

Gaia Is Life in a Wasteworld of By-products

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Volk, Tyler. Gaia is life in a wasteworld of by-products. In *Scientists Debate Gaia*, edited by S. H. Schneider et al., MIT Press, pp. 27-36, 2004.

Abstract

I offer here an essay of personal history of grappling with Gaia theory, with conclusions. These are as follows: The relatively steady states in the global environment are simply the expected, natural results of a system containing chemical reactions, many of which involve life. There is nothing special about the existence of both positive and negative feedbacks in this system; these are to be expected. Certainly much of the global environment has been, and is being, transformed by life into a state very different from that of a planet without life—but what is this state? I suggest that the global environment is, in essence, a wasteworld: a system of by-products (and their effects). This wasteworld plus life creates a complexly structured dynamical system, because life is not passive. Organisms make metabolic products aimed to ensure their success at living and reproducing, not aimed at transforming or controlling the global environment. But in making these products, organisms also produce by-products, and these often build large-scale environmental side effects. The environmental consequences of the by-products are inadvertent but do create a system with evolutionary and population feedbacks—for instance, the biogeochemical cycles. The dynamics of this system are such that some forms of life alter the environment, and then all other forms within that altered environment must adapt or perish. Life thus shoves the environment around, subject to limits at various extremes. Are there general principles of this wasteworld? At the end, I spell out some directions that I see for the future of Gaia theory.

Introduction

This chapter is a personal essay about Gaia theory. I will reflect a bit on what became for me major lessons about the theory. I hope readers will not be put off by this more informal format. I want to show the evolution of my thinking. Admittedly, I will not attempt a survey of all work in Gaia theory, and thus will necessarily leave out many substantial attempts by other

researchers to solve outstanding issues. For this I apologize. I focus on those principles and concepts that have emerged over time as the solid truths I carry around as a foundation for continuing work.

Let me start by thanking James Lovelock and his colleagues, who proposed and promulgated what started as the Gaia hypothesis but has come to be known as Gaia theory. Since the 1980s my thinking has been influenced and inspired by the Gaia theorists.

In the early 1980s I was working on my Ph.D. dissertation. Its published title was *Multi-property Modeling of the Marine Biosphere in Relation to Global Climate and Carbon Cycles* (Volk, 1984, see also Volk and Hoffert, 1985). I now would change one word. Let's say *Biota* rather than *Biosphere*, because I prefer to reserve "biosphere" to encompass all life (biota) and its global environment.

In fact, I take "biosphere" as essentially equivalent to Gaia. I define *Gaia* as the system that includes all Earth's surface life, the soils, oceans (all surface water), and atmosphere (Volk, 1998). I also include in Gaia the active interface of rocks that are contributing on the thousand-year timescale to the chemistry of the rest of the biosphere. Soil, air, and ocean are unified over about a thousand-year ocean mixing cycle, making all life linked into what is essentially a synchronized moment in global biogeochemical evolution.

Tim Lenton (chapter 1, this volume) uses a somewhat more flexible definition of the Gaia system, in which the lower boundary of Gaia deepens as the timescale under consideration expands. I can concur with his reasoning, and I hope the system's boundaries will become clearer the more we are able to elucidate the dynamics of this special system. I also wish to acknowledge another opinion. Axel Kleidon, in his review, suggested that the term *Gaia* is value laden and should be restricted to Lovelock's original concept. In this chapter I will stick with my preferred heuristic of a definition: equating Gaia with the biosphere.

The MIT Press
Cambridge, Massachusetts
London, England

Back to the 1980s. Somehow during this time I became aware of Lovelock's Gaia hypothesis. I read his book *Gaia: A New Look at Life on Earth* (Lovelock, 1972). It was eye-opening. Could he be right? Could salinity, temperature, and atmospheric and ocean chemistry have a single explanation behind their apparent stability over long periods of time? Could this explanation have to do with the global activities of life that maintain those conditions for life's very own benefit? Are there feedback loops in Gaia (Lovelock used the analogy of a thermostat) that hold conditions relatively constant, and possibly even adjust them for thermal and chemical comfort on a global scale? Are we, in fact, living in a gigantic super-organism that in some ways behaves like the manner in which our body creates its remarkable, internal homeostasis?

I also studied two key journal papers (Lovelock and Margulis, 1974; Margulis and Lovelock, 1974). Certainly from the viewpoint of my dissertation on the marine biota, I was open to their persuasive ideas. My work involved modeling marine life at the biosphere scale, aiming to place life in the equations for marine carbon dioxide, phosphate, nitrate, alkalinity, and oxygen. The concentrations of these constituents, varying with water depth, are profoundly affected by life. Life does have an indisputably powerful influence on global ocean chemistry.

As a theoretician I was drawn to any hint of general principles for these global patterns. I recall at the same time also looking into nonequilibrium thermodynamics, as well as chaos theory, nonlinear dynamics, and fractals. What theoretical framework might give insight about the biosphere? Lovelock's Gaia hypothesis seemed particularly relevant because it specifically dealt with life: life as the central organizing factor for Earth's surface system.

Where I subsequently went with the Gaia hypothesis in my work, how my ideas about Gaia developed as a result of early explorations, and how I see the current status of Gaia theory's present and future are the subjects of the body of this chapter.

Positive and Negative Feedbacks from Life's By-products in Steady States

In the mid-1980s, as a newly minted Ph.D. and then professor, I drew inspiration from a paper in *Nature* by Lovelock and Whitfield (1982). They noted that life enhances the chemical weathering of soil minerals. This is because the soil CO₂ level, compared to that of the atmosphere, is elevated by respiration from plant

roots, soil animals, and microbes. And weathering takes place in the soil, releasing calcium ions from silicates (to simplify). These ions then flow via rivers to the ocean, where they are precipitated out as calcium carbonate, thus carrying CO₂ into a rock burial, removing it from Gaia (in other words, from the biosphere).

At the same time, I was aware of the important BLAG model of this so-called geochemical carbonate-silicate cycle, named after the authors Berner, Lasaga, and Garrels (Berner et al., 1983). BLAG provided a framework for computing CO₂ levels over multimillion-year time periods. It specified weathering as a function of atmospheric CO₂ (among other factors). But significantly, BLAG did not include life as an active player. As noted, life is a major factor in determining the CO₂ levels where weathering occurs, and thus I was motivated to add life and soil to the BLAG model, to make it more "Gaian" (Volk, 1987).

Constructing a "lively" BLAG model required quantifying a crucial loop: atmospheric CO₂ affects plant growth, which by direct respiration of roots and the supply of photosynthesized organic detritus to soil respirers affects soil CO₂, which in turn affects the weathering rate of soil minerals, which then, via the eventual burial of ocean calcium carbonates, circle back to affect atmospheric CO₂. The loop is a negative feedback, as Lovelock and Whitfield perceptively pointed out. How strong is the feedback, I wondered. Does it create homeostasis—a key term that appears in Lovelock's first book and his early papers with Lynn Margulis?

After formulating the relevant dynamics, I examined how the lively BLAG model responds to an increase in volcanic emissions (a chemical forcing into Gaia from beneath Gaia). How much would atmospheric CO₂ rise with a given extra input flux of volcanic CO₂ in a lifeless BLAG model, compared to the model with life and its lively feedback loop? I found that the biota could roughly perform what I preferred to call "mitigation" rather than "regulation."

By "regulation" I was looking for homeostasis, which meant holding the atmospheric CO₂ and global climate nearly constant in the face of external forcing. "Mitigation," on the other hand, would be less powerful. David Wilkinson has pointed out to me that he regards regulation as any bounded condition in which perturbations amplified by relatively weak positive feedbacks over short times scales are ultimately constrained by negative feedbacks that dominate over longer time periods. But then what are the logical

bounds on the use of "regulation"? I don't know. Furthermore, even the lifeless BLAG model contains a negative feedback. Does the existence of any degree of negative feedback warrant the use of "regulation"? Not in my opinion. As I found, the additional negative feedback added by life in the lively BLAG system is relatively weak; thus, at the time I felt (and still feel) more comfortable with "mitigation."

How much is this mitigation? About 30 percent for a reasonably strong forcing. For instance, if volcanoes in the lifeless BLAG model create a new steady-state climate 3°C higher in the forced condition, then with my lively BLAG the temperature increase is only about 2°C. Life mitigates (reduces) the increase by about 1°C. This is significant. But it is definitely not anywhere near perfect regulation.

Why even expect regulation to be perfect? At that time, in ignorance, I had not given enough thought to why we might even theorize about homeostasis as a property of the biosphere. I suppose that in my mind something along the lines of Lovelock's analogy with a thermostat made sense. But what could possibly create the mechanisms of such tight regulation within a biosphere that contained organisms as evolving entities? Eventually I came to realize that negative feedback associated with life, as in the lively BLAG model, is not a property to be expected to follow from evolution any more than positive feedback does. I will explain further.

Trees are not been positively selected by evolution to have roots that pump lots of CO₂ into the soil. Just the opposite: trees whose root cells are more efficient and generate less CO₂ as metabolic waste will be at a reproductive advantage. Along the same lines, grasses are not selected by evolution because, at the end of their growth season, their bodies wither to feed the earthworms and microbes with detritus, so that these soil respirers elevate soil CO₂. The elevation in soil CO₂, which happens to increase chemical weathering, is a result of waste by-products of soil's life-forms. Consider, too, actively released substances such as phosphorus-dissolving enzymes, which are secreted by soil microbes to liberate nutrient ions from soil minerals. The resultant lowering of the steady-state value of atmospheric CO₂ as a consequence of these enzymes is a by-product, a side effect.

Life's influence on atmospheric CO₂ is a collateral effect of chemical weathering in the soil. Again, elevated soil CO₂ is itself a by-product of waste from respiration. There is no evolutionary pressure that drove life to mitigate excursions of atmospheric CO₂, computed in the lively BLAG model. The reason the

model's negative feedback is 30 percent just happens to be that way, given the quantitative dynamics of photosynthesis and chemical weathering.

So far I have been discussing the value of a particular negative feedback between life and the global environment. But there is no reason for the sign of feedback between life and its environment to be negative. Schneider (1986) pointed this out in an important paper that questioned some of the logic applied in Gaia theory. At that time it was becoming evident that Earth's Pleistocene Ice Age cycles of about 100,000 years were at least partially due to positive feedbacks between life and the environment. Although the cyclic Ice Ages are still a mystery and the reasons still unresolved why, for example, CO₂ was lower during the cold periods, clearly life was involved somehow in amplifying the pacing signal from the changes in Earth's orbit.

David Wilkinson's point above is apropos here: that positive feedbacks will in general be bounded in extent and time by longer-term, stronger negative feedbacks. I agree, although in the case of Ice Ages the bounds might have been set by the orbital cycles themselves. I do generally agree, however, with his point: Gaia is a system with both types of feedbacks, and the system will tend to settle into stable states bounded by negative feedback.

Thus naturally there will be steady states in which life plays a major role. But the creation is a side effect, an inadvertent consequence of life's by-products. Life creates these states—but life did not evolve to create these states. This logical distinction is crucial. (See also Kirchner, 2002; Volk, 2002). I will deal with the issue of ultimate environmental limits later.

Here is how I have come to see the Gaia system: The biosphere is a vessel containing chemical reactions. There are flows of matter into this vessel (considering input flows from volcanoes and rock weathering). As described in the example of lively BLAG, life can influence the weathering rate, which puts elements from rocks into the circulation of the Gaia system.

In addition, there are exiting flows from the biosphere vessel, primarily by the burial of materials in sediments and by chemical exchanges at ocean vents. These exit fluxes, too, can be influenced by life. But the fluxes are also modified by purely inorganic processes, such as entrapment of solid materials as sediments accumulate, with subsequent passage out of the active biosphere.

What goes on inside the chemical vessel of the biosphere? Some of the internal reactions don't require

life—equilibrium-seeking exchanges between bicarbonate and carbonate ions in the ocean, for instance. But as noted and emphasized, life participates in many internal transformations. Specifically, photosynthesis can be written as an equation with reactants and products. Nitrogen fixation can be written as an equation. And so forth. The reaction rates of these processes are not simply driven by the chemical free energy of the reactions alone. As Axel Kleidon has emphasized to me, forms of life actively degrade free energy between input and output, thereby building up free energy inside their bodies as complex chemical compounds. Therein lies the challenge to find simple rules that capture how organisms determine the rates of their metabolic equations. But just the same, as a foundational starting point, life's chemical equations contain reactants that go to products, with the release or addition of energy, just as we find in the abiotic chemical processes of soil, air, or water.

Now, let us consider once more, in conclusion, Wilkinson's idea of a nesting of feedbacks. Assume for comparison two chemical systems or cases. The first case has no life. The second case has life. Each system contains a number of reactions. States are determined by the entering fluxes, the exiting fluxes, and internal reactions. In both systems, the soup of chemicals inside the vessel will likely reach a steady state, given relatively steady input fluxes (these change as forcings, of course, but usually more slowly than the rates of reaching steady states). In dynamical systems of chemicals, other behaviors are possible as well. We might find cycles in the chemical concentrations. We could have chaotic attractors. But whatever the case, the systems generally arrive at distinct, bounded behaviors. This is because there will be regions of phase space for the systems where negative feedbacks dominate and act to bound any fluctuations caused by positive feedbacks. These will be the regions into which such systems will settle.

With life, the behavior is essentially the same as without life: for example, steady states occur in the both the lifeless and lively BLAG models. I emphasize: It's not the situation (at least no one has shown this to be generally true) that without life the system is wild, whereas with life the system is steady. I don't question that life influences the concentrations of the steady state. It's just that we cannot elevate life to a status of creator of the steady state.

Because life participates in causal loops of positive and negative feedbacks, the levels of the steady states will be different when comparing a lifeless "biosphere" to one with life. But it's not the existence

of positive and negative feedbacks that makes life special. Causal loops of both positive and negative feedbacks exist as well without life. Life makes the biosphere more complex, certainly. But is that complexity qualitatively different? Are we talking about an entirely different dynamic behavior, such as stable versus unstable, when we compare a planet with life to one without? I don't think so. I haven't seen the evidence.

Change in the Biosphere from the Evolutionary Output of By-products

I now return to personal history. At the 1988 Chapman Conference on the Gaia Hypothesis, I met David Schwartzman of Howard University. Soon after the meeting, having seen my presentation on the lively BLAG model, he called me. We eventually collaborated on a series of papers whose results can be used to look at the issue of life as maintainer of stability or creator of change.

I remember that first phone conversation well. David said that life influences weathering to a much greater degree than in my lively BLAG model. How much, I asked? He said that in addition to my maximum enhancement of perhaps 2 to 3 times via elevated soil CO₂, other biological factors create a weathering enhancement of 100 to perhaps 1000 times over what should be considered the true baseline comparison for Gaia theory—the abiotic rate of weathering. These factors include release of acids by soil organisms, the retention of water by humus (no water, no aqueous dissolution reactions), and the structure of soil as a matrix of fine particles held in place over long enough time periods to be chemically weathered.

By looking at the available data, we estimated that such magnitudes for the overall "biotic enhancement of weathering" were plausible. What did that mean for quantifying life's influence on Earth's atmospheric CO₂ and temperature? We found that life might currently cool the biosphere by about 35°C (Schwartzman and Volk, 1989). This number is interesting because the current global temperature is about 15°C, and our calculated temperature for an abiotic Earth of 50°C (at today's solar flux) is about the upper temperature limit tolerated by any eukaryote life-forms. So without ancient bacteria that created a biotic enhancement of weathering on a pre-eukaryotic earth (with cryptogamic soils as our reference), then perhaps we would see no elephants, birds, amoebas, or people. It became evident that earlier microbial life

created cooler conditions that led to more complex organisms, which presumably needed those cooler conditions to evolve and survive.

We then extended this work to specifically treat the biosphere over time, in which the biotic enhancements to weathering took place in a series of stages (Schwartzman and Volk, 1991; especially see Schwartzman, 1999). In this work we computed a history over 4 billion years of atmospheric CO₂ and global temperature. There were several forcings whose relative impacts we examined. The effects of these forcings were isolated in my book (Volk, 1998); here I discuss the results and what I have gained from them with regard to Gaia theory.

Three major abiotic forcings exist on the geochemical carbonate-silicate carbon cycle. First, the sun has increased in intensity by about 30 percent, which, when isolated in the model, causes a 6°C warming over 4 billion years, from 66°C to 72°C. (The initial temperature is set to be about 66°C, to yield today's state with all the forcings applied, abiotic and biotic.) In addition, there are two major geological forcings: first, the growth of the continents, which especially in Earth's early history added raw area for weathering reactions; second, the decrease in the release of Earth's deep heat, which lessened the CO₂ emitted by volcanism (see discussion in Schwartzman, 1999, for formulations and justifications). Both of these long-term changes act to decrease the steady-state level of atmospheric CO₂ over time, thus gradually cooling the climate. When the forcings from sun, continental growth, and volcanism are combined, as they would be in reality, the two geological forcings "win," with the net result of a 20°C overall cooling, from 66°C to 46°C.

Now add life. As Schwartzman and I have argued, the evolution of life would have caused a progressive series of enhancements in the biological impact on chemical weathering, starting with the earliest prokaryotes on land and ending with modern soils created by as well as supporting vascular plants. With everything combined in the model—sun, geology, and the evolution of life—Earth's temperature progressively moved from 66°C 4 billion years ago to today's 15°C, an overall cooling of 51°C.

Thus, in our scenario, life has not stabilized the planetary surface temperature; it has helped to destabilize it. This isn't the place to review uncertainties and controversies over the weathering formulations, or whether or not methane, rather than CO₂, was important as the early greenhouse gas, or what prelife temperatures were. The point is that we attempted to

assemble, in a common geochemical framework, reasonable best estimates for the main effects on CO₂ and temperature.

Does this biologically determined weathering effect on global temperature support Gaia theory or not? That depends on what is meant by Gaia theory.

In the traditional view of Gaia as stabilizer of biosphere conditions (a la Daisyworld), the progressive cooling from weathering enhancement is not Gaia. But to my mind, the cooling of the planet due to the progressive and evolutionarily driven biotic enhancement of weathering is as much "Gaia" as a theory gets because of the intimate coupling of life and environment.

But suppose Gaia theory says that some aspects of the global biota are stabilizing and some are destabilizing. Then I submit that if Gaia exhibits both stabilized and destabilized trends, and that's our conclusion about Gaia theory, then we are not saying much—other than whatever is, is Gaia. If stability is Gaia, and if change is Gaia, then what is Gaia? There is no non-Gaia state, no null hypothesis. Sometimes Gaia is stable, due to some inadvertent negative feedbacks that create steady states (which must exist, as I argued earlier). But life also creates forcings on the biosphere's chemistry by way of evolution. So is that Gaia, too?

Lovelock (2003) has said that "Gaia theory clearly states that the Earth self regulates its climate and chemistry so as to keep itself habitable and it is this that is the sticking point for many, if not most, scientists." (See my comments to Lovelock in Volk, 2003a.) In the Schwartzman and Volk model, the temperature without life varies from 66°C to 46°C. With life the temperature varies from 66°C to 15°C. All right—I admit that at all these temperatures the Earth is "habitable." But "life" did not keep things more or less habitable, because as Schneider (1986) pointed out, it depends on what you are referring to. In this case is it hyperthermic microbes or tundra grasses?

The biosphere is a co-evolved entity consisting of life and what primarily are the by-products of life and the effects of those by-products (such as the waste CO₂ in the soil affecting the weathering rate). It's one big wasteworld. My calculations show that regarding the atmosphere's CO₂, more than 99 percent of the entire reservoir has recently been ejected by a living respirer rather than a volcano. For nitrogen, more than 99 percent has been discharged from living denitrifiers rather than volcanoes. And for methane and many other trace gases, more than 99

percent has been expelled from living prokaryotes rather than volcanoes. The atmosphere is one giant waste dump.

The great influence of life on the environment was one of the key insights of James Lovelock, and I salute him for that. And Tim Lenton has asked me to emphasize that the "production of waste by-products is an inevitable aspect of being alive." But I also will emphasize that I don't see any particular "optimization" or even securing of "habitability" in the numbers above. What I see is that life produces by-products and side effects that can shove the environment around into various chemical states. All organisms, linked in the chemical vessel of the biosphere, must adapt to these states or go extinct.

Why? Why can't organisms direct the global environment for their own benefit? Why can't they put substances into, say, the atmosphere that improve the atmosphere relative to their needs?

The main problem has to do with the dynamics of evolution and the issue of "cheats." Others have recognized this problem for Gaia theory and the resultant need to incorporate what is essentially a concept of by-products into the theory (Lenton, 1998; Wilkinson, 1999; Lenton, this volume). In particular, Ken Caldeira (1989) published a key paper that looked into the problem of cheats and the inability of organisms to be selectively evolved to change the global environment. I incorporated his work into a preliminary view of the biosphere as a wasteworld of by-products (Volk, 1998).

Caldeira attended the 1988 Chapman Conference on the Gaia Hypothesis as a graduate student in my department at New York University. I was later proud to serve on his dissertation committee. At the meeting, Caldeira became interested in the CLAW hypothesis (Charlson et al., 1987), that DMS (dimethyl sulfide) released to the atmosphere by marine plankton creates brighter clouds and cools the Earth, and is somehow connected to a feedback loop that impacts the plankton producers. Did some species of plankton evolve specifically to alter the clouds?

Caldeira analyzed this question. Could certain species of plankton have evolved to create DMS to create clouds above them for their own benefit (for example, perhaps the resulting cooler water stirred up more nutrients for the plankton)? Caldeira wanted to weigh these presumed benefits against the metabolic costs to the plankton of producing the precursor molecule to DMS. He liberally estimated an enhancement of growth from an increased stirring of nutrients. He conservatively tallied the metabolic costs. The finding:

no contest. Metabolic costs outweigh climatic benefits by a factor of a billion or more (Caldeira, 1989).

With such a skewed ratio of costs to benefits, mutant cheater plankton would proliferate. They could live mixed in with the DMS producers and derive all the benefits of upwelled nutrients without paying the huge metabolic costs. The lesson: Phytoplankton must synthesize the DMS precursor solely because it benefits their individual growth and reproduction while it is inside their bodies, not because this chemical affects the atmosphere. The precursor has indeed been proven to help cells regulate their ion contents relative to the surrounding salty water. Plankton don't even want to release DMS; it is forced from them in predation by zooplankton or bacteria. The survival-promoting, internal function of the DMS precursor is the reason why the genetic heritage of synthesizing it is passed on by the generations, not because it has a climatic effect when it is altered into a gas spreading across the sky.

What if DMS were in fact not beneficial but detrimental to marine life? More reflective clouds, for example, dampen photosynthetic potential by reducing the light that reaches the surface. In this case, the DMS emitters are actually hurting all the other life in their locale. But the emitters would still keep on emitting because of the huge survival benefits of regulating their internal ions. The numbers are of the same magnitude as before: The climatic detriment would be only a ripple on the ocean of the real evolutionary math going on within the organism. On the Gaian scale, whether DMS as a diffuse gas causes large-scale benefits or detriments (or both) may not matter, because the climatic effects forge intimate links among all organisms living within the DMS-determined climate. A world that is cooler because of DMS would have different climate zones, rainfall patterns, and ocean circulation.

If the world average temperature is now 5°C cooler because of DMS, and 35°C cooler because of the progressive biotic enhancement of weathering, then the whole living world is to some extent adapted to a physical reality vastly influenced by some forms of life. Tens of millions of species are united by DMS and the biotic enhancement of weathering. The situation is awe-inspiring: neither biogenic DMS nor the biotic enhancement of weathering evolved *because* it cooled climate, and yet their existence perpetrated free Gaian effects that profoundly link all life.

To conclude this section, note that the issue of by-products involves levels in space. The result of an organism's metabolism has to be to promote its own

reproductive potential. This means it will behoove the creature to keep the effects of its beneficial substances as close to its body as possible. Sending a costly substance out to change the atmosphere is not a good way to do this because the effects become so diffuse and easily shared with others, even halfway around the world. These others, if cheats, are not penalized for the metabolic costs of creating the effects, yet derive the same presumed benefit. We can start citing the different kinds of wastes that organisms produce, and the litany of side effects or by-products will grow substantially. To me, this litany, when eventually understood as a complex system of chemical interactions, is the structure of Gaia; this litany is fundamental to the dynamical shape of the biosphere.

Conclusion: By-products and Cycling Ratios Are Crucial to the Future of Gaia Theory

Although in earlier work I elaborated on the importance of by-products for Gaia theory and explicitly used the language of by-products and side effects (Volk, 1998), as I mentioned above, there were others who noted this phenomenon as well (though using different terminology and sometimes with different logical architecture). Tim Lenton (1998) developed the concept of "growth feedback" versus the stronger Gaia process of "selective feedback." I also wish to acknowledge David Wilkinson (1999) for seeing that the "cheater" problem is solved by considering global environmental effects as side effects.

Specifically, Lenton (this volume) says, "Indeed, many (and perhaps most) globally important biotic feedbacks appear to be based on by-products of natural selection." He goes on to identify one important pattern of Gaian dynamics associated with the effects from by-products: constraints on life that occur as the effects create extreme levels of environmental values which feed back to limit life (and thus those levels). Oxygen serves as an example. I think Lenton would basically agree with me that life's production of oxygen is crucial in creating a steady state of oxygen and that this state has been altered and generally increased over Earth's history into different values over many orders of magnitude. I agree with him that when a very high value of oxygen is reached (approximately not much higher than today's 21 percent), constraints can come into play that limit its further growth.

For example, photosynthesis, which is responsible for oxygen production, is biochemically limited as oxygen rises. Also, if terrestrial photosynthesis becomes limited by increased fires during excursions

into higher oxygen, phosphorus weathering (via the biotic enhancement of weathering) decreases, suppressing the supply to marine photosynthesizers and further limiting the production of oxygen (Lenton and Watson, 2000; Lenton, 2001). Thus oxygen might be constrained to about today's value by feedbacks involving life. I agree with Lenton that searching for constraints of this kind will be an important part of future science of Gaia theory. And I emphasize that such feedbacks were not evolved to constrain oxygen. They are by-products.

Lenton (this volume) agrees with me that there is nothing special in the mere existence of steady states in Gaia, that both living and nonliving systems typically reach steady states. Instead, he says, "what is of interest for Gaia is the degree of regulation." Lenton (2002) proposes two main properties to evaluate the degree of regulation: resilience and resistance. Does life make the chemical system of Gaia more resistant to changes? Does life make the system more resilient to changes in that the return to some steady state (not necessarily the original state) is quicker following an external perturbation?

Lenton tentatively answers "yes" to both questions, offering evidence from models and from Earth observations. How can we determine the truth of these proposals, given limited modeling studies? It does seem likely that systems with life could be more resilient (Volk, 2002). This is because shorter turnover times of elements in the reservoirs of ocean, air, and soil are implied by the increased rates of chemical fluxes that life creates in the environment. Shorter turnover times generally mean more rapid returns to steady-state conditions following perturbations. I also allow the possibility that systems with life will be more resistant, but I don't yet see any general reasons why this should be, given a wasteworld containing numerous positive and negative feedbacks that are side effects from by-products. Perhaps the mere fact of an increased number of feedbacks in a system with life ups the probability of regions of phase space in which the system is particularly stable.

I do want to go on record here that I think the word "regulation" should stop being used in Gaia theory. Its definition is too vague and subject to too many interpretations. The word is difficult to use precisely in a way that will be agreed on by everyone. For example, sometimes "regulation" means just the dynamics that create a relatively bounded steady state, a meaning that David Wilkinson used in a communication to me. Sometimes it has been used in discussions of Gaia to refer to a homeostasis of truly

beneficial conditions. Sometimes the word is limited to certain types of feedbacks with life compared to feedbacks without life, not in reference to the steady state itself (Lenton and Wilkinson, 2003). Because of this problem of shifting meanings and shades of meanings that change from paper to paper or even within papers, I never use the word.

To move toward my conclusions and to generalize, I submit that it's all by-products. It's all a world of life-forms interacting primarily with each other and their wastes. No one, as far as I am aware, has yet come forth with an example on the Gaia scale of an environmental effect that is selected for (in the evolutionary sense) to exist as a trait that costs the organism something to create. So if Gaia is built from by-products, then where do we stand with regard to Gaia theory?

First, we must throw out any concept that organisms are constructing the environment for their own benefit. Gaia is built from by-products. Lenton (this volume) and Lenton and Wilkinson (2003) agree that this statement about by-products is mostly true, and I see this as a major convergence among some of us involved in Gaia theory. But Lenton and Wilkinson also note that the specific favoring by natural selection of effects that enhance life as a whole might be true in specific cases. While I don't say this is impossible, I predict that the concept of global effects built from by-products will either always be true or so commonly true that the few cases in which the concept is not true will be trivial in our understanding of the dynamics of the biosphere. See Volk (2003b) for a critique of Lenton and Wilkinson (2003).

Second, we should realize that the effects of by-products released for free from organisms will shove the environment around into different states. For example, oxygen levels have varied by probably about six orders of magnitude over Earth's history, and carbon dioxide by three or more orders of magnitude.

Third, following Lenton's lead, we should consider that this shoving around of the environment will be subject to constraints which generally occur toward extremes when life overall is diminished as a result of the change. This diminishment will include not only the life-forms that create the push toward extremes but most other life-forms as well.

Fourth, we should look into Lenton's possibility of increased resistance and resilience as natural consequences of by-products released and merging into a complex system of fairly contained dynamics (the biosphere vessel). Currently I lean more strongly to-

ward the possibility of increased resilience, given the reasons outlined earlier.

Fifth, and finally, we should think about how by-products from certain groups of organisms are used by others. In a point stressed to me by Axel Kleidon, wastes still contain much chemical potential energy—for example, the feces of animals and the sloughed-off parts of plants. The entire human body enters the category of waste at death, but this is far from implying that the corpse is a chemical dead end, as the hordes of bacteria waiting to gobble us well know. Thus wastes to some creatures are actually foods for other organisms able to use the by-products as sources of energy or sources of necessary elements. Wilkinson (2003) and I have been emphasizing this aspect of Gaia, by which creatures become linked in a complex matrix of chemical exchanges with other, different creatures.

My proposal along these lines is to think about the biosphere as composed of organisms grouped in "biochemical guilds" (Volk, 1998). I was influenced by Ron Williams's book *The Molecular Biology of Gaia*, which deserves closer attention from the Gaia community (Williams, 1996). Williams discusses the main molecules of the nitrogen cycle, ranked by the magnitudes of different types of transformations of nitrogen. Glutamine synthetase, for example, ranks foremost in the pantheon of nitrogen enzymes by virtue of the sheer mass of nitrogen that it channels as an essential step in making all the nitrogen-containing compounds essential for life. The second most important molecule is nitrate reductase, key in synthesizing nitrite from nitrate, and the third is nitrogenase, which catalyzes nitrogen fixation.

I was motivated by Williams to think of Gaia's parts as sets of organisms grouped by their key molecular transformations—the "biochemical guilds." These can be conceptualized for different elements by grouping organisms that perform similar chemical transformations. Components of biochemical cycles are then formed by linked guilds. One biochemical guild produces a by-product waste as output that is the input flow to another biochemical guild. For instance, consider the photosynthesizers and respirers, in which the wastes from each (O_2 and CO_2 , respectively) become the gaseous "food" for the other.

Photosynthesizers and respirers together form a binary loop, but to fully map the carbon cycle we would have to add methanogens and methanotrophs, as well as other guilds. The nitrogen cycle is also composed of many biochemical guilds; the major ones are the

nitrogen fixers, denitrifiers, nitrifiers, ammonium assimilators, nitrate reducers, and ammoniificators. One can do the same analysis for sulfur, phosphorus, and all the nutrient elements essential for life. Ultimately, one would have a list of the guilds for all biochemical transformations mediated by life.

In conceptualizing the biosphere as linked guilds, it is clear that this is why global photosynthesis is greatly amplified over what it would be if it were limited to the sum of the fluxes of key elements into the biosphere from below. These supply fluxes are basically from rock weathering, ocean ridge exchanges, and volcanic emissions. For the example of carbon, these sources total about 0.5 billion tons of carbon entering Gaia each year.

Now let us conduct a thought experiment. Assume the products of photosynthesis are unusable. In other words, no molecule of fixed carbon from any plant or algae can be recycled to carbon dioxide by consumers. Thus assume totally indigestible bodies of photosynthesizers, which are all buried upon death and become parts of rocks such as shales. Photosynthesis in this imaginary case could still exist, but its global total would be limited to the flux each year into the biosphere, the 0.5 billion tons of carbon. That is a pittance compared to the actual global value of about 100 billion tons of carbon per year going into the bodies of photosynthesizers. The "extra" 99.5 billion tons comes from respirers.

One can form a ratio between today's value of the flux of a given element into photosynthesizers and the flux into the biosphere—"the cycling ratio" (Volk, 1998). For carbon the cycling ratio is about 200 (100/0.5). For nitrogen it's somewhere on the order of 500 to 1300. For sulfur it's only about 10. Thus the structure of the biosphere can be studied from the viewpoint of the cycling ratio.

The cycling ratio could be a metric for Gaia (Volk, 2002). A metric is a number we might use to compare states of systems involving life, across space (watersheds versus the global ocean) and across time. Perhaps there will be patterns that appear. Does the cycling increase over time as new guilds evolve to use what were once only wastes that exited unutilized from the biosphere system? Steve Schneider (1986) asked how we about might compute the Gaia-ness of Gaia. By biomass? By diversity? I suggest the cycling ratio.

In contrast to the cycling ratio, Kleidon (2002) proposed global productivity as a metric for Gaia. But note that in Kleidon's proposal if the supply from

beneath Gaia of some limiting element is suddenly doubled, and photosynthesis doubles as a result, we would call the new state "more Gaia." But I don't think we want to give the label "more Gaia" to such a simple response to what is essentially fertilization from outside the biosphere. "More Gaia" should come about from internal changes in the dynamics of some forms of life coupled to the dynamics of other forms, plus the environment of wasteworld. The cycling ratio as a metric captures that possibility. In addition, the cycling ratio as a metric in a model of Gaia dynamics has been successfully investigated in an evolutionary model by Downing and Zvirinsky (1999).

I don't know if we will find general principles that enable us to make Gaia theory more robust with precise language and hard-core findings. I hope so. In general, I think the quest to further Gaia theory will be helped by clearer attention to the world as it is as a source for data and ideas for models. In particular, we should continue to seek for and test principles via models and by thinking about patterns in Earth history, perhaps investigating Lenton's resistance and resilience, perhaps thinking along lines of an evolutionary drive toward higher cycling ratios by the successive evolution of new biochemical guilds that discover how to use wastes as food, and, finally, perhaps through developing concepts not even yet thought of.

Acknowledgments

I am indebted to Jim Lovelock for his inspiration to think big, for his invitations to the Oxford Gaia conferences, and for his courage to span disciplines. For formally requested comments on the earlier version of this chapter, I thank Tim Lenton, Axel Kleidon, and Lee Kump. I also value the more informal comments I received from Amelia Amon, David Schwartzman, and David Wilkinson.

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