

# THE GAIA HYPOTHESIS: CONJECTURES AND REFUTATIONS

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**Abstract.** The uncertainties surrounding global climate change provide ample evidence, if any were necessary, of the need for a whole-system view of the Earth. Arguably the most visible – and controversial – attempt to understand Earth as a system has been Lovelock's Gaia theory. Gaia has been a fruitful hypothesis generator, and has prompted many intriguing conjectures about how biological processes might contribute to planetary-scale regulation of atmospheric chemistry and climate. In many important cases, however, these conjectures are refuted by the available data. For example, Gaia theory predicts that the composition of the atmosphere should be tightly regulated by biological processes, but rates of carbon uptake into the biosphere have accelerated by only about 2% in response to the 35% rise in atmospheric CO<sub>2</sub> since pre-industrial times. Gaia theory would predict that atmospheric CO<sub>2</sub> should be more sensitively regulated by terrestrial ecosystem uptake (which is biologically mediated) than by ocean uptake (which is primarily abiotic), but both processes are about equally insensitive to atmospheric CO<sub>2</sub> levels. Gaia theory predicts that biological feedbacks should make the Earth system less sensitive to perturbation, but the best available data suggest that the net effect of biologically mediated feedbacks will be to amplify, not reduce, the Earth system's sensitivity to anthropogenic climate change. Gaia theory predicts that biological by-products in the atmosphere should act as planetary climate regulators, but the Vostok ice core indicates that CO<sub>2</sub>, CH<sub>4</sub>, and dimethyl sulfide – all biological by-products – function to make the Earth warmer when it is warm, and colder when it is cold. Gaia theory predicts that biological feedbacks should regulate Earth's climate over the long term, but peaks in paleotemperature correspond to peaks in paleo-CO<sub>2</sub> in records stretching back to the Permian; thus if CO<sub>2</sub> is biologically regulated as part of a global thermostat, that thermostat has been hooked up backwards for at least the past 300 million years. Gaia theory predicts that organisms alter their environment to their own benefit, but throughout most of the surface ocean (comprising more than half of the globe), nutrient depletion by plankton has almost created a biological desert, and is kept in check only by the nutrient starvation of the plankton themselves. Lastly, where organisms enhance their environment for themselves, they create positive feedback; thus Gaia theory's two central principles – first, that organisms stabilize their environment, and second, that organisms alter their environment in ways that benefit them – are mutually inconsistent with one another. These examples suggest that the further development of Gaia theory will require more deliberate comparison of theory and data.

## 1. Introduction

My title is a whimsical tip of the hat to Popper's (1963) classic collection of essays, in which he puts forth the view that science progresses by an iterative process of conjecture and refutation, as theories are speculatively proposed, tested against observations, revised, and tested again. With the benefit of hindsight one can see a



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similar process underway with Gaia, although in my view there has been rather a lot of conjecture, and rather too little willingness to recognize that these conjectures are often refuted by the available data. I emphasize that in spite of this, I believe that Gaia has been fruitful as a metaphor and a hypothesis generator, and I have consistently said so in print (Kirchner, 1989, 1991, 2002).

In this contribution I have three objectives. The first is to address specific points raised by Lenton and Wilkinson (2003) in their response to my recent commentary (Kirchner, 2002) and the commentary by Volk (2002). The second is to use Lenton and Wilkinson's comments as a springboard to expand and clarify my views on Gaia and the Earth system. The third is to outline new directions for Gaia theory, in the hope that it can contribute to the further development of Earth system science.

Particularly because I have been a vocal critic of the Gaia hypothesis, it is important to make clear that I substantially agree with many of its central themes. I agree with Gaia, in the sense that I think that no view of the Earth system can be complete – or even approximately correct – without accounting for the pervasive influence of biological processes on Earth's surface chemistry and climate. I agree that coupling between the atmosphere and biosphere should naturally give rise to feedback. I also agree that coupled feedback systems can exhibit 'emergent' behaviors, including self-regulation. And most importantly, I agree that it is essential to understand the Earth system as a *system*, rather than as a set of disconnected components.

At a mechanistic level, I think that Gaia's supporters and I largely agree about how the Earth system works. I think we disagree, however, about how to characterize the behavior of that system. Specifically, I do not think that the data warrant the generalizations that Gaia's supporters have put forward, to the effect that biological feedbacks generally enhance the self-regulation of the atmosphere-biosphere system, or that organisms generally alter their environment to their own benefit. I think that given the currently available data, we need to seriously consider the possibility that in many cases, Earth's climate has remained relatively stable in spite of biologically mediated feedbacks rather than because of them.

## 2. Should One Generalize about Gaia?

One of my tasks in this contribution is to respond to points raised by Lenton and Wilkinson (2003) – hereafter denoted as LW – where I believe a response is required. LW caricature Volk's recent commentary on Gaia (Volk, 2002), saying 'Volk criticizes Kleidon and Lenton for giving only a finite number of examples to support their arguments'. In fact, Volk criticized Kleidon for giving only *two* examples to support the sweeping generalization that 'life has a strong tendency to affect its environment in a way that enhances the overall benefit'; Volk then gave two counter-examples to show how shaky this generalization is. And Volk did not criticize Lenton for giving 'only a finite number of examples' at all; instead he questioned whether Lenton's treatment was even-handed, asking, 'how can we be

sure that Lenton is not giving more weight to evidence that fits his pre-selected conclusions?' This is a fair question in the context of the past 30 years, during which Gaia's proponents have vigorously advanced the view that life stabilizes Earth's climate, while largely ignoring the substantial body of evidence that biological feedbacks also can (and do) destabilize Earth's climate. It is also a fair question in the context of Lenton (2002), despite LW's assertion that 'an effort was made to objectively balance available evidence'. While Lenton clearly acknowledges the *theoretical possibility* of biologically mediated positive feedbacks, in 14 pages he makes only a few passing references to the biological feedbacks that *actually do* destabilize Earth's climate.

Later in the same paragraph, LW say, 'Volk does not level the same criticisms at his own attempts to generalise or those of Kirchner. To make progress, criteria for what constitutes a reasonable argument must be applied in a consistent manner'. This kind of indirect accusation is a debater's trick: with no supporting evidence of any kind, it simultaneously insinuates that Volk and I have indulged in generalizations similar to Kleidon's, and accuses Volk of applying a double standard. Where is the unwarranted generalization – or the generalization of any sort – in Volk's paper or my own?

Indeed, I have been arguing for more than a decade that the quest for grand generalizations is *part of the problem*, because it can blind us to the diversity of feedback processes in the Earth system (Kirchner, 1989). I certainly agree with LW that, 'We should not expect there to be universal truths about the behavior of such a complex system . . . Life is not always going to enhance gross primary productivity . . . or any other metric of the system'. But I disagree with their view that 'What matters is the balance of examples: do they suggest a tendency in one direction?' In my view, what matters is not 'the balance of examples', what matters is *how the Earth system works*, in all its intriguing diversity and complexity. To be useful, generalizations need to be almost universally true, and this is unlikely given the great diversity of life (and environments) on Earth. Even if there is a 'tendency' one way or another, the exceptions will make any generalization misleading as a guide to how the system works.

This is not to say that generalizations are not useful *as hypotheses*, and therefore as spurs to investigation. It makes perfect sense to put forward the hypothesis that biological feedbacks increase the Earth system's resistance or resilience to perturbation, or increase its habitable range of conditions, and Lenton's framing of terms in this way has been helpful. This hypothesis can be useful as an organizing concept, as a means of focusing attention, and as a spur to inquiry, and years ago I said the same thing about its precursor, the 'homeostatic Gaia' hypothesis (Kirchner, 1989). Hypotheses like these, *as questions*, motivate us to look at mechanisms in the Earth system and ask what their consequences are for its regulatory behavior.

But we should be careful not to confuse the question with the answer; it is the journey (the process of inquiry) that is helpful here, not the putative destination (a proclamation that the hypothesis is or isn't proven). What we should expressly *not*

do is tally up the examples for and against, and – presuming that there were more and better examples in favor – consider the hypothesis to be proven and apply it as a generalization, despite the exceptions. That would convert a perfectly fertile hypothesis into a sterile orthodoxy.

Science is a process, a journey toward a better collective understanding. It is not a mere contest, in which all one needs to do is to declare a winner and a loser. Thus the most useful answer to a question such as, ‘Do biological feedbacks increase the Earth system’s resistance to perturbation?’ is *neither* ‘Yes, they do’ nor ‘No, they don’t’. The most useful answer instead is, ‘These mechanisms do, and those mechanisms don’t, and here are their implications for how the system functions. And here are all the other things we need to figure out as a consequence’.

Particularly given the conceptual plasticity of the Gaia concept, one should be cautious about even a well-meaning search for confirmatory examples. The risk is not that such an effort might fail, but rather that it will always succeed through open-ended re-interpretation of the theory, the observations, or both. It is worth recalling the impact of other theories that invited similar re-interpretation of observations, and that were similarly heralded as fundamental breakthroughs in human knowledge some time ago:

These theories appeared to be able to explain practically everything that happened within the fields to which they referred. The study of any of them seemed to have the effect of an intellectual conversion or revelation, opening your eyes to a new truth hidden from those not yet initiated. Once your eyes were thus opened you saw confirming instances everywhere: the world was full of verifications of the theory. Whatever happened always confirmed it. Thus its truth appeared manifest; and unbelievers were clearly people who did not want to see the manifest truth . . . (Popper, 1963).

Watching from outside, I have the sense – and I want to emphasize that this is just my subjective impression – that some of those involved with Gaia theory are caught in the uneasy tension between two impulses. The first impulse is to interpret the history of the Earth as an epic tale in which the organisms play heroic starring roles. The second impulse, driven by a broad-minded curiosity, is to probe the complexities of the Earth system puzzle wherever they may lead. I have the sense (again subjectively) that over time, the second impulse is having a growing influence on the development of the Gaia concept. In my view this is all for the good.

### 3. Gaia and Planetary Regulation

Just as LW caricature Volk’s critique, they caricature mine as well, saying ‘Kirchner suggests that some Gaia theorists are still arguing for universal or overwhelming negative feedback as a feature of the Gaia system, as if this were a prerequisite for regulation’. I did not say that Gaia’s proponents argue for ‘universal or

overwhelming negative feedback'. What I said was precisely this: 'Gaia's proponents appear to view the Gaia hypothesis as combining elements of what I have termed "Homeostatic Gaia" (i.e., biologically mediated feedbacks stabilize the global environment) and a qualified form of "Optimizing Gaia" (i.e., biological modifications of the environment make it more suitable for life)' (Kirchner, 2002). That is, if anything, a highly *conservative* interpretation of the written record, as the following examples illustrate:

The notion of the biosphere as an active adaptive control system able to maintain the Earth in homeostasis we are calling the 'Gaia' Hypothesis. (Lovelock and Margulis, 1974, titled 'Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis').

The Gaia hypothesis ... postulates that the climate and chemical composition of the Earth's surface are kept in homeostasis at an optimum by and for the biosphere. (Lovelock and Watson, 1982).

Planetary life must be able to regulate its climate and chemical state ... the greater part of our own environment on earth is always perfect and comfortable for life ... Through Gaia theory, I see the Earth and the life it bears as a system, a system that has the capacity to regulate the temperature and composition of the Earth's surface and keep it comfortable for living organisms (Lovelock, 1988).

The Gaia hypothesis, when we introduced it in the 1970s supposed that the atmosphere, the oceans, the climate, and the crust of the Earth are regulated at a state comfortable for life by and for the biota. Specifically, the Gaia hypothesis said that the temperature, oxidation state, acidity, and certain aspects of the rocks and waters are at any time kept constant, and that this homeostasis is maintained by the organisms at the Earth's surface. It is important to recognize that the Gaia hypothesis so stated is wrong ... Through Gaia theory I now see the system of the material Earth and living organisms on it, evolving so that self-regulation is an emergent property. In such a system active feedback processes operate automatically and solar energy sustains comfortable conditions for life. The conditions are only constant in the short-term and evolve in synchrony with the changing needs of the biota as it evolves (Lovelock, 1995).

The Gaia theory proposes that organisms contribute to self-regulating feedback mechanisms that have kept the Earth's surface environment stable and habitable for life (Lenton, 1998).

The Gaia hypothesis of Lovelock states that life regulates Earth's functioning for its own benefit, maintaining habitable, or even optimum conditions for life (Kleidon, 2002).

The Gaia theory proposes that the Earth system self-regulates in a habitable state (Lenton, 2002).

From these three decades of re-statements of what Gaia means, one can discern both enduring themes and important changes over time. The most important change is that the notion of an Earth regulated ‘by and for the biosphere’ has generally been abandoned, nowhere more explicitly than in Lovelock’s 1995 revisions to his 1988 book. The two enduring themes – reflected in the passages quoted above, but more so in the surrounding body of work on Gaia – are that biological feedbacks contribute to the regulation of the environment, and that they help to maintain habitable or comfortable conditions for ‘life’ (which presumably means the life forms that are dominant under those conditions). I agree that such feedback processes exist, and I have consistently said so in print (Kirchner, 1989, 1991, 2002). I have also consistently argued that we need to pay more attention to cases in which biological processes *destabilize* the environment or make it *less* comfortable for life.

#### 4. Biotic Destabilization of Earth’s Environment

Think about it: in the Gaia literature, where can one find detailed elucidations of the biologically mediated feedbacks that are thought to *undermine* the stability of the Earth’s climate (e.g., Lashof, 1989; Lashof et al., 1997; Woodwell et al., 1998; Cox et al., 2000)? When have Gaia’s advocates proposed a biologically mediated *positive* feedback mechanism? The one example that I can think of is the DMS hypothesis, but that was originally proposed when DMS appeared to act as a global thermostat (Charlson et al., 1987); only later did it become apparent that this ‘thermostat’ is hooked up backwards, serving to make the Earth cooler when it was cool and warmer when it was warm (Legrand et al., 1988, 1991; Kirchner, 1990; Watson and Liss, 1998). In Gaian interpretations of the history of the Earth, periods of rapid change are often attributed to external perturbations rather than inherent instabilities in the Earth system. Likewise, destabilizing feedback is often presented as an aberration that arises during the breakdown of regulatory mechanisms (e.g., Lovelock and Kump, 1994), rather than an intrinsic characteristic of many biologically mediated processes. Thus it seems to me that the Gaia literature selectively emphasizes biologically mediated processes that produce stabilizing feedbacks rather than destabilizing ones.

In response to my summary of biological feedbacks affecting global warming, drawn from reviews by Lashof (1989), Lashof et al. (1997) and Woodwell et al. (1998), LW note that, ‘When considering future global warming, it is most important to know the *overall sign* of feedback, which cannot simply be deduced from how many feedbacks are positive and how many are negative’ (italics in original). I agree. But if LW are familiar with this literature, they should be aware that Lashof (1989) has answered precisely this question, by estimating the strength of a large number of biologically mediated climate feedbacks (including the negative feedback resulting from direct fertilization of vegetation by CO<sub>2</sub>). Lashof concluded that *the overall sign is positive*, with the net effect of *amplifying* the sensitivity of

the Earth system to anthropogenic climate change. In Lashof's analysis, the overall feedback gain for biologically mediated climate feedbacks is 0.08–0.44, compared to an estimated gain of 0.17–0.77 for the sum of the water vapor, cloud albedo, and snow albedo feedbacks. The uncertainties in any such calculation are substantial, and Lashof's analysis may not be the final word on the subject, but it is currently the best available quantitative summary of the best available data. As such, Lashof's analysis is an empirical refutation of Lenton's hypothesis that biological feedbacks make the Earth system more resistant to perturbation.

Although the available evidence indicates that biological feedbacks will amplify global warming, the buildup of greenhouse gases in the atmosphere has been slowed by biological uptake of anthropogenic CO<sub>2</sub>, as LW point out. But again it is important to estimate the quantitative strength of this feedback. Anthropogenic carbon emissions have raised the concentration of CO<sub>2</sub> in the atmosphere from a pre-industrial concentration of roughly 275 ppm to its present value of roughly 370 ppm, an increase of approximately 35%. The best available estimates indicate that this increase in atmospheric CO<sub>2</sub> has prompted an increase in the net rate of carbon uptake into the terrestrial biosphere of roughly 2 or 3 Pg C per year (Schimel et al., 2001), whereas gross primary productivity and gross respiration of the terrestrial biosphere are each roughly 120 Pg C per year (Schlesinger, 1997). Thus the terrestrial biosphere's gross primary productivity has increased (or its gross respiration rate has decreased) by only 1.7–2.5%, in response to a 35% increase in atmospheric CO<sub>2</sub>. Viewed in these quantitative terms, the coupling between atmospheric CO<sub>2</sub> and carbon uptake by the biosphere is weak, consistent with Lashof's (1989) estimate of a negative feedback gain of only –0.02. From an ecological perspective this is not surprising, since CO<sub>2</sub> is not a limiting nutrient in many ecosystems.

Nor does this picture change when uptake by the ocean is included. Gross carbon uptake by the ocean is roughly 90 Pg C per year (Schlesinger, 1997), and has increased by roughly 1.8 Pg C per year, or 2%, again in response to anthropogenic increases in atmospheric CO<sub>2</sub> totaling 35% (Schimel et al., 2001). Thus both terrestrial and oceanic uptake are only weakly coupled to atmospheric CO<sub>2</sub>. Note in particular that whereas Gaia theory would predict that increases in atmospheric CO<sub>2</sub> should have a much stronger effect on terrestrial ecosystem uptake (which is biologically mediated) than on ocean uptake (which is primarily abiotic), the available data indicate that both are about equally *insensitive* to atmospheric CO<sub>2</sub> concentrations.

The Gaia hypothesis holds that the composition of the atmosphere is tightly regulated by biologically mediated feedbacks. Yet anthropogenic releases of carbon have pushed atmospheric CO<sub>2</sub> far beyond the range of concentrations seen on Earth for the last 400,000 years, and this anomalously high concentration has persisted for much longer than the mean lifetime of CO<sub>2</sub> in the atmosphere. If atmospheric CO<sub>2</sub> were tightly regulated by the Earth system, the increase in atmospheric CO<sub>2</sub> could have been prevented by adjustments of only 3–4% in the gross fluxes between

the atmosphere, the oceans, and the terrestrial biosphere. The fact that this has not happened demonstrates that atmospheric CO<sub>2</sub> is *not* tightly regulated by the Earth system, even though CO<sub>2</sub> is an important controller of Earth's climate, and even though CO<sub>2</sub> participates directly in the most fundamental processes of life. Thus the failure of the Earth system to tightly regulate atmospheric CO<sub>2</sub>, at least on human timescales, is another empirical refutation of the Gaia hypothesis.

The Vostok ice core record shows that to the extent that the Earth system regulates CO<sub>2</sub>, CH<sub>4</sub>, and DMS in the atmosphere, all three of these planetary 'thermostats' are hooked up backwards, functioning to make the Earth cooler during glacial periods and warmer during interglacials (Petit et al., 1999). LW claim that this behavior is consistent with Gaia theory, noting that 'many complex systems undergo transitions between states in which positive feedback predominates'. I agree that complex systems often undergo transitions driven by positive feedback. But it makes no sense to call such behavior 'regulation', just as it would make no sense to say that a drunkard was 'regulating' the path of his truck as it swerved down the street, alternately smashing into parked cars on the right and the left. To the extent that biologically mediated feedbacks control CO<sub>2</sub>, CH<sub>4</sub>, and DMS, they apparently *destabilize* Earth's climate on timescales of 100,000s of years. Thus the ice core data provide yet another empirical refutation of the Gaia hypothesis.

### 5. Is Gaia More Consistent with the Distant Past?

Perhaps recognizing the extent to which the current behavior of the Earth system tends to contradict the Gaia hypothesis, LW note that, '... we must be clear about the *timescale* of concern. Gaia theory is concerned with over 3.5 billion years of Earth history. Focusing on the coming centuries and the past ~1 million years is unlikely to give a representative picture, especially if we happen to live at an unusual time of transition' (*italics in original*). I agree that we might live in a time of transition, but I see no reason to believe that times of transition are anomalous. The geological record of the distant past does not necessarily paint a less dynamic picture than the present, particularly when we recognize that the geological record often disguises abrupt fluctuations by averaging them out (and it does so more strongly, the farther back we look). New high-resolution isotopic measurements for the more distant past are now becoming available, and they reveal abrupt fluctuations in temperature and atmospheric composition scattered throughout the geologic record at least as far back as the Cretaceous (Arens and Jahren, 2000; Jahren et al., 2001; Zachos et al., 2001) and the Permian (Retallack, 2002).

Referring to the hypothesis that 'negative feedback is stronger in the presence of life', LW argue that, 'Just because it is falsified at present on relatively short timescales does not mean it is falsified on longer timescales or throughout Earth history'. We need to keep in mind that the recent past is the part of Earth history that we know the best, and the present is the *only* part of Earth history in which we



can directly observe Earth system processes at work. To the degree that the Gaia hypothesis is contradicted by recent Earth history, where our observational data are relatively good, one is not entitled to assume that it will necessarily fare any better in the distant past, where our data are relatively poor. Indeed, in isotopic records stretching back at least to the Permian, peaks in paleotemperature correspond to peaks in paleo-CO<sub>2</sub> (Retallack, 2002). Thus, if CO<sub>2</sub> is biologically controlled as part of a global thermostat, the data suggest that this thermostat has been hooked up backwards for at least the past 300 million years.

We also need to keep in mind that as we look farther and farther back in time, our interpretation of the geological and palaeontological record becomes more speculative and ill-constrained. Particularly because Gaia theory and ‘geophysiology’ invite open-ended re-interpretation (Kirchner, 1989, 1990), it is hardly reassuring that Gaia might be able to explain the behavior of the Earth system in the distant past, where the theory and the data are *both* sufficiently ill-constrained that they could be re-interpreted to make them consistent with each other.

Finally, whether or not Gaia theory adequately explains the Earth system’s behavior a billion years ago, the fact that it is so plainly contradicted by many prominent feedbacks in the present-day Earth system ought to put to rest any notion that Gaia theory provides ‘the essential theoretical basis for the putative profession of planetary medicine’ (Lovelock, 1986; see also Lovelock, 1991 and chapter 7 of Lovelock, 1995). Indeed, given the pervasiveness of destabilizing biological feedbacks, it is appropriate to question whether the Earth system has been stabilized by biological feedback processes, or *in spite of* them.

## 6. Biological Feedback at the Limits of Habitability

There are ultimate constraints to the extent to which biologically mediated feedbacks can destabilize Earth’s climate. A biologically mediated feedback mechanism cannot drive the environment to extremes that would cause the extinction of the organisms responsible for that same feedback (Kirchner, 2002). Thus, as Lenton (2002) has put it, ‘feedbacks involving life *automatically* tend to stabilise habitable conditions, because they involve biotic effects that can (by definition) only operate under habitable conditions’ (*italics in original*). This would seem to be virtually a proof-by-definition of the Gaia hypothesis, and to some extent it is. However, it is important to remember that the single term ‘life’ encompasses a vast diversity of organisms, and the range of conditions that are ‘habitable’ for *some* organism or another is very broad indeed – encompassing, for example, temperatures spanning over 60 °C and oxygen concentrations spanning at least two orders of magnitude. Thus, while a biologically mediated positive feedback cannot push environmental conditions beyond the range that is habitable for the organisms responsible for it, it *can* push conditions outside the habitable range for other organisms, and thus drive them to extinction. This is not just a hypothetical pos-

sibility. It has happened in Earth history, nowhere more dramatically than during the Proterozoic, when a biologically driven rise in atmospheric oxygen drove the previously dominant life forms (anaerobic bacteria) to extinction, everywhere that they were exposed to Earth's atmosphere (though they survive today in anaerobic refuges, such as sediments and our own digestive tracts).

Nonetheless, I agree with LW that at the limits of habitability (for the specific organisms involved), biologically mediated feedbacks should generally be stabilizing. A good example of such a self-limiting biotic feedback is the tendency for populations to grow until they have depleted their environments of essential resources (nutrients, water, food, light, etc.) so severely that their further growth is constrained. This phenomenon, which has recently (and aptly) been termed 'biotic plunder' by Toby Tyrrell of Southampton University, has been widely recognized since at least the time of Malthus:

Among plants and animals the view of the subject is simple. They are all impelled by a powerful instinct to the increase of their species, and this instinct is interrupted by no reasoning or doubts about providing for their offspring. Wherever therefore there is liberty, the power of increase is exerted, and the superabundant effects are repressed afterwards by want of room and nourishment . . . (Malthus, 1798).

Likewise the growth of populations can be constrained by the wastes that they produce, as populations 'foul their own nests' and thus make their environments less suitable for themselves (Kirchner, 1989). This is just another case of biotic plunder, in which the resource that has been plundered is the environment's capacity to handle wastes. If one organism's wastes are another organism's food, then a symbiotic interaction between them may serve to relax those particular resource constraints. In that case, the population continues to grow until the biotic plunder of some other resource (ultimately either light or another source of free energy) leads to such severe resource depletion that further growth is impossible.

This behavior is clearly stabilizing, as Lenton (2002) points out: '...any biotic effect that pushes environmental conditions towards the boundaries of what is tolerable to the responsible organisms will be stopped by self-limiting negative feedback'. But this is hardly a beneficent mechanism that creates *favorable* conditions for the biota. Instead it acts as the ultimate constraint to the organisms' capacity to make their environment wholly uninhabitable. This kind of feedback often achieves stability at the outer limits of habitability; in the language of 200 years ago, 'misery is the check that represses the superior power of population and keeps its effects equal to the means of subsistence' (Malthus, 1798). A good example is the 'biotic plunder' of nutrients from the surface ocean as plankton take up nutrients, die, and sink (Volk, 2002). This biologically mediated process has created a biological desert over most of the world's oceans, constituting over half of Earth's surface area. Biotic plunder by plankton is limited only by the nutrient starvation of the plankton themselves.

These negative feedbacks at the outer limits of habitability might be termed a form of regulation – just as, in my whimsical metaphor above, the parked cars along the side of the street could be said to ‘regulate’ the path of the drunkard’s careening truck as it smashes into them, and thus is deflected back into the roadway. Semantically speaking this may be ‘regulation’, but an environment that is regulated in such a manner is hardly one that is ‘always perfect and comfortable for life’ (Lovelock, 1988).

## 7. Gaia and Natural Selection

LW misrepresent my argument when they say, ‘Kirchner raises a theoretical problem that many evolutionary theorists have had with Gaia, that of “cheats”’. I have *never* raised the problem of ‘cheats’; neither the term nor the concept appears anywhere in any of my papers on Gaia. Since my argument has been so thoroughly misunderstood, let me briefly try again; for a more complete explanation, see pp. 401–403 of Kirchner (2002).

The environment is, by definition, that which is shared among organisms. To the extent that a trait improves or degrades the environment, it will affect its carriers and its non-carriers equally. For a trait to spread via natural selection, it must give its carriers an advantage over its non-carriers. Therefore, to the extent a trait improves the environment rather than the individual, and thus benefits its carriers and its non-carriers equally, natural selection will have *no effect* on it.

This fact may offend our sense of fairness, but it is an inevitable result of how natural selection works. If a trait benefits individuals, its carriers will fare better than its non-carriers and produce more offspring. As a result, that trait will become more common in each successive generation. By contrast, if a trait benefits the shared environment, it will benefit its carriers and non-carriers alike and they will both produce equal numbers of offspring. Thus that trait will not become more common in the gene pool over time. Therefore, natural selection will generally favor traits that benefit individuals, whether they enhance the environment or degrade it.

That was my central argument for why one should not generally expect natural selection to favor environment-enhancing traits (or, for that matter, environment-degrading traits). As I also pointed out, this argument may not hold if the environment is *not* shared alike between carriers and non-carriers (such as in metapopulations, e.g., Kirchner and Roy, 1999). In such cases, it is theoretically possible for natural selection to favor environmental altruism, that is, to favor traits that benefit the environment at a cost to the individual. For this to occur, at least two conditions must be met. First, the ecosystem must be partitioned into a collection of local organism/environment assemblages which compete with one another, leading to a form of group selection. Second, the distribution of altruistic individuals must be patchy, such that altruists are more likely to find themselves

among other altruists, and thus are more likely than non-altruists to share in the benefits of altruistic behavior (Sober and Wilson, 1998). These conditions can arise in spatially patchy populations with limited dispersal, where organisms' environmental effects are localized in the immediate vicinity. If these conditions are met, then whether environmental altruism is favored will depend on the relative strength of selection between groups (favoring altruism) versus selection among individuals within groups (favoring selfishness). Thus the hypothetical possibility of Gaian altruism is not inconsistent with natural selection, but the hard work has not yet been done; one needs to show that the necessary conditions arise in the real world, and one needs to show that inter-group selection is sufficiently strong. One cannot simply assume that traits will be favored by evolution because they are good for the environment or the group; as Sober and Wilson (1998) have put it, 'Many people axiomatically assume that societies, species, and ecosystems have evolved to function harmoniously. It is not easy to grasp the fragility of this assumption, and once grasped, the lesson learned is often troubling'. I think that LW and Volk share my view that this assumption is particularly fragile in the case of Gaia. In particular, to the extent that Gaia is principally concerned with the atmosphere and oceans (which cannot be readily partitioned among groups) and concerned with the global biota (comprising organisms with conflicting needs) it is difficult to see how global-scale altruism can evolve, even through group selection.

In some cases, of course, traits that benefit the individual may also *coincidentally* enhance the environment. Nitrogen fixation in nitrogen-limited ecosystems is one such example, as LW suggest. Natural selection will favor these traits, but it will generally favor them to the degree that they benefit the individual, not the environment. As evidence of this, consider that legumes have a special structures (root nodules) that help them retain as much of their hard-won nitrogen as possible, thus minimizing the benefit that they provide to their environment. The benefit to the environment comes from the nitrogen that inadvertently leaks out as a by-product of nitrogen fixation.

Traits that benefit the individual may also degrade the environment; for example, many organisms are highly evolved to sequester resources for themselves, even at the cost of impoverishing their environments. Natural selection will promote the spread of such traits if they are beneficial for individuals, even though their end result is 'biotic plunder' and widespread resource depletion. In human affairs, the counterpart to this phenomenon is termed the 'tragedy of the commons' (Hardin, 1968).

## 8. Feedback on Selection

If traits alter the environment in ways that affect their carriers and non-carriers differently, then their environmental consequences can affect natural selection. This is 'feedback on selection' in Lenton's terminology. Using LW's example of nitro-

gen fixation, as nitrogen fixers become more common in an ecosystem, nitrogen becomes more widely available, thus diminishing their fitness advantage over non-nitrogen-fixers. Over time, this negative feedback will modulate the abundance of nitrogen fixers and non-fixers in response to changes in nitrogen availability, as LW point out.

As another example, consider the traits that enable organisms to hoard resources for themselves, thus depleting their environments. As resource-hoarding organisms become more common (and thus resources become scarcer), organisms that efficiently hoard resources will gain an ever-growing advantage over those that do not. This positive ‘feedback on selection’ serves to turbocharge the process of ‘biotic plunder’, with the end result being a highly depleted environment and organisms that are highly efficient at hoarding resources.

It is important to recognize that whether or not natural selection is mediated through environmental changes (that is, feedback on selection), it cannot and will not systematically favor traits that confer a general environmental benefit. I think that LW understand this, but I belabor the point because many others do not. Traits that are beneficial to the individual *may* also confer a broader benefit as a by-product (in the case of nitrogen leakage by nitrogen fixers), as LW and Volk (1998, 2002) have both pointed out. Alternatively, they may degrade the environment as a by-product (as with resource-hoarding). Natural selection will favor them equally in either case (at least in the absence of group selection). If a trait gives its carriers an advantage over its non-carriers it will spread by natural selection, whether it enhances or degrades the environment as a result.

## 9. Environmental Enhancement and Natural Selection

Discussions of Gaia often feature the notion that organisms generally alter their physical and chemical environments in ways that benefit them. LW misrepresent my argument on this point, attributing to me the view that ‘the observation that the environment is remarkably well suited to life does not *necessarily* mean that the predominant process has been for life to alter the environment’ (emphasis added). In fact I argued that this does *not at all* mean that life has altered the environment to its benefit. What I said was that claims such as ‘rainforest vegetation influences its climate to its own benefit . . . are semantically correct *but mechanistically misleading*, because they suggest that the environmental conditions have somehow been adjusted to the needs of the organisms. Instead, it is more mechanistically accurate to say that natural selection has made rainforest organisms dependent on rainforest conditions, which are partly of their own making’ (emphasis added).

Rainforest vegetation flourishes in the damp of the rainforest, and transpiration by the dense vegetation contributes substantially to that dampness. But rainforests are *not* wet because rainforest vegetation likes it that way. Even when such notions are semantically purged of their teleological overtones, they still utterly fail as

mechanistic explanations for why rainforests are wet. There is simply no mechanism by which the affinity of rainforest vegetation for dampness could be translated into a process of natural selection that makes the rainforest wetter. Instead, the particular organisms that will thrive in a rainforest are those for whom its wet, dark environment is advantageous, whether or not they contribute to those wet, dark conditions.

It is crucial to keep in mind that natural selection acts primarily on individuals (Goodnight and Stevens, 1997), and that there is an inherent asymmetry between individuals' consequences for their environment, on the one hand, and the environment's consequences for individuals, on the other hand. How much is the rainforest environment altered by the addition or removal of a single tree (not an entire tree species, just a single individual tree)? A little bit, but not much. By contrast, the survival of each and every tree depends *entirely* on the physical, chemical, and biological characteristics of its local environment.

In other words: each individual of each species has only an *incremental* effect on its local environment, but the characteristics of the local environment *completely determine* which individuals survive there and which don't. Therefore the process by which organisms become well-matched to their environments is overwhelmingly one of natural selection of organisms that happen to conform to local environmental conditions, not one of the environment being somehow adjusted to the benefit of the organisms that happen to live there. Claims that life alters the environment to its benefit, which appear widely in the Gaia literature – including in much of Lovelock's work, in Kleidon (2002) and at least three times in Lenton (1998) – are fundamentally misleading. *Of course* the species that we find in a rainforest benefit from the rainforest environment; if they didn't, they wouldn't survive there, and we would find other species there instead!

The key point that is missing from Gaian discussions of organisms and their environments is that the composition of the biota is not fixed in advance. Ecosystems are open systems; their boundaries are porous to continuous dispersal of organisms from other ecosystems. Organisms are continuously subject to competition, not only from other species in their ecosystem but from species dispersing from other ecosystems as well. This process of competition determines the species composition of the ecosystem, and guarantees that the dominant organisms will be those best suited to the local environment.

As anyone who has walked through a forest knows, the local environmental characteristics – the availability of water, the amount of light streaming through the canopy, the slope and aspect of the terrain, the abundance of pathogens and parasites, the nutrient levels in the soil, and so forth – change continuously from place to place. Each point on the terrain is bombarded by seeds and spores; some of these originate in the local environment and others are would-be colonizers from other environments. Only a tiny fraction of these seeds and spores will survive to reproduce themselves. On average, the ones that survive and thrive will be the ones that are best suited to the environmental characteristics of the particular point

on the terrain where they happen to land. It is primarily through this process of natural selection among competing species (and secondarily through the much slower process of evolutionary ‘adaptation’ of the traits of individual species) that the organisms found at any point on the landscape become well-matched with their local environmental characteristics.

The local environment is also incrementally altered by each individual that lives there. Thus, as the species composition at each location changes, so do the net effects on the environment. Through time, this process of natural selection leads to the self-assembly of a collection of organisms (metaphorically termed a ‘community’) that can survive and thrive in the conditions that they and their co-occurring species have created. This is hardly a Gaian notion; ecologists have been studying this process for decades.

Thus I agree with LW that there is a feedback loop between an ecosystem’s species composition and its environmental conditions; I have consistently said so, and I know no ecologist or Earth scientist who thinks otherwise. I have also consistently said that the cumulative effect of a collection of organisms on their environment can be substantial. But *membership* in that collection of organisms – and thus the match between those organisms and their environment – is overwhelmingly determined by the causal arrow that points from the environment to the biota, not the other way around. Each individual alters its environment only incrementally, and it does not necessarily do so in ways that enhance the environment for its needs.

The same principles apply at the global scale. Although we refer to ‘the global environment’ in the singular, we are actually referring to a diverse collection of ecosystems, encompassing a vast range of environmental conditions. The processes of dispersal and colonization described above are constantly at play across these environmental gradients. As environmental conditions change, they shift the boundaries between different communities, and thus alter the predominance of membership in the global biota. Thus during ice ages we may have more tundra, and during interglacials we may have more tropical forests. These shifts in ecosystem boundaries in turn affect the global climate, for example by altering the planet’s albedo, latent heat budget, and atmospheric composition. Thus the climate and the biota co-evolve. As the global environment evolves, the composition of the global biota will shift, because those organisms whose needs are well met by the environment will flourish: more penguins during glacial times, perhaps, and more toucans during interglacials. Therefore, Gaian notions that environmental conditions on Earth ‘evolve in synchrony with the changing needs of the biota as it evolves’ (Lovelock, 1995) are, from a mechanistic standpoint, exactly backwards. The environment is always well-suited to the needs of the predominant organisms, precisely because that is *why* those particular organisms are predominant.

In the case of the rainforest environment, LW propose that one can test ‘whether organisms are flourishing primarily because of their impact on the environment or

primarily because they have adapted to the environmental conditions that they have partly created', as follows:

If alteration of the environment and the resulting feedback dominates over adaptation we would expect the rainforest-climate system to be prone to rapid transitions when sufficiently perturbed, e.g., a switch to an arid pasture/desert state. If adaptation has been the main shaping factor, we expect no such collapse. Some models have predicted catastrophic collapse . . . We wait pessimistically to see how the real system behaves.

I agree with LW that the rainforest-climate system may collapse if it is extensively disrupted. I think that we also agree, at a mechanistic level, about *why* it is vulnerable to collapse: the rainforest environment is partly a by-product of dense rainforest vegetation, and a shift to a drier climate could prompt a thinning of rainforest vegetation, a reduction in local recycling of transpired water through the atmosphere, and an invasion of other species better suited to the drier environment. Species that thrive in a drier environment will typically transpire less water (because they can't afford to waste it), thus making the environment drier still. So LW and I agree that feedback occurs here, but we disagree about how to characterize it. To me, it makes little sense to describe the rainforest environment as having been altered to suit the needs of rainforest vegetation, just as it would make little sense to describe dryland vegetation as altering its environment to its benefit when it refrains from transpiring too much water (even though one could claim that this helps to prevent a transition to a rainforest environment, which would be fatal for it). Instead, I think the only mechanistically sensible view is this: the particular organisms that we find in the rainforest are those for whom the rainforest environment is suitable, and the rainforest environment is partly the result of the organisms that live there. Thus rainforest species thrive in a rainforest environment that is partly of their own making. But rainforests are not wet because rainforest species like it that way; instead, it is precisely whether an organism thrives in those damp, dark conditions that determines whether it is found in a rainforest or in some other environment instead.

Proponents of Gaia theory do not readily acknowledge that its two central principles – first, that organisms stabilize their environments, and second, that organisms alter their environments in ways that benefit them – are mutually inconsistent with one another (Kirchner, 1989). Consider the rainforest as an example. Because rainforests are wet, vegetation can grow densely in them. Thus rates of transpiration (and subsequent re-precipitation) of moisture are high, and the canopy is tall and dense; all of these factors make rainforests even more humid. This in turn permits even denser vegetation, which makes the rainforest even more humid, and so on. This positive feedback process cannot go on forever, because it is ultimately constrained by the finite supply of sunlight. But it *is* a positive feedback process, and it is therefore *destabilizing*, as illustrated by the possibility of a rapid spiraling collapse, described in the paragraph above. The rainforest moisture feedback is destabilizing (and thus violates the first principle of Gaia theory) precisely be-



cause it involves environmental effects of dense vegetation that promote still denser vegetation (consistent with the second principle of Gaia theory).

## 10. Evolution of the Gaia Hypothesis

Reiterating almost verbatim an argument that has been made by Gaia's proponents for at least a decade (see Lovelock, 1990), LW say reactions to Gaia in the scientific community have been progressing through the three classic stages – first 'it is obviously wrong', then 'there may be something in it', and finally 'we have known it all along'. It seems to me that the community's reaction to Gaia has changed largely because Gaia itself has changed. The early versions of Gaia made extravagant claims, such as 'global homeostasis by and for the biosphere', that indeed *were* 'obviously wrong', as Lovelock (1995) now agrees. By contrast, recent statements to the effect that 'The Gaia theory proposes that the Earth system self-regulates in a habitable state' (Lenton, 2002) are so self-evident that indeed we all really *have* 'known it all along' – we've known that Earth self-regulates (since there is no external agent to do the regulating), and we've also known from the fossil record that Earth has been in a habitable state for much of its history.

As I said in my first Gaia commentary, it invites confusion when the single term 'Gaia' is used to refer to observations that are self-evident and propositions that are highly speculative. That confusion persists today. Just compare the first sentences of Kleidon (2002) and Lenton (2002): does Gaia mean only that 'the Earth system self-regulates in a habitable state', or does Gaia mean that 'life regulates Earth's functioning for its own benefit, maintaining habitable, or even optimum conditions for life?' Is Daisyworld merely a 'parable' (Watson and Lovelock, 1983) that was 'never intended... to be more than a caricature' (Lovelock, 2000), or is Daisyworld 'a cybernetic proof of the Gaia hypothesis' (Lovelock, 1983) that implies that 'seventy-five years of neo-Darwinist science will need to be rewritten' (Lovelock, 2000)? If Gaia's proponents cannot be clear and consistent about what Gaia means, it is unrealistic to expect the broader community to intuit its meaning on their behalf.

Like it or not, there is a legacy associated with the Gaia label, resulting from the extravagant claims of the 1970s and 1980s and from the ensuing New Age hype. Many scientists' impressions of Gaia are inevitably colored by the outlandish claims that were stridently publicized under the Gaia label in the early years (and were not directly retracted until 1995). Gaia's supporters decry this situation, and imply that the community's views on Gaia are outdated. But it is simply myopic to expect otherwise. Beyond the narrow sphere of Gaia supporters, it is unrealistic to expect the community to keep up with the continually shifting definitions of what Gaia means. It is easy to understand why many in the Earth system science community want nothing to do with the Gaia label, because of the connotations that it carries.

Thus my own view is that if there is to be a future for Gaia theory, it will involve Gaia's supporters integrating themselves into the larger Earth system science community, and abandoning the notion that Gaia stands apart from (or perhaps even in opposition to) that broader effort. I think this will also require abandoning the Gaia label, for the reasons outlined above.

Since this is likely to be the last commentary that I will write on Gaia for some time, I would like to take the liberty to suggest several ways forward for Gaia theory, in the hope that it can play a productive role in the further development of Earth system science.

First of all, it is important to *move beyond Daisyworld*. Daisyworld has served a useful purpose in illustrating how simple feedback relationships can produce self-regulating behavior without conscious control. For those without prior training in systems analysis, this is an important lesson to learn, and Daisyworld teaches it effectively. For those unaccustomed to systems thinking, a first glimpse of the phenomenon of systems-level emergent behavior often comes as a revelation, and permanently alters one's outlook. Daisyworld is now widely used as a teaching tool for precisely this purpose, and that is all for the good. My only reservation is that I think that Daisyworld has almost nothing useful to say about how climate is regulated on the real Earth. By this I do not mean simply that on the real Earth, vegetation albedo is only weakly coupled to climate (Schneider, 2001), or that this coupling, however weak, is probably a *positive* feedback, just the opposite of what the Daisyworld model assumes (Kirchner, 1989, 2002). Rather, my concern is that even as an abstract model, Daisyworld's generality – and thus its applicability to the real world – has been exaggerated.

Daisyworld is widely interpreted as demonstrating that atmosphere-biosphere systems will always self-stabilize near the biological optimum. Daisyworld indeed does this, but only because of a specific assumption embedded in the model. In the real world, natural selection will generally favor behaviors that benefit individual organisms, whether they improve the environment or degrade it. But in Daisyworld, the *only* behaviors that benefit individuals are those that also improve the environment. Thus, Daisyworld to some extent assumes what it sets out to prove (for a more detailed discussion, see Kirchner, 2002). Although many elaborate Daisyworlds have been developed over the years, to my knowledge they all retain this built-in bias from the original Daisyworld model.

This bias can be reversed by making a biologically plausible change in a single parameter. This simple parameter adjustment converts Daisyworld into a bi-stable system that strictly *avoids* the biological optimum, as I showed over a dozen years ago (see Figure 3 of Kirchner, 1989). What is most interesting about this alternative Daisyworld is that when subject to perturbations, its climate would undergo unstable, positive-feedback transitions between its two end-member states, which is at least qualitatively consistent with the ice core data (Kirchner, 1989).

But instead Daisyworld has, perhaps inadvertently, been configured to be pathologically stable. Daisyworld is a one-feedback model; there is only one en-

vironmental variable and it is regulated by extremely strong feedback with the simplest possible biosphere. Such a simple model necessarily exhibits simple behavior. By contrast, on the real Earth many different environmental variables are coupled simultaneously, through many different feedback relationships, with a highly complex biosphere composed of organisms with diverse (and often incompatible) environmental requirements. Such a complex system can exhibit many kinds of behavior that a simple Daisyworld model cannot. I fully understand the reasons for making highly simplified models, but the first rule of model-building is to preserve the core features of the system that one is trying to study. The problem is that Daisyworld is intended to explore the stability properties of hypothetical atmosphere-biosphere systems, but the stability properties of a one-feedback system like Daisyworld are fundamentally different from those of more complex systems, let alone *realistically* complex systems.

When I say there is a need to move beyond Daisyworld, I am not advocating the construction of equally heuristic models of ever-greater complexity. In order to be anything more than illustrations of abstract concepts in systems theory, models must be *mechanistically plausible* and *quantitatively realistic* in relation to the system under study. Otherwise, with a handful of feedback loops and arbitrary coefficients, almost any model can produce almost any behavior. It is also essential that model behavior be comparable against real-world behavior at comparable scales (Schneider, 2001); otherwise models cannot be tested against data. Building and testing quantitatively appropriate models of real-world atmosphere-biosphere interactions, although harder work than building hypothetical Daisyworlds, is likely to yield more relevant insights for Earth system science. Recent modeling efforts by Lenton and colleagues (Lenton, 2001; Lenton and von Bloh, 2001; Lenton and Watson, 2000) are a step in the right direction.

Second, it is important to *move beyond simply theorizing*. Nothing would do more to promote Gaia's acceptance in the broader community than a successful test of an a priori prediction, for which the canonical example is Eddington's confirmation of general relativity in 1919. Lovelock's observation that Earth's atmosphere is maintained in extreme chemical disequilibrium was a palpable early success, but by itself this simply demonstrated biology's pervasive influence on the chemistry of the atmosphere (which in any case was already largely understood by biogeochemists – see Hutchinson, 1954), rather than the regulatory coupling envisioned by Gaia theory. After several decades and several iterations of Gaia theory, there is an urgent need for that theory to be tested against data. Unfortunately, Gaia theory makes predictions that are abstract and qualitative, making them difficult to test in the real world.

However, the simple models developed by Gaia theory might be testable against laboratory microcosms, which they somewhat resemble. At the AGU Chapman conference on Gaia in 1988, I remember attendees asking why nobody had built laboratory microcosm experiments to demonstrate that organisms could meaningfully regulate their own environment, the way Gaia theory says they should.

Hamilton (1995) reiterated this challenge seven years later, and as of today (seven years still further on) the challenge remains unanswered, to the best of my knowledge. Unless one can demonstrate that Gaia theory can correctly predict how a simple microcosm experiment will evolve under controlled laboratory conditions, is there any reason to expect that Gaia theory can correctly predict how the global atmosphere-biosphere system will evolve under real-world conditions?

When testing models of Gaia, it is important to test them against observations, not against one's preconceptions of how the world ought to behave (Kirchner, 1989). For example, Lovelock has repeatedly touted the fact that strong environmental coupling strongly stabilizes ecosystems in Daisyworld, even when the model includes many interacting species. This, according to Lovelock (1995), shows the superiority of Daisyworld models over conventional biological models:

What is it, then, that confers the great stability and freedom from cyclical and chaotic behavior on the Daisyworld models? The answer is that in Daisyworld the species can never grow uncontrollably; if they do, the environment becomes unfavorable and growth is curtailed. Similarly, while daisies live, the physical environment cannot move to unfavorable states; the responsive growth of the appropriate colored daisy prevents it. It is the close coupling of the relationships which constrain both daisy growth and planetary temperature that makes the model behave.

But the problem is that 'making the model behave', in Lovelock's view, entails making the model behave *placidly*, whereas this is rarely how real-world ecosystems behave. Indeed, the whole reason that ecologists began modeling ecosystems in the first place was to explain the highly *unstable* behaviors that often characterize population dynamics in the real world – the boom and bust cycles, the local extinctions, and so forth. These real-world population dynamics are an empirical refutation, both of Daisyworld and of preconceptions that the natural world is necessarily a tranquil place, harmoniously regulated at delicately adjusted equilibria.

Third, it is important to *move beyond generalities about 'life' and 'the global environment'*. The Gaia literature is marked by numerous conjectures about how life affects the global environment, but one needs to recognize that neither life nor the global environment are monolithic. The seductively simple term 'life' encompasses a vast array of organisms with diverse and often contradictory environmental requirements. The equally seductive term 'the global environment' encompasses a complex spatial patchwork of environmental conditions spanning, at a single point in time, more than 60 °C in temperature, 7 units of pH, three orders of magnitude in ambient pressure, and several orders of magnitude in the concentrations of many biologically important chemical constituents – and that's just the *habitable* environment. Thus attempts to generalize about either life or 'the environment' can be fraught with conceptual difficulties.

Many of the proposed tests for Gaia are based on assessing whether Earth's surface environment would be different without life. Would an abiotic Earth be

less resilient and resistant to perturbation (Lenton, 2002)? Would the environmental conditions prevailing on an abiotic Earth be less conducive to biological productivity (Kleidon, 2002)? These hypotheses have the advantage of being fairly precise, but the disadvantage of being untestable in practice. They also have the more serious disadvantage of being far removed from the most pressing issues in Earth system science – namely, how the climate system works and how it will evolve in the future. We know that a planet without life would be radically different from the one we all live on now. Thus I think Kleidon could be correct that gross primary productivity is higher on the present-day Earth than it would be under the environmental conditions that would prevail on an abiotic Earth (particularly with a present-day biota). But what would that prove? One is tempted to say that it would prove the Gaia hypothesis, but it would only prove one specific conjecture based on Gaia – and one with little relevance to understanding the current Earth system. How would that conjecture, assuming it were proven, help us to understand the phenomenon of biotic plunder? Likewise I think Lenton could be correct that the present-day Earth is more resistant to perturbation than an abiotic Earth would be. But how would that help us to understand why, according to the best available evidence, biologically mediated feedbacks are likely to *amplify* the effects of anthropogenic global warming? The urge to seek generalizations is always strong, but here I think a more nuanced approach is needed.

Fourth, it is important to *keep the dialogue civil*. My criticism of Gaia over the years has been pointed, but I have always tried to be precise, factual, and fair, and I have never engaged in name-calling. I regret that Lovelock's response has been to characterize me as a 'figure of the Inquisition' (Lovelock, 1990) and to characterize my critique as a 'polemic' (Lovelock, 1995) and as 'sophistry, not science' (Lovelock, 2000), while refusing to acknowledge that my critique is available in print, thus preventing his audience from drawing their own conclusions on the issues at hand. Scattered through the Gaia literature are gratuitous slams such as 'Geologists have tried to persuade us that the Earth is just a ball of rock . . . and that life is merely an accident, a quiet passenger that happens to have hitched a ride on this rock ball in its journey through space and time. Biologists have been no better' (Lovelock, 1995). These kinds of comments are unfair and counterproductive, and they should stop. To pretend that Earth scientists and biologists live in completely separate worlds is to deny the existence of the entire field of biogeochemistry, which predates Gaia by decades (Kamen, 1946; Hutchinson, 1950, 1954; see also Gorham, 1991).

Lovelock's scorn for evolutionary biologists takes me aback: 'A paradoxical saying goes, "The measure of a scientist's eminence is the length of time he, or she, holds up progress in the field". If confirmation were needed of Charles Darwin's eminence this measure provides it . . . zealous disciples of Darwin by taking his words as if they were revelations, not just the thoughts of a scientist, are making a creed for biology and so hindering its natural development . . . In such a climate of almost religious intolerance it was hardly surprising that the Gaia hypothesis

never stood a chance' (Lovelock, 1995). The biologists of my acquaintance are not narrow-minded zealots. Most of them disagree with Gaia, but they have valid reasons for doing so. Most biologists and Earth scientists are good people, and the way they have been caricatured in the Gaia literature (particularly in books written for the general public, who are in no position to know any better) is a disservice to science.

Gaia has helped to raise interest in the whole-system view of Earth, and that is all for the good. It has helped to introduce systems concepts like feedback and emergence to a wider audience, and that is an important contribution as well. Yet Gaia remains marginalized. One reason is certainly Gaia's New Age connotations, but I believe that a larger problem is that many are put off by the tone – simultaneously defensive and self-congratulatory – of much of the Gaia literature. Here too, however, there appears to be recent progress. The new generation of Gaia supporters appears to be less eager to antagonize the rest of the community, and I hope that this heralds the beginning of a new trend.

Finally, it is important to *stay focused on the things that matter*. It should not matter whether the current version of Gaia theory survives intact. It should not matter whether the Gaia label endures. It certainly should not matter who is perceived to have 'won' the Gaia 'debate'; as I said early in this essay, science is a journey of exploration, not a paltry contest. What should matter is that we all keep moving forward, toward a clearer understanding of how the Earth system works.

In exploring big questions, where our comprehension is puny compared to our incomprehension, the most treacherous obstacle is a misguided sense that we already know the answers. My greatest worry about Gaia is that it could lead to a false confidence that once one accepts that biological systems are intrinsically self-regulating, understanding the Earth system is easy. The only check against this kind of facile complacency – to return to where this commentary began – is the scientific process of conjectures and refutations. It is essential to remember that theories are no more than conjectures, and to resist becoming entranced by them. And when the data contradict those conjectures, it is essential to see them for the refutations that they are. This is not easy – our first instinct is often to rescue the theory by denying or reinterpreting the data – but in the long run, it is the only way forward.

We have made considerable progress toward unraveling the complexities of the Earth system, but what we know is still dwarfed by what we don't know. What controls the magnitude and duration of glacial/interglacial climate cycles, and why have they changed over time? Why has the anthropogenic increase in atmospheric CO<sub>2</sub> so far resulted in a global temperature increase of only 1 °C or so, rather than the much larger rise that one would expect from the correlation between temperature and CO<sub>2</sub> in the ice core data (Kirchner, 2002)? What controls the patterns of extinction and diversification in the fossil record, and how are they linked to changes in climate? Anyone can come up with a long list of unanswered questions like these, and the Earth system no doubt holds many other important puzzles that we have not even imagined yet.

And it is our home. Mankind's impact on the atmosphere and the biosphere is growing daily, and growing at an ever-faster rate. We need to understand the consequences of these trends for the global environment and the biota. We also need to understand how to react constructively to this predicament. These are crucial matters, and it is crucial to be clear-headed about them. We must see things as they are, not as we wish they were. Let us go forward, then, with all the dedication, skill, insight – and clear-headedness – that we can marshal for the task.

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