

Open systems living in a closed biosphere: a new paradox for the Gaia debate

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While energetically open, the biosphere is appreciably closed from the standpoint of matter exchange. Matter cycling and recycling is hence a necessary and emergent property of the global-scale system known as Gaia. But how can an aggregate of open-system life forms have evolved and persisted for billions of years within a planetary system that is largely closed to matter influx and outflow? The puzzling nature of a closed yet persistent biosphere draws our attention to the course of evolution of fundamental metabolic strategies and matter-capture techniques. It suggests a facet of the Gaia hypothesis, framed in terms of persistence. The oceans, atmosphere, soils and biota constitute a complex system which maintains and adjusts matter cycling and recycling within the constraints of planetary closure such that open-system forms of life can persist. This weaker version of the Gaia hypothesis may be useful because it readily lends itself to at least one form of test. What is the solution to the closed biosphere puzzle, and does it indicate that Gaia merits status as a discrete entity? We suggest several disciplines within the field of biology that might provide tools and perspectives toward reaching a solution. These disciplines include artificial closed ecosystems, prokaryote evolution, the nexus of thermodynamics and evolutionary biology, and hierarchy theory in ecosystem modeling and evolution theory.

Keywords: Biosphere; Closed systems; Endosymbiosis theory; Evolution; Gaia; Geophysiology; Hierarchy theory.

Introduction

In the 1970s, Lovelock and Margulis introduced the Gaia Hypothesis, postulating that the biota, oceans, atmosphere, and soils comprise a global-scale system which is self-regulating and, in their view, "living" (Lovelock and Margulis, 1974; Margulis and Lovelock, 1974; Lovelock, 1979). One piece of evidence cited in support of the Gaia Hypothesis was drawn from the paradox of the Faint Young Sun, first articulated by Sagan and Mullen in 1972. Sagan and Mullen, and subsequent authors (Newman and Rood, 1977), noted that models of stellar evolution suggest that the sun has increased in luminosity since the formation of the solar system. The paradox is this: "Solar evolution implies, for contemporary albedos and atmospheric composition, global mean

temperatures below the freezing point of seawater less than 2.3 aeons ago, contrary to geologic and paleontological evidence... It is unlikely that extensive liquid water could have existed anywhere on Earth with such global mean temperatures." (Sagan and Mullen, 1972) And yet it is widely accepted that the earth has harbored life for more than 3 aeons.

Sagan and Mullen suggested that the paradox would be resolved if the early atmosphere had contained a greater concentration of greenhouse gases than today's atmosphere contains. While they initially proposed ammonia as the likely greenhouse gas, subsequent authors (Owen et al., 1979; Walker et al., 1981) argued that a substantially elevated level of carbon-dioxide was the more likely mechanism. The question then became whether the downward drift in carbon-dioxide concentration through time was a chance event or whether thermostasis was a necessary

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outcome of natural processes. And if the latter, were these processes biotic or abiotic?

Walker et al. (1981) developed a model based on a possible abiotic negative-feedback mechanism by which thermostasis is achieved through temperature-dependent weathering of silicate rocks, followed by deposition of carbonates. Lovelock and Whitfield (1982) and Lovelock and Watson (1982) argued in favor of biotic control. A model was developed, "Daisyworld", to portray the logic by which global thermostasis could be achieved by the biota "without foresight and planning", but based instead upon accepted principles of population dynamics (Watson and Lovelock, 1983). Later works have identified possible biotic mechanisms of climate control that operate through manipulation of atmospheric carbon-dioxide (Lasaga et al., 1985; Volk, 1987, 1989a,b; Schwartzman and Volk, 1989), or cloudiness (Charlson et al., 1987; Rampino and Volk, 1988), or both carbon-dioxide and cloudiness (Klinger, 1989).

The Faint Young Sun paradox, therefore, has been a powerful stimulus for earth-system research, fostering development of new models and postulation of both abiotic and biotic processes that might affect or even regulate earth's climate. It has also provided a firm basis for scientific inquiry and debate concerning the Gaia hypothesis. In this paper, we propose another puzzle or paradox which we believe could stimulate fruitful scientific inquiry and debate.

Introducing the Vernadsky paradox

While the Faint Young Sun paradox drew attention to presumed changes in planetary energy influx and outflow through time this paper draws attention to the global flow of matter within a planetary system that is known to be appreciably closed. The puzzle is this: How can an aggregate of open-system life forms evolve and persist for billions of years within a global system that is largely closed to matter influx and outflow?

The question is intriguing in several ways. First, an opposing property (closure) exists at a hierarchical level above those other levels (ecosys-

tems, communities, organisms, tissues, cells) which are characterized by a large measure of openness. The nesting of open living systems that themselves both contain open subsystems and are contained within larger open systems ends at the planetary level. This disjunction in character which appears between the planetary scale and lesser scales presents, at minimum, a curiosity. However, if one views the biosphere as a living system (whether its coherence is greater or lesser than that exhibited by ecosystems) then a puzzle emerges. The highest level in the hierarchical sequence of living systems is distinctly different from all the lower levels.

Second, we know that closure, if applied on a local level, would be lethal for consume-and-waste organisms. Empirical evidence drawn from experimentation with artificial "ecospheres" provides confirmation. Almost all artificially designed, closed ecosystems self-destruct and become lifeless within a few months (due to depletion of vital resources or concentration of toxins); while those few that have persisted for several decades may yet suffer a similar fate (Botkin, 1985; Skoog, 1985). Much of the research carried out today on materially closed (or nearly closed) living systems is conducted through NASA's CELSS Program (Controlled Ecological Life Support System). It is significant here to note that NASA investigators working on the design of human life-support systems for extended space travel and colonization conclude, "The dynamics of material flow within the system will require monitoring, control, stabilization and maintenance imposed by computers." (MacElroy and Bredt, 1985).

If human designers find it difficult (perhaps impossible) to create closed or even nearly closed systems in which life can persist, how much greater a challenge indeed for a system lacking foresight and planning! And unlike human designers, the biosphere has no opportunity for trial-and-error at a global scale; at least within our solar system, the biosphere exists as a population of one. How is it, then, that the inputs and outputs of a myriad open-system forms a life mesh in such a way that material closure as a boundary condition of the planet does not destroy the organized subsystems? Why, during the course of at least

three aeons, has life on Earth not come to a halt either because a vital element becomes trapped physically or in a chemically inert form or because of a toxic accumulation of unprocessed metabolites? Viewed in this light, the closed biosphere puzzle becomes a paradox: all living systems are open systems; yet the biosphere is a living system that is closed.

Those who might call upon the Anthropic Principle to squelch inquiry at this point would do so unscientifically. Calling attention to the persistence of life in a closed biosphere is not the sort of wonderment that characterizes inquiry as to why various numerical or qualitative primitives in our universe (apparently essential for life) happen to be "just so". The closed biosphere puzzle refers not to one-time events or properties of matter, but to a self-organized planetary process that, presumably, has faced risks or difficulties many times following the initial hurdle of simply getting started. And even if we are "just lucky", and our planet represents the one success in a billion Gaian failures throughout the universe, surely there is something scientifically useful to be gained by examining the underlying processes and the critical junctures.

The processes of biological evolution will figure prominently in any proposed solution of the puzzle, but solutions are not readily apparent. This is because a third facet of the puzzle emerges if one contrasts biospheric evolution with evolution at lower hierarchical levels. Natural selection can operate at the organism and perhaps species and higher levels because all of these entities exist as populations greater than one and can therefore withstand the culling by death of less successful variations. But on the level of the biosphere, evolution or development must occur internally. Whyte (1965) drew attention to various internal factors in the evolution of organisms, notably the fact that embryological development must satisfy essential "coordinating conditions" before the organism is even exposed to the test of natural selection. Koestler (1967) called this aspect of evolution "internal selection". The concept of internal selection may have even greater relevance at the level of the biosphere.

But one cannot simply assert that natural sel-

ection operating at the organism level is the means by which the biosphere maintains essential coordinating conditions through time. Because the atmosphere is shared by all, one cannot necessarily invoke differential reproductive success of organisms adapting to and modifying *local* environmental conditions as the process by which a balance of atmospheric inputs and outputs is maintained. Moreover, while evolution of species and relative shifts in populations are surely part of the answer to biosphere persistence, these processes might also destabilize balanced flows of materials. Thus the same processes that might account for persistence also present dangers of unravelling a functioning system.

If the closed-biosphere puzzle articulated here does indeed contribute to fruitful inquiry regarding the evolution of the biosphere, we suggest that it be given a formal name that pays tribute to the founder of biogeochemistry, Valdimir I. Vernadsky. The "Vernadsky paradox" draws from the ideas of this Russian scientist who, in the early part of this century, looked beyond the morphologies of organisms (which was and still is the focus of empirical work in biological evolution) to the manifestation of biological evolution at the planetary level: biotic circulation of materials (see, for example, Kamshilov, 1976.)

Life in open and closed systems

Before we explore the ramifications of the closed biosphere puzzle, it may be useful to distinguish the terms open and closed systems. In thermodynamics, these terms have precise meanings; open systems exchange both energy and matter with the environment, while closed systems exchange only energy. (Isolated systems exchange neither energy nor matter.) Bernal (1951) has concluded that life is manifest only in the form of open systems. Lovelock and Margulis (1974) cite Bernal's definition in their own work, "Life is one member of the class of phenomena which are open or continuous reaction systems able to decrease their entropy at the expense of free energy taken from the environment and subsequently rejected in a degraded form."

Bertalanffy (1952, pp. 124—125) also found thermodynamic openness to be an essential feature of life, and we quote him here at length.

When we compare inanimate and animate objects we find a striking contrast. A crystal, for example, is built up of unchanging components; it persists with them perhaps through millions of years. A living organism, however, only appears to be persistent and invariable; in truth it is the manifestation of perpetual flow. As a result of its metabolism, which is characteristic of every living organism, its components are not the same from one moment to the next. Living forms are not in being, they are happening; they are the expression of a perpetual stream of matter and energy which passes the organism and at the same time constitutes it . . .

This dynamic conception of the organism can be counted among the most important principles of modern biology. It leads to the fundamental problems of life, and enables us to explore them.

From the standpoint of physics *the characteristic state in which we find the living organism can be defined by stating that it is not a closed system with respect to its surroundings but an open system which continually gives up matter to the outer world and takes in matter from it*, but which maintains itself in this continuous exchange in a steady state, or approaches such steady state in its variations in time. (*emphasis added*)

Despite the clarity of thermodynamic definitions of open and closed systems, we have detected some ambiguity in present usage of these terms in the context of the life sciences. Life scientists today (Odum, 1983, p. 4) often make no distinction between matter and energy transfer across the membranes of living systems for one very good reason: all forms of life yet known exchange both matter and energy with the environment. In his book, *Living Systems*, Miller (1978) uses the term "matter-energy" in his definition of open system, thus erasing any distinction. Yet for our purposes, it is essential to keep the two concepts separate. Not only does the closed biosphere puzzle turn on the distinction between matter and energy flows, but we suggest that those who wish to portray Gaia as "living" might profitably reflect on what their assertion portends for a thermodynamic definition of life.

The biosphere's degree of closure

Degree of closure depends on observer choice of (1) system boundaries and (2) time scales. First, where does the system end and the environment

begin? System boundaries have not yet been rigorously defined or debated by participants in the Gaia controversy; but then, there has been no apparent need for precision. Lovelock and Margulis (1974) delineated the boundaries of Gaia as "the outer reaches of the atmosphere. There is also to a lesser extent an inner boundary represented by the interface with those inner parts of the Earth as yet unaffected by surface processes."

We are inclined to draw system boundaries in the fashion articulated by ecologists who use hierarchy theory as a tool for scientific research. Allen and Starr (1982) characterize boundaries as natural break points at which one observes a sharp change in the frequency of exchange. Allen et al. (1984) suggest that researchers demarcate boundaries by looking for "a change of frequency, sandwiched between high frequency behavior inside and low frequency behavior outside."

Sundquist (1985) identified the natural hierarchical subsystems within the carbon cycle. He lumped into a single box the atmosphere, oceans, marine biota, terrestrial biota and soils, and the most reactive marine and terrestrial sediments. He then placed this lumped box into a network of flows with other boxes, such as those for the marine and terrestrial organic and carbonate sediments. The lumped box (approximately Lovelock's Gaia) had an eigenvalue, or characteristic response time, about 4 orders of magnitude lower than the sediment boxes. This indicated a clear discontinuity, an abrupt change in frequencies.

Figures 1 and 2 show examples of the biogeochemical cycles of oxygen and carbon, superimposed with our interpretation of the delineation of Gaia by natural break points. This demarcation of Gaia encompasses both the largest fluxes and the reservoirs with smallest masses. While Gaia's lower boundary is somewhat fuzzy, the upper boundary is crisp. A clear discontinuity in rate processes exists between the atmosphere and space, since the supply of total material from space (probably only 10,000 to 100,000 tons per year; Tuncel and Zoller, 1987) is many many orders of magnitude smaller than the fluxes within earth's biogeochemical cycles. This huge dis-

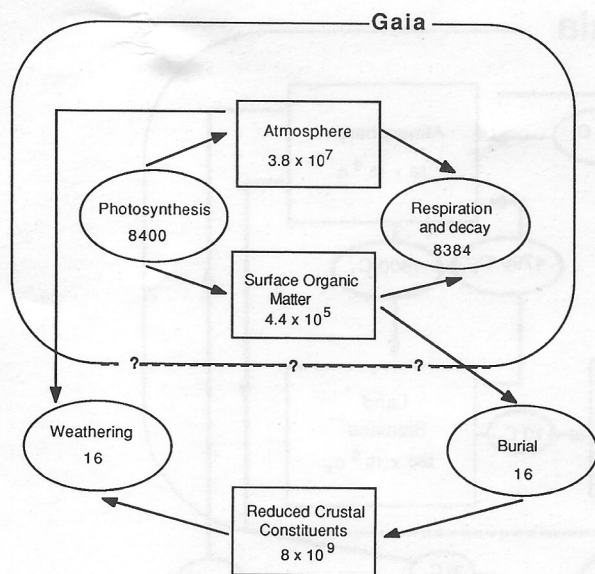


Fig. 1. A simplified representation of the biogeochemical cycles of oxygen. Circles denote processes in units per year, while rectangles denote stores of either oxygen or reduced matter with which oxygen can combine. All units are 10^{12} moles of oxygen or capacity to combine with oxygen (Walker and Drever, 1988). Demarcation of Gaia added by authors.

continuity serves as a triple upper boundary of the atmosphere itself, of a surface biogeochemical system (Gaia), and of a still higher-level system, Earth, which is the coupled Gaia and deep-earth system. A hierarchical approach to system demarcation can therefore explain why Lovelock and Margulis so clearly identified Gaia's upper boundary, but found that the inner boundary was apparent "to a lesser extent".

Degree of closure depends not only on observer choice of system boundaries, but observer choice of time scales. In our delineation of Gaia, the boundaries themselves were chosen to correspond with marked changes in the frequencies of interactions. The closed biosphere puzzle emerges when one compares the fluxes between Gaia's subsystems (atmosphere, oceans, and biomass) with the fluxes between Gaia as a whole and the deep-earth system (see Fig. 2.) Gaia is not substantially closed to exchange of matter with the earth's mantle on a time scale of millions of years, but it is essentially closed on shorter time scales of

hundreds or thousands of years. And those shorter time scales are most relevant to life processes. At today's scale of living biomass, the turnover time of all the carbon in the atmosphere due to biotic processes is approximately 12 years. The turnover time of all the carbon in the atmosphere and hydrosphere combined is less than 500 years. This means that Gaia's own subsystems necessarily must be capable of effecting cycling and recycling of materials critical to life on time scales too short for deep-earth processes (with fluxes generally three orders of magnitude smaller) to make an impact. The puzzle of the closed biosphere is precisely the persistence of life through thousands of these "instants" of geologic time.

The Soviet scientist M.I. Budyko begins his book, *The Evolution of the Biosphere* (1986), with a discussion of the relative degrees of closure between the major earth subsystems and draws conclusions similar to those above. Budyko uses the term "biosphere" to designate nearly the same aggregation of spatial systems as Lovelock and Margulis (and we here) have incorporated within Gaia:

In this book, as well as in the author's previous works, the biosphere is defined as the zone in which modern living organisms exist. Thus, the biosphere includes the organisms themselves and embraces the troposphere, the hydrosphere and the upper, comparatively thin layers of the lithosphere. This definition is commonly used by many scientists. (p. 1)

The biosphere takes a certain amount of matter from outer space (mainly as a result of falling meteorites) and releases a small portion of molecules of gases outwards, from the upper layers of the atmosphere. However, the exchange of matter between the biosphere and outer space is insignificant compared to the cycling of matter within the biosphere itself. Much more substantial is the exchange of some types of matter between the biosphere and the lithosphere. Although this exchange is of great importance in the evolution of the biosphere, it is less intensive than the cycles of the same matter in the biosphere itself.

It is important that the cycles, formation and destruction, of living matter in the biosphere as a whole are completely closed. These cycles are not closed in individual ecological systems nor in the individual spheres of existence of the organisms (i.e. in the atmosphere, hydrosphere and lithosphere). This is further evidence that the biosphere is more integrated than its component parts. (p. 2)

Every planet is, of course, surrounded by the same utter emptiness of space. What makes Earth

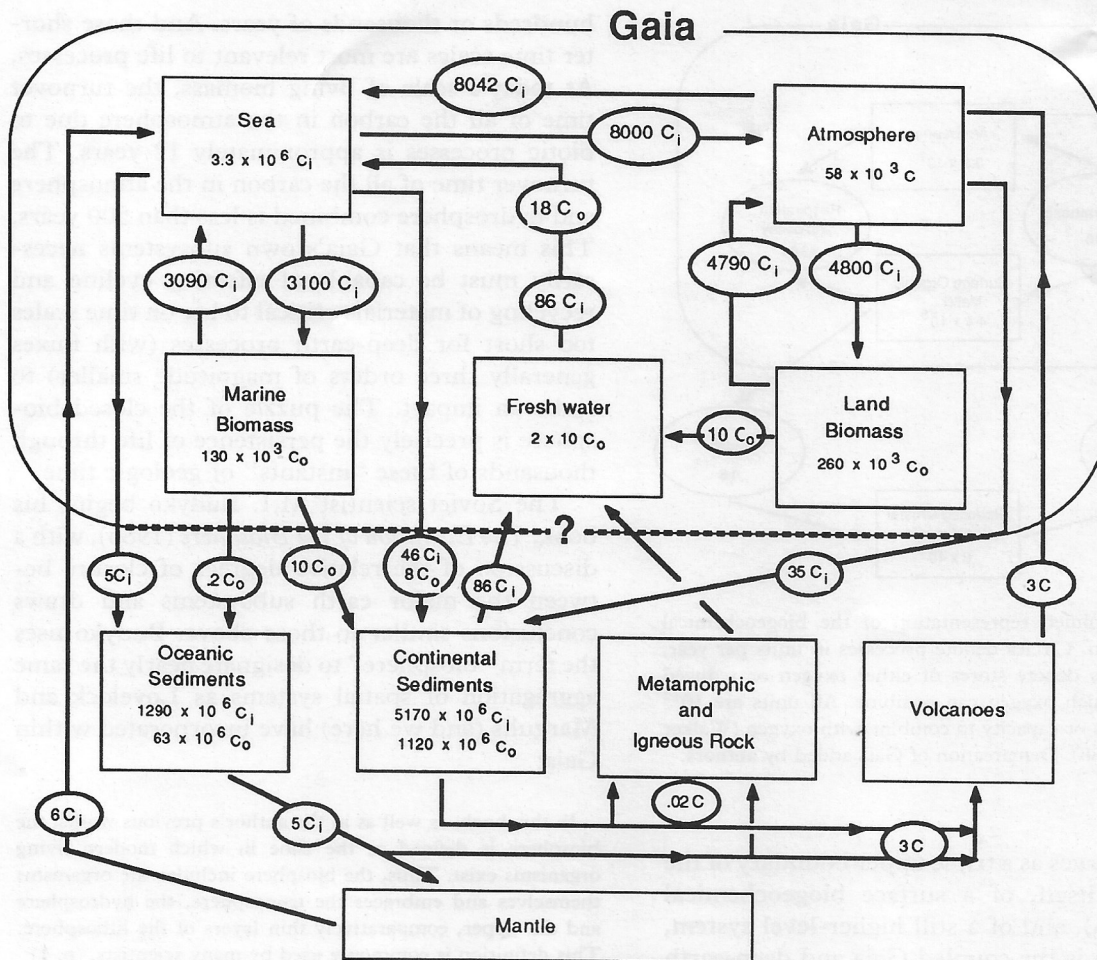


Fig. 2. Biogeochemical cycles of carbon. Reservoir units are 10^{12} moles C/year. C_i indicates inorganic carbon (carbonate or carbon dioxide); C_o indicates organic carbon (Holser et al., 1988). Demarcation of Gaia added by authors.

distinctive is that it is a living planet. Its combined surficial systems — whether one wishes to call them the biosphere or Gaia — have somehow managed to support a myriad of evolving open-system forms of life for well over three aeons despite the constraint of matter closure. Through the rest of this paper, we will generally use the term Gaia rather than biosphere, as the former is being used by scientists who call attention to characteristics of the surface of our planet which, together, imply the existence of a discrete entity of global scale that is perhaps more autonomous, more self-regulating (or as we suggest, more persistent) than mere ecosystems or their aggregate.

Planetary closure and evolution of metabolic strategies

System closure at the global level necessarily constrains the development of all earth's subsystems. As Allen and Starr (1982, p. 11) state, "Ordered systems are so, not because of what the components do, but rather because of what they are not allowed to do." They observe that constraints, in turn, may give rise to "emergent properties" — macroscopic characteristics of the whole system that are quantitatively or qualitatively distinct from the properties manifest at the subsystem level.

We propose that matter recycling is an emerg-

ent property of Gaia, which arises through the interactions of Gaia's subsystems under the pressure of planetary closure. Matter recycling is a quantitative emergent at the level of Gaia. By this we mean that while matter recycling is manifest at subglobal scales of life, at the scale of Gaia the degree of recycling is significantly greater. Ecosystems do recycle a fair measure of some components (particularly nutrients such as phosphorus, potassium, and sulfur) and thus represent an intermediate stage of material closure. No ecosystem, however, is even substantially closed because the atmosphere is common to all. Carbon, oxygen, and hydrogen (in the form of water) — the elements with by far the greatest mass fluxes in living systems — therefore circulate freely among all ecosystems on Earth.

This concept of matter recycling as an emergent property of Gaia may provide an enlightening framework within which to view the evolution of life, particularly the evolution of prokaryotic life. In their book, *Microcosmos* (1986), Margulis and Sagan survey the major events in the development of prokaryotic life. They observe that in the first two billion years of early life, prokaryotes "invented all of life's essential, miniaturized chemical systems," including fermentation, photosynthesis, oxygen breathing, and the removal of nitrogen gas from the air (p. 15). "If we are ever to design closed ecosystems that replenish their own vital supplies, we must study the natural technology of the earth." (p. 275)

Margulis and Sagan portray the sequence of events in prokaryote evolution as having been triggered by one shortage after another. The first forms of life may have feasted on freely available chemicals and abiotically generated ATP. The evolution of simple fermentation freed life from the limits imposed by the quantity of abiotically generated ATP because abiotically generated sugars could now be consumed to generate ATP. A sugar shortage was followed by the evolution of new forms of fermentation by which bacteria could derive energy from the metabolic wastes (acids and alcohols) of other fermenters. Other bacteria developed metabolic strategies by which ATP was derived from sulfates. Finally, a number of different photosynthetic strategies evolved,

whereby energy from the sun was used to construct carbohydrates out of the ultimate metabolic waste product, carbon dioxide, and some source of hydrogen. Hydrogen gas and hydrogen sulfide (from volcanic vents and the metabolic wastes of sulfate bacteria) placed a limit on the amount of photosynthetic activity that could initially be supported. But when a mutant bacteria was able to extract hydrogen from water, a quantitative leap in biomass potential was effected. As Margulis and Sagan state, "The disastrous loss of needed hydrogen from the gravitational field of the earth led to one of the greatest evolutionary innovations of all time: the use of water in photosynthesis. But it also led to a tremendous pollution crisis, the accumulation of oxygen gas, which was originally toxic to the vast majority of organisms." (p. 237)

In Gaian terms, therefore, prokaryote evolution can be looked upon as the stepwise development of the total of open-system life forms working within the parameters of a closed global system. One shortage after another drove the evolution of metabolic pathways, with the most recent pathway (oxygen respiration) driven by the other face of global closure — the fact that there is no external environment into which Gaia can eject wastes. Indeed, the oxygen-pollution event was an unavoidable consequence of an arguably more important event: life's success in overcoming the hydrogen shortage.

Looked at in this way, the oxygen-pollution event is not at all enigmatic. The photosynthetic release of oxygen was neither a Gaian blunder (making much of the world unfit for anaerobes), nor an instance of Gaian foresight and ingenuity, by which Gaia prepared the way for the evolution of eukaryotes. Rather, in response to the inexorable planetary loss of hydrogen from a low-gravity inner planet, prokaryotic life evolved a new metabolism to overcome this matter constraint. Then taking advantage of a consequent opportunity — freely available oxygen — prokaryotes again evolved another series of metabolic strategies: oxygen respiration of fermentable hydrogen to form water, of methane to form carbon dioxide, of sulfide to form sulfite, and of ammonia to form nitrate. (Note: Biological innovations and adaptations outlined above provide clues, but not

a direct solution, for the closed biosphere puzzle; scenarios that depict biotic evolution as fostering matter cycling and offsetting internally generated perturbations may be a necessary but not a sufficient explanation for the apparent fact that new metabolic strategies have evolved and relative populations have adjusted *whenever necessary* for more than three aeons.)

Evolution of nitrogen-capture techniques serves as another excellent example of the role of planetary closure in the evolution of life. Mancinelli and McKay (1988) chart the steps in the evolution of nitrogen-capture techniques, which we present in Fig. 3. Their discussion of the evolutionary stages of ammonification, nitrate assimilation, nitrification, and nitrogen fixation is built upon the premise that shortages of readily available nitrogen and biological demand for additional sources were the driving forces in such evolution.

Examination of the volume of biomass and the structure of matter and energy throughputs at each of these stages of biosphere history might provide insight into the attributes (if any) of biosphere development, similar to Odum's (1969)

formulation of attributes of ecosystem development. What qualitative parameters or quantitative measurements might be applied to ascertain "degree of Gaia"? Might it be useful to consider the biosphere as having become "more Gaian" whenever a new metabolic strategy or matter-capture technique (1) increased biotic access to planetary matter or chemically-bound energy, (2) contributed to a balancing of materials flow, for example, through recycling of metabolic wastes, or (3) in some way enhanced the biosphere's ability to persist — both with respect to minimization of internally induced perturbations and with respect to resilience to external perturbations (such as extraterrestrial impacts)? In what ways would these attributes of Gaian development differ from attributes of ecosystem development? Would the biosphere, accordingly, appear more or less autonomous, and more or less of a discrete "entity", than an ecosystem? Would there be conflicts among these biospheric attributes — particularly with respect to effects on persistence — as there may be between diversity and stability attributes at ecosystem levels (McNaughton, 1988)?

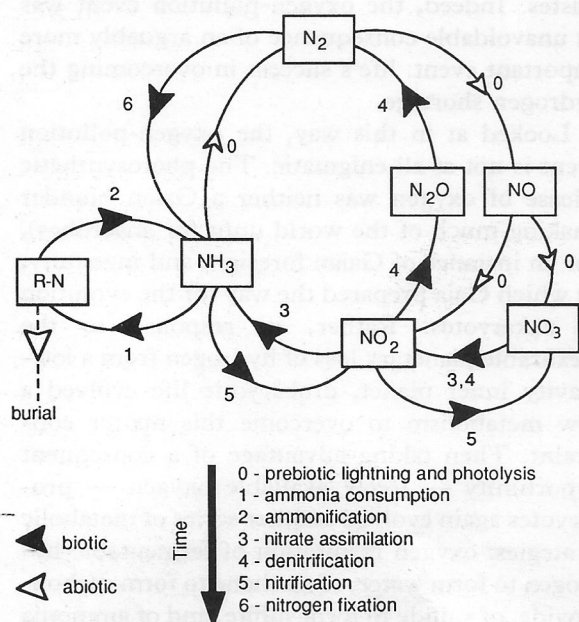


Fig. 3. Evolution of the nitrogen cycle, after Mancinelli and McKay, 1988.

Introducing persistent Gaia

To date, much of the discussion and debate concerning the Gaia hypothesis has revolved around Lovelock's and Margulis' assertion that Gaia is manifest in posited homeostatic tendencies of the biosphere (thermostasis, chemostasis). This version of the Gaia hypothesis has been dubbed "Homeostatic Gaia" (Kirchner, 1989). Our examination of planetary closure as an environmental constraint, and the consequent demand that Gaia manifest matter recycling as an emergent property, has suggested to us an alternative form of the Gaia hypothesis. We formulate "Persistent Gaia" in this fashion:

Persistent Gaia. The oceans, atmosphere, soils and biota constitute a complex system which maintains and adjusts matter cycling and recycling within the constraints of planetary closure such that open-system forms of life can persist.

The notion that persistence is a noteworthy characteristic of the biosphere has been repeatedly emphasized by Daniel Botkin. For example, in his 1982 article, "Can There Be a Theory of Global Ecology?", he asks,

Has the ensemble of the Earth's biota not only changed the Earth's surface, but changed the surface in a way that promotes the persistence — the stability of life? ... Does the complexity of life increase the probability of the persistence of life, or is the complexity merely a curiosity — an historical accident in the sense that it is the result of phenomena that take place in a system that supports life over long periods, but are of little consequence to the system properties including its persistence?

Persistent Gaia may be a useful contribution to the Gaia debate for at least three reasons. First, Persistent Gaia is a weaker form of the hypothesis than Homeostatic Gaia, and yet it still posits something truly interesting and debatable. The system called Gaia need do nothing more than ensure the persistence of life in the face of internal perturbations (resource scarcity or pollution events attributable to open-system forms of life evolving and metabolizing within a closed planetary system) and external perturbations — such as changes in mantle-crust exchanges driven by plate tectonics (Veizer, 1988), the gradual increase in solar luminosity, and catastrophic impacts of large extraterrestrial objects. A weaker form of the Gaia hypothesis may offer the benefit of attracting more scientists to give it serious thought.

Second, Persistent Gaia may be a useful addition to the Gaia debate in that it suggests a ready explanation for the oxygen pollution event, which has been troublesome for versions of Gaia keyed to homeostasis or optimization (Schneider, 1986). As mentioned earlier, the oxygen pollution event need not be viewed either as a Gaian blunder (which forced anaerobes forever into hiding), or as a purposeful action intended to prepare the planet for the evolution of metazoans with their high metabolic demands. The oxygen pollution event was, rather, an understandable outcome of life's tendency to persist (and perhaps expand) in the face of a hydrogen shortage.

Finally, Persistent Gaia may be useful in that it readily lends itself to one form of test. The test is this: What is the solution to the closed biosphere

puzzle? By what specific means does a myriad of open-system forms of life evolve and persist in a closed environment? And is this means best framed cybernetically as a property of the system as a whole or as a property within one or more of Gaia's subsystems? If the means is found to be a property of the whole system, then Gaia may be a useful scientific construct; Gaia may even "exist". If the explanation is, however, attributable to the internal workings of one of Gaia's subsystems, then "Gaia" may be an unnecessary strengthening of the term "biosphere" — though "Biota" (with a capital B) may well deserve recognition. Finally, if the puzzle resists solution, it could be viewed as a kind of koan (a puzzle in the tradition of Zen Buddhism) that gives Gaia status as an entity despite our present inability to comprehend key aspects of geophysiology.

Solving the puzzle: suggestions for an interdisciplinary approach

Several disciplines within the field of biology are especially suited for probing the closed biosphere puzzle. These disciplines include (1) artificial closed ecosystems, (2) prokaryote evolution, (3) the nexus of thermodynamics and evolutionary biology, and (4) hierarchy theory in ecosystem modeling and evolution theory.

Recognition that life on earth must be able to persist within an essentially closed system is conventional wisdom among those scientists who design and study artificial closed ecosystems. Despite significant input of human intelligence and repeated experimental attempts, however, researchers are not convinced that any of the ecospheres are able to support life indefinitely (Skoog, 1985). Investigators with NASA's Controlled Ecological Life Support System may also have insights regarding problems of life's persistence when constrained by material closure. Research on artificial "ecospheres" and NASA projects aimed at space travel and colonization, of course, make no allowance for the evolution of new species or, more importantly, new metabolisms. For this reason, while researchers in these fields might have a great deal to offer in fleshing

out the range and depth of problems inherent in the closed biosphere puzzle, they may not be well positioned to contribute complete solutions.

Scientists specializing in biological evolution might be able to propose solutions to the puzzle, although the field has, in our view, focused too much on the evolution of eukaryote species and morphologies and not enough on the evolution of metabolisms and matter-capture techniques. (Consider the widely quoted assertion that over 90% of living species went extinct at the end of the Permian; does this figure encompass the fate of the Prokaryote Kingdom, for which "species" is a slippery term?) Moreover, the key events in the development of Gaia from the standpoint of the closed biosphere puzzle probably occurred before eukaryotes arose. All of the fundamental metabolisms and matter-capture techniques evolved within the prokaryotic clan (Margulis and Sagan, 1986, p. 15). In addition, the prokaryotes express and disperse mutations in ways utterly foreign to the realm of eukaryotes (Sonea and Panisset, 1983, p. 112).

Scientists who expressly approach evolutionary biology from the standpoint of thermodynamics (we shall call them "entropy evolutionists") have been willing to search for the kind of broad principles that may prove useful in tackling the closed biosphere puzzle. These evolutionists would likely harbor no prejudice against Gaia (and certainly not the "biosphere") as a legitimate object of study in that they view all "dissipative structures" in the world of physics and biology as brethren. Schneider (1988) provides an excellent introduction to the cast of characters, past and present, contributing to this field and the scope of their insights, including Harold Morowitz' classic work (1968). Today, Jeffrey S. Wicken is a prime contributor in this field, and his treatment of living systems as informed autocatalytic organizations is directly relevant to the issues presented in this paper (see, for example, Wicken, 1987, 1989).

Entropy evolutionists, nevertheless, tend to regard matter fluxes and cycles more as a contributor to system energetics than as a process worth studying in and of itself. While ecosystems modelers do investigate both matter and energy

flows, they have not traditionally had to attend to the impact of closed flows of carbon, oxygen, and hydrogen because the atmosphere plays a key role in these cycles. Ecosystems modelers who work within the research program of hierarchy theory (see, for example, O'Neill et al., 1986) may be well equipped to do pioneering research at the scale of the biosphere. Ulanowicz (1986, 1987, 1989) uses hierarchy theory in his work in ecosystems modeling; he suggests that "a flow cycle" could be regarded as "a structure with an existence that is to some degree independent of its constituents" (1986, p. 54). He says:

The crux of autonomous behavior lies in the tendency of simple direct cycles to exhibit positive feedback. Positive feedback can act to select from among variations occurring within the cycle. The behavior of the cyclical structure can strongly influence the makeup of its constituents. Causality can thereby flow down the hierarchy, but this influence can be observed only at spatial scales that encompass whole cycles and over temporal intervals that exceed the period of the cycle. It is fashionable to proscribe discussion of living phenomena at these larger temporal and spatial scales; but this attitude may be overly restrictive and possibly counter productive. (1986, p. 80)

Hierarchy theory has also been embraced by some evolution theorists. Niles Eldredge and Stephen Jay Gould, widely known for their theory of "punctuated equilibria" (Eldredge and Gould, 1972), have advanced bold proposals for reformulating Darwinism in a way that takes account of nature's organization in nested hierarchies (Gould, 1980; Eldredge and Salthe, 1984; Vrba and Eldredge, 1984). We suspect that these scientists and their fellow proponents of hierarchy theory could make substantial contributions toward solving the closed biosphere puzzle.

Nevertheless, Botkin (1982) has noted a general lack of attention by biologists to the biosphere as a distinct system worthy of study:

There is no doubt that a theoretical basis for a science of the biosphere is needed; there is little doubt that a theory for management will develop. But there is great uncertainty that a useful theory, derived from the phenomena and taking into account the special attributes of life-modulating systems, will result. The outcome depends on biologists motivated to develop their own theory, not easily led astray by the mathematical methods that have succeeded in physics and engineer-

ing, nor led elsewhere by claims that the subject is without interest. A theory of the biosphere may not be possible; the attempt to find one is central to biology.

Discussion

In this paper we have introduced a weaker version of the Gaia hypothesis that focuses on the persistence of life through time. Persistence is a characteristic of life on Earth that demands explanation, for how can an aggregate of open-system life forms evolve and persist for billions of years within a global system that is largely closed to matter influx and outflow?

The constraint of planetary closure (named here the closed biosphere puzzle or Vernadsky paradox) is not the only issue that might be fruitfully examined within the context of "Persistent Gaia". The phenomena at the heart of the Faint Young Sun paradox and the theory that mass extinctions were caused by extraterrestrial impacts (Alvarez et al., 1980) are also widely recognized as having posed enormous challenges for the persistence of life. The impact theory, in turn, may add a twist to the closed biosphere puzzle. In a kind of "punctured equilibria" (our playful reworking of the term "punctuated equilibria" coined by Eldredge and Gould), Gaia's success in ensuring matter recycling would have been upset repeatedly by blasts from space that severely depleted Gaia's biotic agents. Research directed not at taxonomic counts but at biogeochemical changes across geological boundaries, such as the K-T boundary (Zachos et al., 1989), may provide important clues about disruptions and subsequent recoveries of the vital metabolic strategies and matter-capture techniques. On the other hand, if some extinction events are not attributable to catastrophic impacts (Gruszczynski et al., 1989), might an internally generated upset in matter cycling, which changes chemical or thermal regimes, be a plausible cause?

Perhaps periodic impacts of extraterrestrial objects are not catastrophes to be withstood, but stresses with some beneficial effects, akin to the role of fire in grasslands and other ecosystems. Might periodic impacts actually help maintain Gaia at a stage of development that is resilient?

Might they clean out the "dead wood" of eukaryotic evolution? Michael Rampino (1989) has posited possible beneficial aspects of extraterrestrial impacts for the Gaian system.

Along these lines, Ulanowicz (1989) suggests that in the normal course of ecosystem development, redundant pathways of material flow tend to be eliminated, as the web of interactions becomes progressively more articulated. He concludes that the elimination of redundancy makes the system increasingly vulnerable to disruptions. Conversely, internal redundancy "affords a system-level strength-in-reserve." Similarly, Wicken (1987, p. 149) finds that with the trend toward specialization in ecosystem development comes vulnerability to external disturbance.

We do not aim in this paper to favor either side of the diversity-stability debate that has engaged ecosystems scientists for two decades (McNaughton, 1988). But we do suggest that the question may have implications beyond the realm of ecosystem development. It may also be relevant for ascertaining the processes that work for or against persistence of the biosphere, and for evaluating the effects of extraterrestrial impacts from the standpoint of biospheric persistence. Perhaps it is time to critically examine Eugene P. Odum's 1969 statement:

In a word, the 'strategy' of succession as a short-term process is basically the same as the 'strategy' of long-term evolutionary development of the biosphere — namely, increased control of or homeostasis with the physical environment in the sense of achieving maximum protection from its perturbations.

Recognition that Gaia is an energetically open, materially closed system might, in itself, suggest intriguing lines of inquiry with respect to definitions of life. Whether or not Gaia is viewed to be "alive" may be more a matter of taste than of science. But by opening our minds to the possibility of a living Gaia, we are led to consider the unique qualities that life would manifest if it did exist (somewhere in the universe) on a planetary scale. Notably, life at the planetary scale would likely operate as a closed system. And this closed-system form of life probably would have evolved out of an aggregation of consume-and-waste forms of life pressed into symbiotic relations by

the constraints of planetary closure. Accordingly, theories that major steps in evolution occurred by symbiosis could then be extended to apply to the evolution of planetary-scale, closed-system life forms. These theories include: (1) genesis of the eukaryotic cell (Margulis, 1981); (2) occupation of deep-sea, sub-photic-zone vents by invertebrates with chemoautotrophic bacteria in their tissues (Cavanaugh, 1985); (3) various theories of the origin of life that posit separate origins, followed by symbiotic merger, of proteins and nucleic acids; and (4) a broad hypothesis that "symbiosis has been important in the origin of species and higher taxa" (Margulis and Bermudes, 1985).

Using the concept of Gaia as a tool to expose overly narrow presumptions about the character of life, we might also examine whether reproduction is an essential trait. Could "internal selection" (which, as discussed earlier, may be based in large part upon natural selection operating at lower hierarchical levels) ensure the continuing fitness of an evolving biosphere? Might Gaia, therefore, evolve (transform might be a better word; see Levins and Lewontin, 1985, pp. 85–86 and Piaget, 1970), but without reproduction and differential death rates of offspring? If matter cycling (including exchanges with the mantle) and a life-supporting thermal regime can be achieved through internal selection — this, of course, is a big "if" — then natural selection at a planetary scale may be unnecessary. For lacking predators, parasites, and competitors, there is little if any environmental pressure that would mark as "unfit" any excursion of Gaia within the possibilities of evolutionary property space. Thus, using Gaia to prod our imagination, we can now envision how a global-scale form of life could evolve in the absence of reproduction and death of the entity itself.

Finally, because of its focus on the development of metabolic strategies and matter-capture techniques, might the closed biosphere puzzle expose evolution at a hierarchical level in which Darwinism has more rigorous explanatory powers? While morphologic changes of eukaryotes may not be predictable even in hindsight, is there perhaps a logic and necessity to the

sequence of events that marks the evolution of metabolic strategies and matter-capture techniques within the Prokaryote Kingdom?

We will close this discussion with quotations from the writings of three scientists whose works, though seemingly antithetical, have provided the impetus for the key ideas in this piece. Quotations here all implicitly refer to the value of scientific "research programmes", as articulated by Imre Lakatos (1970), or "research traditions" (Laudan, 1977). First, Richard Dawkins, a Gaia critic, introduces his extended phenotype hypothesis thus:

The extended phenotype may not constitute a testable hypothesis in itself, but it so far changes the way we see animals and plants that it may cause us to think of testable hypotheses that we would otherwise never have dreamed of . . . D'Arcy Thompson's (1971) celebrated chapter 'On the theory of transformations . . .' is widely regarded as a work of importance although it does not advance or test a hypothesis . . . But our imagination is fired . . . It is possible for a theoretical book to be worth reading even if it does not advance testable hypotheses but seeks, instead, to change the way we see. (Dawkins, 1982, p. 2)

James Lovelock characterizes the Gaia hypothesis as "a novel 'bioscope' through which to look at life on Earth." (1988, p. 12). And in their seminal paper, Lovelock and Margulis (1974) spoke thus:

The purpose of this paper is to introduce the Gaia hypothesis at least for entertainment and for the induction of new questions about the Earth.

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