

DEVELOPING THE GAIA THEORY

A Response to the Criticisms of Kirchner and Volk

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1. Introduction

This paper is a response to the recent criticisms of Gaia theory by Kirchner and Volk, in this journal (Kirchner, 2002; Volk, 2002). As noted by Kirchner, there is a need for more dialogue on this topic, and we write in this spirit with the intention of helping clear a pathway 'Toward a future for Gaia theory', to use Volk's phrase. We agree with Kirchner and Volk on a number of points. Our purpose here is to clarify outstanding differences and suggest how they may be resolved, in the hope that this will help form a basis for developing the Gaia theory.

'Gaia' is a particular type of open thermodynamic system, planetary in scale with abundant life tightly coupled to its environment. Planet Earth hosts the only known example, for which the name 'Gaia' was introduced. The Gaia theory aims to explain the development and functioning of Gaia systems, and is currently restricted to this one example. Our central point is that the functioning of such systems must be consistent with natural selection occurring within them, but this does not mean that planetary-scale regulation has to be the product of natural selection.

We try to move from the more general questions raised by Volk to the more specific issues tackled by Kirchner. We begin by considering what constitutes a reasonable basis for generalising about the behaviour of Gaia systems (Section 2). Then we consider the possible explanations for the persistence of life on Earth (Section 3). We associate the 'Gaia theory' with the idea that regulatory feedbacks are a probable outcome on planets with abundant life, but note that if this is proved wrong and the existence of regulatory feedbacks on Earth turns out to be good luck, this still leaves an important research agenda. We briefly review the basic tenets of the Gaia theory (Section 4), and expand on the facts that Gaia systems are expected to contain both positive and negative feedback (Section 5), and both feedback from by-products of selection (Section 6) and feedback involving natural selection (Section 7). Means of distinguishing the results of environmental enhancement and adaptation to the environment are suggested (Section 8). We conclude by discussing how conceptions of Gaia have contributed to the emerging field of 'Earth system science' (Section 9).



2. Generalising about Gaia: What Constitutes a Reasonable Argument?

Volk appears to be searching for universally true generalities about Gaia. We suggest instead that answers to the big questions about Gaia are always going to be couched in terms of probabilities. We should not expect there to be universal truths about the behaviour of such a complex system. Life is not *always* going to enhance gross primary productivity (Kleidon, 2002), resistance, resilience (Lenton, 2002) or any other metric of the system. There will always be examples for and against. What matters is the balance of examples: Do they suggest a tendency in one direction? For example, is there a tendency toward regulatory feedback or not? The more examples we have, the more confident we can be about answering such questions.

Volk criticises Kleidon and Lenton for giving only a finite number of examples to support their arguments. This is a reiteration of a well-known criticism of Francis Bacon's method of scientific inductivism: namely that it suffers the 'problem of induction', raised by David Hume (Russell, 1946). No matter how many white Swans you see there is always a chance that the next Swan you come across will be black, therefore you can never rigorously generalise to 'all Swans are white'. Volk also asks: 'how can we be sure that Lenton is not giving more weight to evidence that fits his pre-selected conclusions?' noting: 'It is gratifying that he does offer counter examples' (Volk, 2002). An effort was made to objectively balance available evidence. 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.

3. Regulation and the Long-term Persistence of Life

One of the big questions about Gaia is how has life survived and flourished for so long? The Earth's surface is subject to gradual changes in forcing (increasing solar luminosity, changing volcanic and tectonic activity driven from within the Earth, etc.) as well as rapid perturbation (e.g., asteroid impacts). Given this, the long-term persistence of life can be explained in three ways:

- (a) *Pure luck*. Life on Earth has survived by chance alone. Earth possesses no regulatory feedback mechanisms.
- (b) *Lucky Gaia*. The persistence of life is due in part to the existence of regulatory feedbacks, but it was good luck that the coupling between life and its planetary environment turned out to be regulatory.
- (c) *Probable Gaia*. There is something about the behaviour of planets with abundant life that leads one to expect regulatory feedbacks to predominate (at least statistically, if not in every case).

We owe this subdivision and the idea of ‘Lucky Gaia’ to Andy Watson. One of us (Lenton, 2002) has framed the possible explanations as hypotheses, where ‘Innate Gaia’ is equivalent to ‘Probable Gaia’ here. By ‘regulation’ we mean more than just the tendency for the system to return to a stable state after perturbation (alteration in state variables) or change in forcing. That stable state must be habitable and the dynamics of maintaining it should involve regulatory feedback. We define ‘regulatory feedbacks’ as those which tend to speed the recovery toward stable state after perturbation (increase resilience), reduce the change in the stable state under a change in forcing (increase resistance), or increase the range in forcing over which a habitable state can be maintained (introduce bi-stability) (Lenton, 2002). The latter definition equates to tending to prolong the persistence of life and is a special case of increasing resistance.

It is important to differentiate between (a) and (b), both involve luck but only (b) involves regulatory feedbacks. Also note that (b) and (c) must involve an element of luck if Earth has the potential to be struck by sterilising asteroid impacts. Pure luck (a) is easily dismissed as the sole explanation on the grounds that Earth does possess regulatory feedback mechanisms (Kump et al., 1999; Lenton, 2002). Thus the real situation is either (b) or (c).

We associate the Gaia theory with ‘Probable Gaia’ and think this is nearest to being the correct explanation. But let us stress that if ‘Probable Gaia’ is proved wrong and ‘Lucky Gaia’ turns out to be the case, it is still important. Volk gives the impression that ‘Lucky Gaia’ is of no interest because it lacks a general principle, e.g.: ‘what appear to be benefits are *just* chemical wastes’ (Volk, 2002, p. 429, our emphasis). However, ‘Lucky Gaia’ stresses that some principal feedbacks must contribute to maintaining the planet in a habitable state, for life to have survived so long. *Both ‘Lucky Gaia’ and ‘Probable Gaia’ suggest a strong research agenda: to find and understand these feedbacks.*

4. Gaia Theory

The Gaia theory is based on four basic tenets:

1. Life alters its environment.
2. Life forms grow and reproduce.
3. The environment constrains life.
4. Natural selection occurs.

From the first three one can derive:

- 1 + 2 \Rightarrow global environmental effects,
- 1 + 3 \Rightarrow environmental feedback,
- 1 + 2 + 3 \Rightarrow global environmental feedback.

Taken together, 1, 2 and 3 are sufficient conditions for global environmental regulation to occur. Thus, natural selection is not a *necessary condition* for regulation. The resulting type of feedback has been termed feedback on growth (Lenton, 1998) and is based on by-products of selection (Volk, 1998), in the sense that changes made to the environment do not influence the selection of the responsible traits.

However, we live in a world where natural selection occurs. If changes in the environment due to life do affect the selection of the responsible traits then there are the further possibilities of:

- 1 + 3 + 4 \Rightarrow environmental feedback on selection,
- 1 + 2 + 3 + 4 \Rightarrow global environmental feedback on selection.

Such feedback on selection (or ‘selective feedback’; Lenton, 1998) can form the basis of a different type of environmental regulation. There are important distinctions between regulation that involves selection and that which does not, which we will expand upon in Sections 6 and 7.

5. Positive and Negative Feedback

First we must stress that both growth and selective feedback can be positive or negative. Furthermore, a combination of positive and negative feedback does not preclude regulation. On the contrary, many cases of regulation in complex systems involve a mix of negative and positive feedback. Even a single effect on a single environmental variable can give rise to both positive and negative feedback, when the responsible organisms have a peaked growth response to that environmental variable and the effect is sufficiently strong.

At this point, let us clear up some semantic confusion. Kirchner notes that: ‘in the Gaia literature, mechanisms linking organisms to their environment are generally termed “Gaian” only if they create negative feedbacks, and only if they are beneficial to the organisms involved, or to the biota as a whole’ whereas ‘Positive feedbacks, or those that seem detrimental, are typically referred to as “non-Gaian” or “anti-Gaian” mechanisms’. The association of negative feedback with ‘Gaia’ and positive feedback with ‘non-Gaia’ or ‘anti-Gaia’ is wrong and is not widespread in the literature. Kirchner promotes this misconception of the theory by using the terms in this way. The association of beneficial effects with ‘Gaia’ and detrimental effects with ‘non-Gaia’ or ‘anti-Gaia’ (Kleidon, 2002) is flawed and we have both (Lenton, 1998; Wilkinson, in press) been guilty of this error. Consider, for example, that detrimental environmental effects can generate negative feedback. Furthermore, if one is talking of Gaia as the name for a system, then the term ‘anti-Gaian’ applied to things within that system makes little sense, and the term ‘Gaian’ takes on a different, all-encompassing meaning. We suggest that in future the terms ‘Gaian’, ‘non-Gaian’ and ‘anti-Gaian’, be avoided as descriptors of environmental effects or feedbacks.

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. Confusingly, he labelled this the ‘Homeostatic Gaia’ hypothesis (Kirchner, 1989). Yet homeostasis often involves a combination of positive and negative feedback. A good example is the Daisyworld model, where the growth of the daisies is intrinsically a positive feedback process (the more daisies there are, the more daisies they can beget) and when the system is establishing, recovering from large perturbations or collapsing, the sign of feedback on temperature is often positive. We do not support a hypothesis of overwhelming negative feedback. Lovelock also has drawn attention to the positive feedback during the recent glacial-interglacial transitions and the dangers of positive feedback on human-induced global change (Lovelock, 1991; Lovelock and Kump, 1994). Kirchner uses similar evidence to conclude that ‘Homeostatic Gaia’ is incorrect. Yet many complex systems undergo transitions between states in which positive feedback predominates. ‘Homeorhesis’ and ‘punctuated equilibria’ have both been applied to Gaia in an attempt to describe the notion of long intervals of relative stability (predominance of negative feedback) interspersed by shorter transitions (predominance of positive feedback).

We differ with Kirchner somewhat over the interpretation of current and recent past global change. The ice age cycles between remarkably constant bounds of temperature, CO₂ and CH₄ could be generated by a combination of rapid positive feedback and slower negative feedback (which sets the bounds). This is a common cybernetic recipe for generating oscillation. As Lovelock suggests, such oscillation may indicate that the Gaia system is nearing a transition (Lovelock, 1991; Lovelock and Kump, 1994). 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. At present, we can be clearer about the subsidiary issue of the overall sign of feedback on atmospheric CO₂. That is currently negative: typically (over the last two decades) more than half of the CO₂ emitted to the atmosphere each year from fossil fuel burning and land-use change is taken up by combined land and ocean carbon sinks (Prentice, 2001). There is also reason to expect that most of the anthropogenic-emitted CO₂ will eventually be removed from the atmosphere by negative feedbacks on timescales of 10⁴–10⁵ years (Archer et al., 1998).

When considering which feedbacks predominate, we must be clear about the *timescale* of concern. Gaia theory is concerned with over 3.5 billion years of Earth history. Focussing 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. More generally, it is possible that positive feedback dominates on shorter timescales and that negative feedback dominates on longer timescales. The hypothesis that life increases the resistance of the Earth system (Lenton, 2002) amounts to a hypothesis that negative feedback is stronger in the presence of life. This is clearly not true in some cases of biologically mediated positive feedback,

but it was not meant to be a universal generalisation. Just because it is falsified at present on relatively short timescales does not mean it is falsified on longer timescales or throughout Earth history. Kirchner and Volk dismiss it because it is not universally true. In so doing, they ignore the importance of accounting for the long-term (millions of years timescales) regulation of ‘master variables’ of Gaia such as atmospheric O₂, CO₂ and surface temperature.

6. Feedback from By-Products of Natural Selection

Let us now consider the basis of important environmental feedbacks. Kirchner suggests the Gaia theory proposes that regulatory feedback ‘should arise by Darwinian natural selection’ (Kirchner, 2002). We wish to clarify that this is *not* a requirement for regulation (although it could happen in some cases). Regulation is an emergent property in many systems even where there is no active selection for regulation. An example is the density dependent control of populations (Hamblen, 1997; Wilkinson, submitted). Before the 1960s it was often assumed that population regulation was a product of natural selection, but it is now clear that it is an emergent property of ecological systems.

Kirchner raises a theoretical problem that many evolutionary theorists have had with Gaia, that of ‘cheats’. In both reality and mathematical models, co-operation would often be an advantageous strategy (Cohen, 1998), but ‘co-operation invites cheating, and nowhere is this more apparent than when different species cooperate’ (Yu, 2001). This is seen as a problem for Gaia when it is assumed that the Gaia system must be a product of natural selection. However, the problem of ‘cheating’ disappears if, instead, Gaia is built of by-products (Volk, 1998, 2002). There is no selective advantage to any individual withholding its by-product, indeed if there is a cost associated with such withholding (a likely situation when the by-product is a waste product) then such ‘cheating’ on the relationship would be more costly to the individual than co-operation (Wilkinson and Sherratt, 2001). Several mechanisms have been suggested for stabilising non-by-product co-operation between individuals of different species (Herre et al., 1999; Wilkinson and Sherratt, 2001), however these are unlikely to work at the scale of Gaia.

Many (and perhaps most) globally important biotic feedbacks appear to be based on by-products of selection (Lenton, 1998; Volk, 1998, 2002). The resulting type of regulation often maintains an environmental variable in a limiting state, which in turn can be remarkably resistant and resilient to change. Regulation can occur because the spread of environment-altering traits is ultimately subject to constraints. When the spread of a particular trait alters an environmental variable in a manner that reduces the growth rate of the organisms carrying it, then negative feedback on growth (the spread of the trait) occurs, and a steady state is approached. Non-carriers are equally affected and the trait remains selected for, but it is still constrained. When the spread of a particular trait alters an environmental

variable in a manner that increases the growth rate of the organisms carrying it (together with non-carriers) then positive feedback on growth occurs. If the effect of the trait on the environment is sufficiently strong, and there is a peaked growth response to the environmental variable, then the positive feedback regime will be transited and the system will stabilise in the negative feedback regime, with the environmental variable in a limiting state. If the effect is insufficiently strong, or there is no peak in growth response, the system can stabilise whilst still in a constrained positive feedback regime (Lenton and van Oijen, 2002).

Important examples of by-products of selection include dimethyl sulphide production (Charlson et al., 1987; Caldeira, 1989; Lenton, 1998; Volk, 1998), the sink of CO₂ from biological amplification of silicate weathering (Lenton, 1998; Volk, 1998) and the source of O₂ from biological amplification of phosphorus weathering (Lenton, 2001). Feedbacks arising from the latter two effects are involved in regulating atmospheric CO₂ at a lower limit (Lenton and von Bloh, 2001) and atmospheric O₂ at an upper limit (Lenton and Watson, 2000b; Lenton, 2001). This type of regulation toward constraints (involving by-products) is qualitatively different from the type of regulation toward an optimum (involving selection) in the original Daisyworld model (Lenton, submitted; Volk, personal communication).

7. Feedback Involving Natural Selection

Kirchner and Volk are particularly sceptical about the possibility of feedback involving natural selection. We agree that it is not valid to *generalise* that 'Life enhancing effects would be favoured 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.

An important real world example is that arising from the process of nitrogen fixation. Nitrogen fixers increase their own supply of available nitrogen and ultimately this 'leaks out' to increase the amount of available reactive nitrogen in the environment (their surroundings). If reactive nitrogen is deficient in the environment, relative to other essential elements, then organisms that can fix nitrogen gain a selective advantage over non-fixers (as long as the benefits exceed the considerable energetic cost of nitrogen fixation). However, as the fixed nitrogen leaks out into the environment (and becomes available to the non-fixers as well) this selective advantage is reduced. Thus systems with nitrogen fixers and non-fixers should tend towards a stable state with deficits in the input of available nitrogen being met by a corresponding increase in nitrogen fixation. If the supply of nitrogen relative to other essential elements is perturbed then the system will respond in a manner to counteract the change. Reduced nitrogen input will lead to more nitrogen fixation, increased nitrogen input to less nitrogen fixation. This mechanism has been observed in terrestrial ecosystems (e.g., pasture) (Smith, 1992), some lakes

(Schindler, 1977; Howarth et al., 1988), and is thought to play a key role in the nutrient balance of the global ocean (Tyrrell, 1999; Lenton and Watson, 2000a).

8. Environmental Enhancement and Adaptation

It has been proposed that on average the biota alters the physical and chemical environment in a manner that benefits them (without this being teleological). Gross primary productivity (Kleidon, 2002) and ‘cycling ratios’ (Volk, 1998) have been suggested as metrics of this. In response, Kirchner (2002) notes 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. Adaptation of the organism to suit the environment and alteration of the environment to suit the organism both result in a good match between organisms and their environments. Thus it is not obvious 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.

We suggest that the dominant process should be apparent when the life-environment system is perturbed or collapses. A system with strong environmental feedback will be prone to rapid transitions between states, whereas one where adaptation dominates will change more gradually. This has been observed in two-dimensional variants of the Daisyworld model (Ackland et al., 2003). The rainforest (which Kleidon and Kirchner discuss) may be a good real world test case. 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, either due to deforestation or climate drying (Cox et al., 2000) passing a critical threshold. We wait pessimistically to see how the real system behaves.

Other critics of Gaia (Robertson and Robinson, 1998) have assumed that life can adapt to almost any environmental condition, in response to which we must stress that not everything can be achieved by adaptation, because of the existence of constraints. There are at least three important types of constraint in this context:

1. Environmental limits to carbon-based life (Lenton and Lovelock, 2000). The discovery of new extremophiles continues to ‘push the envelope’ of the environmental limits life can tolerate, but it does not remove them. Adaptation often becomes increasingly costly as environmental limits are approached. Life requires liquid water and this sets a geophysical constraint that a habitable planet must be sufficiently warm to avoid a global freeze and sufficiently cold to avoid losing all its water via hydrogen escape to space.

2. Trade-offs between organisms' performance in different areas (Wilkinson, in press). Consider plants, for which very different adaptations are required to do well in low nutrient and high nutrient conditions (Grime, 1979). This makes it unlikely that the same plant could excel under both conditions, especially in the presence of competitors.
3. Historical contingency (Gould, 1989). Many aspects of the biochemistry of organisms are so deeply rooted in their functioning that they cannot be altered by adaptation because it would involve crossing a fatal trough in their 'fitness landscape'. For example, the biochemistry of photosynthesis has not adapted to the oxygen levels in the current atmosphere.

Kirchner mentions Redfield's observation that the proportions of P, N and O₂ in ocean waters match very closely the requirements of marine organisms for these elements (Redfield, 1958). This is a good example of a situation where adaptation does not explain the remarkable fit between organisms and their environment. The requirements of primary producers for a particular ratio of N, P and C, is effectively set by deep-rooted biochemistry. The requirement of consumers for a particular amount of O₂ to respire the resulting organic matter is set by thermodynamics. Feedback involving nitrogen fixing and denitrifying organisms has brought the proportion of N to P in ocean water close to biological requirements (Redfield, 1958; Lenton and Watson, 2000a). In contrast, the correspondence between O₂ supply and demand appears to be partly a matter of chance (Lenton and Watson, 2000a).

9. Conclusion: Gaia's Contribution to Science

It is 30 years since Jim Lovelock introduced the name 'Gaia' (Lovelock, 1972) for the concept he had been formulating (Lovelock, 1965; Hitchcock and Lovelock, 1967; Lovelock and Giffin, 1969) and the system to which it refers. It is often parodied that a scientific theory goes through three phases towards acceptance: first 'it is obviously wrong', later there is a begrudging acceptance that 'there may be something in it', and finally it is ignored because 'we have known it all along'. (The whole process typically takes the order of 40 years.) Reactions to Gaia are shifting gradually through this sequence. Over the last decade, biological scientists (especially evolutionary theorists and ecologists) have recognised that Gaia is worthy of serious thought (Hamilton, 1995; Wilkinson, 1999; Cohen and Rich, 2000; Dagg, 2002) because there are remarkable things to be explained. Meanwhile some more Earth-orientated scientists have gone a stage further. Kirchner claims: 'If Gaia meant only that organisms influence their environment, and that these interactions may give rise to interesting system-level behaviours, then Gaia would add little – apart from different language and different metaphors to the general consensus of the biogeochemical community' (Kirchner, 2002). But has the biogeochemical community really known it all along? Our reading of the literature suggests not.

Rather, 30 years ago most biological and Earth scientists were happily viewing their domains as separate. There are of course wonderful historical exceptions e.g., Darwin (1881), Redfield (1958).

We suggest that Jim Lovelock's conception of Gaia and his popularising has been the single most important driver of an ongoing perception shift toward viewing the Earth as a whole system. Future historians of science will have to be the final judge of this. At present we note that Lovelock's contribution is being obscured by a number of factors.

There is an ongoing widespread objection amongst scientists to the name 'Gaia' because of its metaphorical and religious connotations (the currently in-vogue alternative being 'Earth system'). Other non-scientific names for theories (e.g., 'selfish gene', 'Red Queen') could attract similar criticism (Midgley, 2001). As scientists we shouldn't be too worried about the name, after all it is just 'a convenient four-letter word' as Jim Lovelock puts it. The emphasis should be on understanding the system, and on this point we agree wholeheartedly with Kirchner and Volk.

There is some ignorance of the contributions of Lovelock and co-workers amongst the scientific community. For example, we can't help feeling that: 'the view that organisms have no effect on the environment has not been taken seriously for several decades now' (Kirchner, 2002) largely because Jim Lovelock's realisation that life has transformed the Earth's atmosphere dates back to 1965. John Lawton appreciates this point, writing in a *Science* editorial on 'Earth System Science' that: 'James Lovelock's penetrating insights . . . were major stepping-stones in the emergence of this new science' (Lawton, 2001).

Many scientists are working with early renditions and interpretations of the Gaia hypothesis that its originator and developers have long since discarded. Thus, much of their criticism is misguided. For example, many ecologists assume that 'Gaia' refers to a global 'superorganism' that has evolved by natural selection. Such conceptions date back to the 1970s and were rejected in the early 80s. It is true that Lovelock continued to use the term 'superorganism' in his 1988 book 'The Ages of Gaia' (Lovelock, 1988) but with a broader meaning than that accepted by evolutionary theorists, of a tightly coupled system of life and its material environment. Everyone involved in the debate should grasp the fact that the Gaia theory itself has evolved over time and will continue to evolve.

Aspects of the Gaia theory do continue to cause great controversy. This has the benefit that by generating interest and debate it is drawing attention to a new way of viewing and studying the world. Importantly, it causes us to ask different kinds of questions about the Earth. In this capacity as a hypothesis generator, Gaia has more than proved its worth. Lovelock challenges us to go a stage further and develop a theory of the functioning of Gaia systems. We hope that other scientists will be inspired to join in developing it.

Acknowledgements

We thank James Kirchner, Tyler Volk and Marcel van Oijen for helping us clarify our thoughts on Gaia, and Steve Schneider for encouraging this dialogue.

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(Received 21 June 2002; in revised form 8 January 2003)

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