider: at some key point in evolutionary history, bacteria must have joined to form the first complex cell with organelles (Margulis 1981). But this earth-shaking event would have petered out through accident or mutational misfortune had the initial complex cell not gone on to reproduce and bring about a viable population that could withstand culling of the unlucky and the unfit.

Similarly, although even ardent critics of Gaia might grant that something interesting, something coherent, could from time to time emerge at the global scale, same-level selection would be impossible thereafter. Thus, darwinian processes could not account for the further refinement and persistence of a nascent apparatus for biospheric self-regulation.

Evolutionary biology, therefore, cannot now explain the genesis of a global-scale Gaia that has no ancestors and is starkly alone in the emptiness of space. W. Ford Doolittle (1981, 1991), Richard Dawkins (1982), Paul Ehrlich (1991), and David S. Wilson and Elliott Sober (1989) all dismiss Gaia for this very reason. In the words of Wilson and Sober, "Natural selection at any level requires a population of units, and there is only one earth."

### Strengths and weaknesses of Daisyworld

Lovelock and collaborator Andrew Watson (an oceanographer at England's Plymouth Marine Laboratory) responded to criticism from evolutionary biologists by developing a numerical model that they called Daisyworld (Lovelock 1988, Watson and Lovelock 1983). The model pur-

ports to demonstrate how standard darwinian selection of black and white daisies on an imaginary planet could regulate global temperature despite the increasing luminosity of its star.

In the early eons when the star is dim, the black, light-absorbing daisies are the first to gain a foothold on the lifeless planet. Besides warming themselves, their collective absorption of light warms the whole planet, enabling more daisies to thrive. In later eons, when the star's luminosity has strengthened, white daisies prevail, and their reflective properties cool the planet. Thus, natural selection at the organismic level accounts for Daisyworld's thermal self-regulation.

Although the daisies' planet may be imaginary, the star is not; Watson and Lovelock employed a function of the sun's 25% increase in luminosity since the origin of life. The problem of a dim early sun is in fact the puzzle that impelled some earth-system scientists to respond favorably to the Gaia concept and others (Walker et al. 1981) to take it seriously enough to develop abiotic models to explain Earth's modulation of solar influx.

Lovelock and Watson have succeeded in making their Daisyworld model self-regulating. The model works because the local heating or cooling effect of the color of a single black or white daisy acts in exactly the same direction and on the same time scale at the planetary level. A continent of white daisies cools the planet just as a single white daisy cools itself by reflecting sunlight.

But what about characteristics that may play out globally in a different way from the local costs and benefits experienced by the organism generating the causal agent? Do Daisyworld dynamics apply to the real-world climate?

Lovelock participated in a team effort (Charlson et al. 1987) to determine whether biotic production of dimethyl sulfide (DMS) might affect climate. Biologists know that DMS is produced by plankton to mediate salinity differences between the organism and its seawater environment (Caldeira 1989). Charlson and colleagues discovered that, when DMS diffuses into the atmosphere, it oxidizes to sulfate aerosols, which serve as condensation nuclei that enhance

the reflectivity of marine clouds. Still unresolved is whether the resultant climatic cooling exerts a negative or positive feedback on the growth of DMS-producing plankton (Watson 1991).

Discerning whether an organic process modulates perturbations or even regulates Earth's chemistry or climate becomes especially difficult when the benefit derived by the organism itself (in the case of plankton, osmotic control) is qualitatively different from the aggregate effect on the biosphere (global temperature). This distinction between Daisyworld and DMS feedback is crucial. Daisyworld fulfills, in a way, Doolittle's (1991) demand for evidence of "proto-Gaias in which those with more self-control left progeny while others perished." Because the temperature effect of color is the same for the daisy as it is for the planet, each daisy in combination with its thin envelope of locally heated air can be viewed as a miniature of the planet itself. But in the dual-effect realm of DMS, there is no semblance of proto-Gaias.

Daisyworld has not, therefore, diminished the criticism of evolutionary biologists. Moreover, Daisyworld is not, strictly speaking, an evolutionary model—unless one regards evolution as nothing more than changes in the frequencies of alleles already present in a population. The source of essential variation is unaccounted for; black and white daisies are presumed to exist, and natural selection simply takes over from there.

Thus, although Daisyworld shows how organisms acting strictly in their own self-interest could exert a modulating, even a regulating, force on the planet, the model does not speak to the processes by which essential evolutionary innovations would be expected to arise. Lineages, more often than not, do go extinct; why should the biosphere be any different? This inadequacy of the Daisyworld model might, however, be viewed as an opportunity. Daisyworld does not now adequately attend to the concerns of many evolutionary biologists, but might it be reworked to do so?

Overall then, Daisyworld in its present form does not satisfactorily explain a geologic record that suggests atmospheric modulation of an intensifying sun. It does not explain

the step-by-step development of interlocking metabolisms through time that ensure recycling of materials vital to life. And it does not obviate the Gaia concept's biggest problem: the problem of the population of one.

### What are the underlying processes?

Daisyworld is Lovelock's attempt to explain the processes underlying biospheric self-regulation within a darwinian framework. He has chosen the label *geophysiological* to distinguish this kind of self-regulation at the planetary level (Lovelock 1989, 1991).

Geophysiology is a neologism coined by Lovelock for both the workings of Gaia and the transdisciplinary study of global processes. Transdisciplinary study may be a preferred way to study the earth, but geophysiology says nothing about the genesis of Gaia. In fact, the organismic analogy invites trouble because it seems to place Gaia squarely within the realm of biology, without first and fully satisfying the criticisms of evolutionary biologists.

Margulis builds her homeorhetic version of a self-regulating biosphere around the concept of autopoiesis (Margulis 1990). Citing Maturana and Varela (1980), Margulis contends that metabolism—self-construction and repair—is the essence of life, in contrast with views that deem replication to be central. Advocates of an autopoietic process description of Gaia are thus largely untroubled by the problem of the population of one. Autopoiesis also denies the dualism of organism and environment: "Life does not 'adapt' to a passive physico-chemical environment as most neodarwinians assume, instead life actively produces and modifies its surroundings" (Margulis 1990).

Gail Fleischaker (in press), a philosopher of biology at the Massachusetts Institute of Technology, also draws from the autopoiesis paradigm in portraying Gaia as "a global ecological individual." The biggest problem with current autopoietic descriptions of Gaia, as with Lovelock's geophysiological phrasing, is that although they may be a fine way to recognize a living system, these descriptions say little about the genesis

of that system. And it is to the question of genesis, recall, that Gaia critics address their harshest words.

But Margulis has not ignored the question of genesis. She has co-authored an article that suggests a means by which local processes could bring about global self-regulation (Brown et al. 1985). Pointing to the interconnected metabolisms within microbial mats that give rise to a substantial degree of matter cycling, Margulis and co-authors suggest that compartmentalization may be the key to biospheric coherence.

Local conditions and responses in billions of distinct microbial communities blanketing the planet would have summed to global effects in the eons before plants and animals evolved. "Growth potential of metabolically diverse populations most likely provides the basis for the responsiveness of the biota to changing environments," conclude Brown, Margulis, and co-authors. Obenhuber and Folsome (1984) assert that further laboratory research to probe the dynamics of microbial communities sealed in glass vessels could "offer insight into the nature of global ecology."

This microbial-partitioning version of Gaia appears to address the problem of the population of one, as each microbial community becomes a proto-Gaia (to use Doolittle's terminology). Its weakest point may be that it does not account for the evolution of diverse and interlocking metabolic pathways in the first place, which is the subject of the origin and diversification of Archean life.

Csányi, the originator of an intermittent version of biospheric self-regulation, believes his autogenetic theory of evolution could explain the genesis of Gaia (Csányi 1989, Csányi and Kampis 1985). Csányi criticizes autopoiesis precisely because it does not address the process of becoming; he casts both reproduction and metabolism in terms of replication. He views reproduction as spatial replication and metabolism as temporal replication. The former yields a new spatial entity, whereas the latter entails replacement through time of worn-out parts in the same spatial entity.

Unlike others who regard replication as the essence of life, Csányi believes that replication at lower levels can give rise to regulatory proper-

ties at the level of the biosphere. He sketches a process by which global self-regulation could emerge (Csányi 1989). His portrayal of evolution would seem to obviate the problem of the population of one, but, before it can do much for Gaia, his version of autogenesis will have to gain converts as a general theory of the evolution of new hierarchical levels.

Richard J. Bagley and J. Doyné Farmer of the Center for Nonlinear Studies, Los Alamos National Laboratory, use computer models to study autocatalytic, or self-generating, systems. Drawing on knowledge of the chemical cycles and dynamics at the core of research on the origins of life and prebiotic chemistry, they posit Gaia as a system with an autocatalytic metabolism (Bagley and Farmer 1992). "The relevant issues bearing on the question of whether or not autocatalytic metabolisms are alive are closely related to those for Gaia" (p. 133).

Bagley and Farmer assert that, like Gaia, an autocatalytic metabolism emerges spontaneously and evolves primarily through the richness of its own dynamics. Moreover, they specifically counter Dawkins' objections pertaining to the problem of the population of one. An autocatalytic metabolism, they respond, may emerge as "the sole inhabitant of its medium," later evolving spontaneously into another species of autocatalytic metabolism through internal competition and cooperation of constituent parts.

Similarly, Stanley Salthe, a biologist emeritus at the City University of New York, sidesteps the problem of the population of one by asserting that Gaia is a developing system (evincing predictable irreversible change), whose details are the product of lower-level evolution (accumulation of historical information). Taking the biosphere out of biology and placing it within the realm of nonequilibrium thermodynamics, Salthe (1990) views the genesis of Gaia—he willingly uses the term Gaia—as no more mysterious than the self-organization of any other thermodynamically dissipative structure.

To Salthe, therefore, the fundamental process questions for Gaia have already been answered. As to the "predictable irreversible change" inherent in a developing system, he predicts for the biosphere the same four "general

phenomenological rules" that he believes apply to all "developing thermodynamically open autonomous systems." Notably, he asserts that senescence is inevitable.

Rod Swenson of the Center for the Ecological Study of Perception, University of Connecticut, grounds his work in the same worldview of nonequilibrium thermodynamics as does Salthe. But Swenson (1989) goes beyond observing that thermodynamically dissipative structures tend to self-organize, absent same-level selection. He posits a final cause, which he calls "the law of maximum entropy production."

The second law of thermodynamics depicts a universe that is irreversibly increasing in entropy; Swenson asserts that the fastest way for the universe to maximize entropy is through the creation of life. For example, the global production of free oxygen by photosynthetic life over evolutionary time (although an internal reduction of entropy at the biospheric level) is achieved by way of a net increase in the amount of incoming short-wave radiation that is converted to outgoing long-wave radiation. In this way, Swenson claims that life is in accord rather than in conflict with the cosmic principle of entropy gain. (Salthe<sup>3</sup> now incorporates Swenson's final cause into his own view of Gaia as an entropy-producing, self-organizing system.)

Life—and Gaia, as a promoter of the longevity of life on a planet—should thus be expected to arise. A thermodynamic perspective, in Swenson's view, "obviates the problem of the population of one" (Swenson 1991). Then too, because the biosphere is seen as a regular member of a class (dissipative structures), rather than as an utterly unique and seemingly inscrutable thing, it becomes more conducive to comparative study and generalization.

Salthe and Swenson may, however, have no more success in convincing evolutionary biologists that principles of thermodynamics satisfactorily account for biospheric coherence than have others (like Bagley and Farmer) who use thermodynamics to account for prebiotic complexification. The

<sup>3</sup>S. Salthe, 1991, personal communication. City University of New York, New York.

final and ultimate causes espoused by Salthe and Swenson will probably need to be translated into proximate and efficient causes that are familiar to ecologists.

Weber et al. (1989) have made just such an attempt. They account for ecosystem and biospheric coherence by treating as the units of selection not individual organisms, or genes, or even populations, but "informed patterns of energy flow" that connect a variety of species within a food web. "Those populations are fittest that best enhance the autocatalytic behavior of the reward loops in which they participate." In this way, "individual interest is contextualized within community dynamics." Weber and colleagues do not, however, account for the regulation of environmental conditions that lie outside the flow of energy and the cycling of materials within the food web; they do not, for example, address the ways in which the biota might affect global temperature in a seemingly directed way.

Despite current inadequacies, the field of nonequilibrium thermodynamics may someday offer considerable insights for evolutionary biology as a whole and the Gaia question in particular. Moreover, if the hierarchy of life and its genesis is to be grasped in its totality—from prebiotic chemical complexification to biospheric organization—a synthesis of thermodynamics and biology must occur.

Pressure for acknowledging the role of emergence in evolution comes not only from the lower and upper bounds of the hierarchy of life but from a middle level as well. Jonathan Schull (1990) argues that "species intelligence" is an emergent property of lower-level selection. Schull, who is in the psychology department at Haverford College, Pennsylvania, shows step-by-step how this can be so. Moreover, he draws not at all from thermodynamics but from the standard darwinian toolkit.

Schull mentions Gaia in his article, and he has since articulated the issue that lies at the heart of both: "Is there a systematic tendency for fitness/adaptation to increase in systems which are not themselves products of natural selection? If so, why and how?"<sup>4</sup>

<sup>4</sup>J. Schull, 1991, personal communication. Haverford College, Haverford, PA.

## Antitheses of Gaia

Both the West and the former communist bloc have half-century or older research communities that view the global biota and the physical environment as co-evolving. Lovelock (1989) attributes the origins of this coevolutionary viewpoint to G. Evelyn Hutchinson and Alfred C. Redfield in the West (recently depicted by Schneider and Londer 1984) and Vladimir Vernadsky (1945) in the Soviet Union. But coevolution and Gaia are world views apart (Schneider 1986).

Lovelock points out that coevolution theory "accepts the dogma of mainstream biology, which is that organisms simply adapt to changes in their material environment modified by the organisms themselves." Coevolution thus makes no provision for active regulation of the chemical composition and climate of Earth by the system comprising the biota and their material environment. Finally, coevolution differs from Gaia because "it does not see the Earth as alive in any sense, nor as a physiological system" (Lovelock 1989).

Furthermore, the coevolutionary viewpoint lacks the explanatory power of the gaian theses. If the atmosphere has in fact changed in tandem with the sun, a coevolutionary framework tells us that both biotic and abiotic processes might be responsible, but fundamentally it is just lucky that these processes happened to work in a way that made the direction and degree of modulation favorable for life as a whole.

Gaia critic Doolittle, for example, contends that although the persistence of life for billions of years may look overwhelmingly improbable in the context of a single planet, a more appropriate sample size would be something on the order of a million planets. Life probably arose independently on an immense number of planets throughout the universe; at least one of those planets would have been favored, strictly by chance, with a long record of unbroken evolution such that questioning creatures might have had a chance to arise. It should not, therefore, be astonishing that things worked out favorably here on Earth. And there is no need to look for an overriding cause like Gaia

(Doolittle 1981).

Wilson<sup>5</sup> tempers his criticism of Gaia with an alternative hypothesis that echoes Doolittle's (1991) focus on the need for proto-Gaias. If earth scientists provide compelling evidence that the biosphere indeed has self-regulated, perhaps the explanation will lie in compartmentalization. Perhaps biotic or abiotic processes or characters (e.g., viscosity of water) sufficiently partition the environment so that the atmosphere is modified and experienced locally by key organisms (e.g., algae). Wilson, a biologist at the State University of New York, Binghamton, also speculates that further developments in nonlinear dynamics, especially chaos theory, will lead to an understanding of how homeostatic qualities emerge from complex interactions.

Interestingly, Wilson's attention to compartmentalization is shared by some Gaia advocates, notably Margulis. And Wilson's speculation that biospheric coherence may hinge on chaotic dynamics has also been voiced within the Gaian research community.<sup>6</sup>

David Resnik, a philosopher at the University of Wyoming, concludes that whether one adopts a gaian or antigaian view of global coherence may depend less on determination of precise processes and more on philosophical predilections: Are the root processes simply processes, or are they evidence of a global-scale entity? (Resnik in press).

Aversion to portrayal of the biosphere as an entity need not, therefore, preclude biologists from contributing constructive ideas toward an understanding of what may lie behind biospheric stability and/or persistence. John Maynard Smith (1988) speaks skeptically but inquisitively of Gaia: "No Darwinist could accept the 'Gaia' hypothesis, according to which the earth is analogous to a living organism, because the earth is not an entity with multiplication, variation and heredity. However, we should not be too contemptuous of that idea, logically flawed as it is, until we can give a better account of

the long-term stability of the biosphere than is at present possible."

## Falsifiable hypothesis or fruitful heuristic?

Perhaps nothing has been more disabling to the Gaia hypothesis than the difficulties of framing it in a testable way. Various biologists believe that because the idea of Gaia may be untestable, it should not be treated as science.

Kirchner (1989) published a detailed Popperian indictment of Gaia, challenging Lovelock and Margulis to formulate a test that would render a preferred version of the Gaia hypothesis falsifiable. Lovelock (1989) responded in the same journal. Fundamentally, he questioned the value of strict standards of falsification when attempting to understand the dynamics of closed-loop self-regulating systems. He did, nevertheless, offer a prediction that might be tested: "Oxygen is and has been regulated during the existence of land plants, within  $\pm 5\%$  of its present level."

Lovelock's prediction, which makes explicit his view of the bounds of global homeostatic control, is far from timid. The debate about Phanerozoic oxygen levels is just warming up. Paleooxygen concentrations are derived from estimates of the burial rates of organic carbon in past ages. Some models (e.g., Berner and Canfield 1989) have generated paleo-oxygen concentrations for the late Paleozoic that approach or exceed Lovelock's asserted ceiling.

Jennifer Robinson, a plant geographer at Pennsylvania State University's Earth System Science Center, reviewed these models and hypothesized that the oxygen peak 320 million years ago was caused by an evolutionary lag in fungal ability to decompose lignin when woody plants first appeared. In her view, "the emerging picture is inconsistent with a Gaian biosphere" (Robinson 1991). Not only does the global biota fail to keep oxygen within the range stipulated by Lovelock, but the biota itself is responsible for the disturbance.

If Lovelock's prediction were to fail, would Gaia fall with it? Would other proponents of Gaia—even Lovelock himself—fold up their tents and go home?

<sup>5</sup>D. S. Wilson, 1991, personal communication. State University of New York, Binghamton.

<sup>6</sup>A. Watson, 1991, personal communication. Plymouth Marine Laboratory, Plymouth, UK.

At base, the Gaia concept may be incapable of being framed within the constraints of a falsifiable hypothesis. It may be more a Kuhnian-style paradigm, a shift in world view that undergirds a new and contending research program. The Popperian strait-jacket of falsifiability would then be replaced by a standard of fruitfulness, and the multiplicity of interpretations becomes a sign of fecundity rather than intellectual lassitude.

A third possibility would be to view the Gaia concept as a heuristic: not a hypothesis, but a hypothesis generator. In this way, Robinson (1991) believes that even a flawed and untestable Gaia concept can play a useful role. "I see the Gaia hypothesis as the functional equivalent of the Turing Machine in computer science, or Maxwell's Demon in physics—as a hypothetical, half-whimsical construct, useful for extending the range of scientific imagination."

Daisyworld codeveloper Watson (1991) also has spoken favorably of a heuristic formulation of Gaia: "Whether it is correct or not, Gaia has acted as a powerful stimulus for creative thinking in the study of the global environment."

Although convinced of the verity of his Gaia concept, Lovelock (1991) has pointed to its heuristic value; Lovelock (1988) calls it "a novel bioscope" through which to look at life on Earth. Thus, Gaia has metamorphosed in the minds of some scientists from a radical hypothesis into a reasonable heuristic that may itself prompt radical hypotheses and perhaps lead to important discoveries.

The fledgling Gaia concept—whether hypothesis or paradigm or heuristic, whether process or entity or whimsy—at this stage is necessarily beset with confusion. It is an open question whether somewhere in that confusion resides an opportunity for new insights or applications of evolutionary biology.

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*Connie Barlow is an independent student of evolutionary biology and a science writer. Tyler Volk is an associate professor in the Department of Applied Science, New York University, New York, NY 10003. Tyler is an earth-system scientist specializing in the global carbon cycle and closed-cycle life support systems for space travel. © 1992 American Institute of Biological Sciences.*



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