NATURAL SELECTION, GAIA, AND INADVERTENT BY-PRODUCTS

A Reply to Lenton and Wilkinson's Response

TYLER VOLK

Department of Biology, 1009 Main Building, Mail code 5181, New York University, New York, NY 10003-6688, U.S.A.
E-mail: tyler.volk@nyu.edu

Abstract. Lenton and Wilkinson (2003), in response to me (Volk, 2002), have offered a number of important ideas for a Gaia theory of 'regulatory feedbacks' between life and the global environment. After what are generally positive comments on a selection of their concepts, I focus my reply on one specific point of disagreement. Contrary to the claim of Lenton and Wilkinson, nitrogen fixation is merely another example of how a by-product affects the shared environment among organisms. For Gaia theory to properly incorporate evolution by natural selection, we must distinguish between life's products and by-products. Because organisms evolve in environments altered by these by-products, I continue to support the idea that feedback loops in the biosphere contain segments based solely upon by-products of organisms' metabolisms.

1. Agreements with Lenton and Wilkinson

To help establish areas of convergence, I first discuss several areas in which I agree with Lenton and Wilkinson's development of Gaia theory. When I said that Gaia theory 'involves the search for general principles of the biosphere' (Volk, 2002), Lenton and Wilkinson have taken it to mean that I require 'universally true generalities about Gaia' (Lenton and Wilkinson, 2003, hereafter LW). Let me be clear: I am in accord with LW that we should not expect universal truths, and, furthermore, what matters is to find tendencies in the dynamical organization of the biosphere (I use 'Gaia' and 'biosphere' as equivalent terms). So we are in agreement over what the search is about. For instance, LW are themselves searching for generalities with regard to what they call 'regulatory feedbacks' (more on that later).

I think we all agree that the Gaia system is complex, that the Earth's surface system is more complex with life than it would be without, that the system has dynamics with both positive and negative feedbacks, and that there are a large number of external and internal variables that exert forcings on the system, for example: the sun, extraterrestrial impacts, Earth's geodynamics, and population fluctuations as well as biological evolution.

I also agree that the tendency of the Gaia system to return to a stable state following a perturbation is by itself not particularly interesting, and I am glad that LW concur; such behavior is not one of the general principles that we would trumpet forth as a keystone of Gaia theory. This is because abiotic systems with chemical

Climatic Change **58:** 13–19, 2003.

reactions will also generally reach bounded conditions in their dynamics, assuming chemical source flows that enter and sinks that leave, because the internal reactions that constitute the system will be linked in numerous feedbacks. In general, such systems with complex phase spaces (whether Earth's biosphere, the atmosphere of Mars, or the core of the Sun), will settle into dynamical regions that are relatively stable, usually because such dynamical regions have stronger negative feedbacks that bound fluctuations caused by weaker positive feedbacks.

I commend LW for their clear statement about what they see as the main substance of Gaia theory. To them, Gaia theory is about 'regulatory feedbacks'. They define these as feedbacks that are either more 'resistant' or 'resilient' in the face of perturbations, compared to feedbacks that would exist in an abiotic state. The generalization that the Earth's surface system has regulatory feedbacks could well be true, in my opinion. They claim that there are indeed regulatory feedbacks and, furthermore, distinguish between a 'lucky' and 'probable' Gaia, depending on whether regulatory feedbacks occur on Earth because of the chances of history or because a planet with life tends to develop such feedbacks. I agree with LW that either case offers an important research agenda, involving the elucidation of these feedbacks. I emphasize, along lines of LW, that it is not the mere existence of feedbacks that constitute a Gaia theory, but the existence of feedbacks that are substantially different in fundamental ways from feedbacks that would exist on an Earth with only abiotic surface chemistry, however complex.

2. Gaia Is Built from By-Products

I have emphasized the importance of by-products for the Gaia system (Volk, 1998, 2002). The basic idea was also put forth independently by Wilkinson (1999). LW also bring this crucial concept to the fore when they state, in their Section 6, that 'many (and perhaps most) globally important feedbacks appear to be based on by-products of natural selection'.

What are by-products? In the simplest example, by-products are wastes from organisms. These wastes (such as carbon dioxide from respirers, or oxygen from photosynthesizers) were not metabolically evolved by organisms to be sent out into the environment for altering its chemistry. Instead, the wastes are substances to be gotten rid of, as unusable or even toxic internal materials created by metabolism. Yet these substances can and do affect the global environment: witness the presence of high levels of oxygen in our atmosphere.

Some substances are by-products not because they are actual wastes but because as products they have additional environmental effects that are different from their metabolic functions for the producing organisms. For example, acids released by soil microbes liberate phosphate from rocks, thus gaining a crucial nutrient for these producing organisms. This process has the side effect of also releasing calcium ions from the rocks, which carry carbon dioxide to a burial in the

ocean as calcium carbonate. Such an impact on Earth's atmosphere and climate is inadvertent, meaning that the evolutionary pressure that led to the existence and evolutionary stability of the microbial acids was upon the direct metabolic benefits of nutrients to the soil microbes. The evolutionary pressure was not to create consequences for the atmosphere.

Assume that some large-scale environmental effect was created as the direct consequence of the evolved metabolism by some organism. I mean, assume that an aspect of a metabolism was selected for during evolution by natural selection, specifically to use metabolic resources to create the large-scale environmental effect. In this hypothetical case (important for Gaia theory were it true), the cheater problem raises it head. Cheats who do not pay the metabolic costs of environmental improvement would soon take over and drive to extinction the producers who are paying the metabolic costs. Thus for large-scale matrixes such as the atmosphere and ocean, the effects from life must be for free, as side effects from by-products.

This much is recognized by LW as true in 'many (and perhaps most)' cases of feedbacks. But then LW offer the case of nitrogen fixation as something fundamentally different. Here I disagree.

Because the nature of my disagreement is so fundamental in the way LW and I view the developing Gaia theory (and thus the actual structure of the biosphere), I must set the stage for discussion by quoting a key paragraph that begins Section 7 of LW:

> Kirchner and Volk are particularly skeptical about the possibility of feedback involving natural section. We agree that it is not valid to *generalize* that 'Life enhancing effects would be favored by natural selection' (Kleidon, 2002). However, it may be true in *specific* cases, when carriers of the responsible traits benefit more from those 'life enhancing effects' than non-carriers. (Italics in original; their citing of Kirchner refers to Kirchner, 2002.)

For clarity, the topic here is life-enhancing effects in the big sense – for life as a whole – not just any limited, specific species of life that creates a substance involved in the global feedback. So, can natural selection favor such life-enhancing effects? Could natural selection create 'better' conditions in atmosphere and ocean? Or are 'better' and 'favorable' only illusions from the apparent match we see between life and the environment, a match perhaps derived solely from the fact that organisms are evolutionarily adapted to whatever inadvertent conditions they themselves or others create through their by-products and side effects?

What exactly am I skeptical about? Let me state it forthwith: I do not think that evolution by natural selection can create creatures that change the large-scale shared environments within Gaia (such as atmosphere and ocean) to be more favorable for life as a whole unless the changes are inadvertent. In other words, effects that enhance life as a whole are not specifically created by metabolisms evolved for the function of making those effects.

In their example, LW posit that nitrogen fixation is a 'real world example' of 'life enhancing effects favored by evolution'. Now, in an e-mail, Lenton has written me that he doesn't claim that 'organisms fix nitrogen because of its effect on their environment'. But the point LW raise about life as a whole is that the nitrogen fixed by the nitrogen fixers 'leaks' out to increase the available nitrogen to other creatures in the environment. Thus all do benefit from the fixers. Furthermore, there is a population selection between fixers and non-fixers, which limits the spread of the fixers as the leaked nitrogen becomes generally available, by operating as a negative feedback on the populations of the fixers.

Here is my point: the leaked nitrogen is merely a by-product! One form of leak occurs because nitrogen-fixers serve as food sources for other creatures, who, in consuming the fixers, living or dead, derive organic nitrogen as well as other elements; thus nitrogen in the fixed state starts circulating among various creatures in the soil or ocean matrixes. Another form of leak is the direct excretion of nitrogenous wastes from the fixers. I emphatically agree with Lenton's statement above: Nitrogen fixers did not evolve to leak nitrogen into the environment. They evolved to bring nitrogen from the gaseous, diatomic state into the fixed state for use in their own bodies. But we must be clear that the 'leakage' to the environment is a by-product. Thus the effects of the leakage upon other creatures, upon the amount of environmental fixed nitrogen, and thus upon the populations of the fixers themselves are effects that result from a by-product that enters into these complex ecological dynamics.

But if leaked nitrogen is a by-product, then what do LW mean by using the case of nitrogen fixation as a real world example of a feedback involving natural selection that enhances life as a whole? I don't know. I do not see any fundamental distinction between the case of nitrogen fixation and the cases cited by LW as feedbacks involving by-products. Their cases of by-products (the first two of which I went into in detail in Volk (1998)) include: (1) the climatic effect of leaked DMS from algae, from a precursor, DMSP, that serves a primary metabolic function as cellular osmoregulatory substance; (2) the effect on climate and carbon dioxide from the biotic enhancement of weathering, with one example of this enhancement being the phosphate-liberating acids discussed earlier; and (3) the effect on the source of atmospheric oxygen from phosphate weathering in the soil (in other words, the biotic enhancement of weathering). Does the case of nitrogen fixation differ?

True, in the example of nitrogen fixation the by-product is the same chemical substance as the product (considering fixed nitrogen as a category that lumps the fixed ammonium ions with ions of nitrite and nitrate, which are all forms of fixed nitrogen). But my point is that the fixed nitrogen, when released into the environment is a by-product, not a product. It 'enhances' other life forms because they are capable of using it. The nitrogen changes phenomenological status from product to by-product when it leaves the bodies of the fixers.

Consider a similar example. Plants fix atmospheric carbon and put it into carbohydrates, proteins, and lipids, which are products the plants make by paying energetic costs for building their bodies, surviving, and reproducing. This fixed carbon then enhances virtually all of life because it becomes available as food for animals, fungi, and microbes. The fixed carbon from photosynthesizers is the source of carbon for all non-photosynthesizers. When in the body of a plant, the fixed carbon is a product it took metabolic costs to create. But as soon as the fixed carbon is leaked out (for example, when a caterpillar eats a leaf), it switches phenomenological status to a by-product because this leakage was not the reason that the fixed carbon was produced.

In an e-mail to me after reading a draft of this paper, Wilkinson told me that he and Lenton raised the issue of nitrogen fixation as a 'possible example of a non by-product system'. He said this possibility is more likely in soil than water. Soil is a site where exceptions occur in my rule that leaks are by-products. In soil, leaks can be confined to local loops that link different, neighboring life forms. For example, plants can leak fixed carbon to nitrogen fixers or mycorrhizal fungi that live in their roots, a case of biochemically intimate neighbors exchanging substances in evolved, symbiotic relationships. This is a specific, closely knit relationship. But note: The leaked carbon from roots is not intended to increase the overall soil carbon for everyone, though it does have that inadvertent side effect.

It will be, I contend, crucial for Gaia theory – which deals with global matrixes of soil, atmosphere, and ocean – to distinguish products from by-products. I have yet to see an example on the Gaia scale (say for the global atmosphere or ocean) of an environmental effect that is selected for (in the evolutionary sense) as a trait that costs the organism something to create. LW's example of fixed nitrogen does not allay my skepticism. The effects on the scale of Gaia will all be side effects from by-products.

3. Conclusion: Natural Selection and By-Products

Where does evolution by natural selection come in? Through trial and error it develops new kinds of creatures with new kinds of metabolisms. These new kinds of metabolisms range from the large-scale phenomena of new biochemical guilds (Williams, 1996; Volk, 1998), for example, the nitrogen fixers (Falkowski, 1997) and nonphotosynthetic sulfide oxidizers (Canfield and Teske, 1996), to the more detailed scale of minor new substances, such as variants of hemoglobin. As organisms evolve, they do so in the context of global environments altered by way of by-products. Thus an evolutionary loop is set up that goes from organisms creating by-products that alter the environment, back to effects on the further evolution of all organisms experiencing the environment (Volk, 1998). And as LW point out, there is another kind of loop from the altered environment back to creatures, as populations adjust in size.

The evolutionary loops just described are key to creating the complex number of feedback circuits in the biosphere that involve populations of categories of organisms, from species to biochemical guilds, as well as the global biogeochemical cycles of carbon, nitrogen, phosphorus, sulfur, iron, calcium, and about a dozen other essential elements.

Recognizing that the effects of life on the global scale are through by-products does not diminish a respect for the complexity of the biosphere. And it does not negate the awe many researchers (including myself) feel as we struggle to understand what might be called a global physiology. But the relationship between organisms and this global physiology follows a logic very different from the relationship between our body's cells and our body. Cells produce products for other cells, insulin for example. Insulin is not a waste. Gaia is different. What organisms give off into the globally circulating environments of air and water are wastes.

I repeat for emphasis: The distinction between products and by-products is crucial for the future of Gaia theory. In some cases, such as cellular DMSP becoming atmospheric DMS, by-products for Gaia come from transformed metabolic products. In other cases, by-products are substances or effects formed inadvertently from the actions of products. For example, the biotic enhancement of weathering affects atmospheric levels of carbon dioxide through a sequence of linked causes and effects. In still other cases, such as the leakage from nitrogen fixation, the by-products are essentially the same as products, but the different location (inside versus outside the cell or organism) makes a difference because the effect when the internal substance becomes an external by-product is an unintended side effect, not the reason that drove the evolution of the metabolism that creates the product.

From one point of view, global feedbacks all involve natural selection, but not because global feedbacks are created from products. Rather, life forms adapt through evolution to the conditions created by the by-products. The life forms are thereby fit to the environment. By thriving for some duration in geological time, they prove themselves able to cope with some degree of the inevitable environmental changes. Perhaps the life forms create different kinds of by-products as a result of evolutionary adaptation or different amounts of by-products as a result of population adjustments. Gaia will be understood as a complex system of feedbacks involving by-products.

Acknowledgements

I thank Tim Lenton and David Wilkinson for their generous consideration of questions I asked and issues I raised during a series of e-mails about Gaia theory, David Schwartzman for ongoing discussions, and Stephen Schneider, with special gratitude, for conducting these ongoing deliberations about Gaia theory.

References

Canfield, D. E. and Teske, A.: 1996, 'Late Proterozoic Rise in Atmospheric Oxygen Concentration Inferred from Phylogenetic and Sulfur-Isotope Studies', *Nature* **382**, 127–132.

Falkowski, P. G.: 1997, 'Evolution of the Nitrogen Cycle and its Influence on the Biological Sequestration of CO_2 in the Ocean', *Nature* **387**, 272–275.

Kirchner, J. W.: 2002, 'The Gaia Hypothesis: Fact, Theory, and Wishful Thinking', *Clim. Change* **52**, 391–408.

Kleidon, A.: 2002, 'Testing the Effect of Life on Earth's Functioning: How Gaian is the Earth System?', *Clim. Change* **52**, 383–389.

Lenton, T. M. and Wilkinson, D. M.: 2003, 'Developing the Gaia Theory: A Response to the Criticisms of Kirchner and Volk', *Clim. Change* **58**, this issue.

Volk, T.: 1998, *Gaia's Body: Toward a Physiology of Earth*, Copernicus Books/Springer-Verlag, New York.

Volk, T.: 2002, 'The Future of Gaia Theory', *Clim. Change* **52**, 423–430.

Wilkinson, D. M.: 1999, 'Is Gaia Really Conventional Ecology?', *Oikos* **84**, 533–536.

Williams, G. R.: 1996, *The Molecular Biology of Gaia*, Columbia University Press, New York.

(Received 11 September 2002; in revised form 8 January 2003)