

Biological Feedback leads to homeostasis:
Biological mediated Feedback makes environment more suitable for life
Feedback comes from natural selection.

THE GAIA HYPOTHESIS: FACT, THEORY, AND WISHFUL THINKING

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Abstract. Organisms can greatly affect their environments, and the feedback coupling between organisms and their environments can shape the evolution of both. Beyond these generally accepted facts, the Gaia hypothesis advances three central propositions: (1) that **biologically mediated feedbacks contribute to environmental homeostasis**, (2) **that they make the environment more suitable for life**, and (3) **that such feedbacks should arise by Darwinian natural selection**. These three propositions do not fare well under close scrutiny. (1) Biologically mediated feedbacks are not intrinsically homeostatic. Many of the biological mechanisms that affect global climate are destabilizing, and it is likely that the net effect of biological feedbacks will be to amplify, not dampen, global warming. (2) Nor do biologically mediated feedbacks necessarily enhance the environment, although it will often appear as if this were the case, simply because natural selection will favor organisms that do well in their environments – which means doing well under the conditions that they and their co-occurring species have created. (3) Finally, Gaian feedbacks can evolve by natural selection, but so can anti-Gaian feedbacks. Daisyworld models evolve Gaian feedback because they assume that any trait that improves the environment will also give a reproductive advantage to its carriers (over other organisms that share the same environment). In the real world, by contrast, natural selection favors any trait that gives its carriers a reproductive advantage over its non-carriers, whether it improves or degrades the environment (and thereby benefits or hinders its carriers and non-carriers alike). Thus Gaian and anti-Gaian feedbacks are both likely to evolve.

1. Introduction

Several years ago I overheard a radio interview with Douglas Adams, the author of *The Hitchhiker's Guide to the Galaxy*, in which he was asked to comment on the Gaia hypothesis. His answer, as best I can reconstruct it now, was roughly this:

Imagine a puddle, waking up in the morning, and examining its surroundings (a brief pause here, to let the audience grapple with this rather odd image). The puddle would say, 'Well, this depression in the ground here, it's really quite comfortable, isn't it? It's just as wide as I am, it's just as deep as I am, it's the same shape as I am ... in fact, it conforms exactly to me, in every detail. This depression in the ground, it must have been made just for me!'

Adams' fanciful image illustrates a central problem in some of the current incarnations of the Gaia hypothesis, and in all other theories that find, in Earth's obvious suitability for our particular form of life, **evidence that the environment must be conforming to life's needs** (e.g., Henderson, 1913; Redfield, 1958). The problem is



Climatic Change **52**: 391–408, 2002.

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this: given that organisms must adapt to the constraints of their environment – or else they don't survive – the particular forms of life that we observe will always be those that are reasonably well matched to their environmental conditions. Those that are not well matched to their environment will not thrive and will not be noticed.

Thus the environment and its life forms will always appear well suited to each other, whether or not the environment is in any sense adjusted to life's requirements. It seems inevitable that sentient life should view its world as an Eden, because if there were any evolutionary lineages for which that world were a Hell, they would not persist long enough to develop intelligent life forms. To me, the Earth seems to be remarkably well suited to human needs. But I also understand that evolution has made it virtually inevitable that I should believe this, since any would-be ancestors of mine for whom the Earth were too hostile would have been removed from the gene pool long before their traits could have been passed on to me. Perhaps this helps to explain how the beneficence of nature has become a theme in human thought. As winners of the evolutionary lottery, it is not surprising that we would view ourselves and the life forms around us – with whom we share the winner's circle – as the beneficiaries of an environment has been tailored to our needs.

What makes the Gaia hypothesis interesting is that it proposes that the beneficence of Nature is neither an accident nor the work of a benevolent deity, but instead is the inevitable result of interactions between organisms and their environment. Simply put, **if organisms have a significant influence on their environment, then**

... those species of organisms that retain or alter conditions optimizing their fitness (i.e., proportion of offspring left to the subsequent generation) leave more of the same. In this way conditions are retained or altered to their benefit (Lovelock and Margulis, 1974a).

Life and the environment evolve together as a single system so that not only does the species that leaves the most progeny tend to inherit the environment but also the environment that favors the most progeny is itself sustained (Lovelock, 1986).

Thus the Gaia hypothesis validates our sense of wonder and reverence for the natural world, by proposing a scientific basis for our sense that the Earth is indeed tailored to our needs, and those of the organisms that share the Earth with us.

Some have hailed Gaia as a profound discovery, while others have dismissed it as a 'just-so story' that is more entertaining than informative. **Here I will argue that Gaia, in its different guises, is a mixture of fact, theory, metaphor, and wishful thinking.** It will be necessary to untangle these from each other, and put each in its proper place, in order to get a clearer view of the Earth system as it is, in all its intriguing complexity. It has been a dozen years since my critique of the Gaia hypothesis appeared in print (Kirchner, 1989; Kirchner, 1991). My intent was to

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clarify and focus the Gaia debate, which seemed to be at risk of becoming a shouting match between disciples and detractors. I pointed out that the singular term, 'the Gaia hypothesis', was being applied to many different propositions, ranging from ideas that most modern Earth scientists would consider self-evident, to notions that most would consider outlandish. The weak forms of the Gaia hypothesis hold that life collectively has a significant effect on Earth's environment ('Influential Gaia'), and that therefore the evolution of life and the evolution of its environment are intertwined, with each affecting the other ('Coevolutionary Gaia'). I argued that abundant evidence supports these weak forms of Gaia, and that they are part of a venerable intellectual tradition (Spencer, 1844; Huxley, 1877; Hutchinson, 1954; Harvey, 1957; Holland, 1964; Sillen, 1966; Schneider and Londer, 1984). By contrast, the strongest forms of Gaia depart from this tradition, claiming that the biosphere can be modeled as a single giant organism ('Geophysiological Gaia') or that life optimizes the physical and chemical environment to best meet the biosphere's needs ('Optimizing Gaia'). I argued that the strong forms of Gaia may be useful as metaphors but are unfalsifiable, and therefore misleading, as hypotheses (Kirchner, 1989). Somewhere between the strongest and the weakest forms of Gaia is 'Homeostatic Gaia', which holds that atmosphere-biosphere interactions are dominated by negative feedback, and that this feedback helps to stabilize the global environment. I argued that if one defines it carefully enough, Homeostatic Gaia may be testable, but I also pointed out that there was abundant evidence that the biota can also profoundly destabilize the environment.

How has the Gaia debate progressed? One can discern several encouraging trends. The view that organisms have no effect on their environment has not been taken seriously for several decades now. The most extreme forms of the Gaia hypothesis have generally been abandoned, particularly those that impute a sense of purpose to the global biosphere, and Gaia's proponents have instead searched for mechanisms by which Gaian regulation might evolve by natural selection. Thus the debate has become focused on a more promising (though somewhat ill-defined) middle ground between the mundane versions of Gaia and the extravagant ones. This is progress, and I wish that I could claim some credit for it, but Gaia enthusiasts have rarely come to grips with my critique (which extends well beyond just the taxonomy outlined above), and Gaia skeptics have generally ignored the debate entirely. Thus the Gaia debate has not been much of a dialogue, with Gaia's proponents repeatedly putting forward their case in print, and Gaia's detractors casually dismissing it rather than taking the time to respond. Therefore, my purpose here is to assess the current, more focused Gaia hypothesis, and to outline the difficulties that it poses.

Gaia contains elements of fact, theory, and wishful thinking. One part of Gaia that is clearly fact is the recognition that Earth's organisms have a significant effect on the physical and chemical environment. Biogeochemists have devoted decades of painstaking work to tracing the details of these interactions. Many important chemical constituents of the atmosphere and oceans are either biogenic

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or biologically controlled, and many important fluxes at the Earth's surface are biologically mediated (see Kirchner, 1989, and references therein). This was well understood among biogeochemists well before Gaia, although Gaia's proponents have helped to educate a much wider audience about the pervasive influence of organisms on their environment. Gaia has also inspired original research exploring several biologically mediated processes, including production of dimethyl sulfide by phytoplankton (Charlson et al., 1987) and microbial acceleration of mineral weathering (Schwartzmann and Volk, 1989). This search for Gaian leverage points has proceeded in parallel with a much larger effort by the whole biogeochemical community to trace the mechanisms regulating global geochemical cycles.

2 Another well-established fact that is incorporated in Gaia is the notion that Earth's organisms and their environment form a coupled system; the biota affect their physical and chemical environment, which in turn shapes their further evolution. In this way, Earth's environment and life co-evolve through geologic time (Schneider and Londer, 1984). Over the long term, organisms do not simply adapt to a fixed abiotic environment; nor is the environment sculpted to conform to fixed biotic needs (as early versions of Gaia appeared to argue, e.g., Lovelock and Margulis, 1974b). A key theoretical element of Gaia is that, as with any complex coupled system, the atmosphere/biosphere system should be expected to exhibit 'emergent' behaviors, that is, ones that could not be predicted from its components alone, considered in isolation from one another. So understanding Earth history and global biogeochemistry requires systems thinking (in addition to lots of reductionist science as well). Gaia's proponents have helped to promote a systems-analytic approach to the global environment, in parallel with a much larger and broader-based effort in the biogeochemical community as a whole.

Up to this point, nothing that I have said about Gaia would seem controversial to modern Earth scientists. These themes in Gaia are consistent with a broad effort in the biogeochemical community to better understand the Earth system, but carried out in parallel, with different emphasis and different language.

At the same time, Gaia's proponents have consistently held that the Gaia hypothesis means something more than just the co-evolution of climate and life, and something more than just the idea that the Earth system can exhibit interesting system-level behaviors. Coupling between the biosphere and the physical environment can potentially give rise to either negative (stabilizing) feedback, or positive (destabilizing) feedback, and the consequences of this feedback can potentially be either beneficial or detrimental for any given group of organisms. But 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 (Lenton, 1998; Gillon, 2000). Positive feedbacks, or those that seem detrimental, are typically referred to as 'non-Gaian' or 'anti-Gaian' mechanisms. Thus 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 qual-

ified form of ‘Optimizing Gaia’ (i.e., biological modifications of the environment make it more suitable for life). As Hamilton (1995) has put it, ‘right or wrong, Gaia presents the claim for an evolution of a supreme “balance of nature”’.

This is what makes Gaia interesting, but this is also what makes Gaia difficult. If Gaia meant only that organisms influence their environment, and that these interactions may give rise to interesting system-level behaviors, then Gaia would add little – apart from different language and different metaphors – to the general consensus of the biogeochemical community. By claiming that organisms stabilize the global environment and make it more suitable for life, Gaia’s proponents advance a much more ambitious argument, but one that is less clearly consistent with the available data, and one that sometimes may be difficult to test against data at all.

2. Gaia and Homeostasis

Do biological feedbacks stabilize, or destabilize, the global environment? That is, is the ‘Homeostatic Gaia’ hypothesis correct? This is not just a matter for theoretical speculation; there is a large and growing body of information that provides an empirical basis for evaluating this question. Biogeochemists have documented and quantified many important atmosphere-biosphere linkages (particularly those associated with greenhouse gas emissions and global warming), with the result that one can estimate the sign, and sometimes the magnitude, of the resulting feedbacks. Such analyses are based on three types of evidence: biological responses to plot-scale experimental manipulations of temperature and/or CO₂ concentrations (e.g., Saleska et al., 1999), computer simulations of changes in vegetation community structure (e.g., Woodward et al., 1998), and correlations between temperature and atmospheric concentrations in long-term data sets (e.g., Tans et al., 1990; Keeling et al., 1996a; Petit et al., 1999). Below, I briefly summarize some of the relevant biological feedbacks affecting global warming; more detailed explanations, with references to the primary literature, can be found in reviews by Lashof (1989), Lashof et al. (1997) and Woodwell et al. (1998):

Increased atmospheric CO₂ concentrations stimulate increased photosynthesis, leading to carbon sequestration in biomass (negative feedback).

Warmer temperatures increase soil respiration rates, releasing organic carbon stored in soils (positive feedback).

Warmer temperatures increase fire frequency, leading to net replacement of older, larger trees with younger, smaller ones, resulting in net release of carbon from forest biomass (positive feedback).

Warming may lead to drying, and thus sparser vegetation and increased desertification, in mid-latitudes, increasing planetary albedo and atmospheric dust concentrations (negative feedback).

Conversely, higher atmospheric CO₂ concentrations may increase drought tolerance in plants, potentially leading to expansion of shrublands into deserts, thus reducing planetary albedo and atmospheric dust concentrations (positive feedback).

Warming leads to replacement of tundra by boreal forest, decreasing planetary albedo (positive feedback).

Warming of soils accelerates methane production more than methane consumption, leading to net methane release (positive feedback).

Warming of soils accelerates N₂O production rates (positive feedback).

Warmer temperatures lead to release of CO₂ and methane from high-latitude peatlands (positive, potentially large, feedback).

This list of feedbacks is not comprehensive, but I think it is sufficient to cast considerable doubt on the notion that biologically mediated feedbacks are necessarily (or even typically) stabilizing. As Lashof et al. (1997) conclude, 'While the processes involved are complex and there are both positive and negative feedback loops, it appears likely that the combined effect of the feedback mechanisms reviewed here will be to amplify climate change relative to current projections, perhaps substantially... The risk that biogeochemical feedbacks could substantially amplify global warming has not been adequately considered by the scientific or the policymaking communities'.

Most of the work to date on biological climate feedbacks has focused on terrestrial ecosystems and soils; less is known about potential biological feedbacks in the oceans. One outgrowth of the Gaia hypothesis has been the suggestion that oceanic phytoplankton might serve as a planetary thermostat by producing dimethyl sulfide (DMS), a precursor for cloud condensation nuclei, in response to warming (Charlson et al., 1987). Contrary to this hypothesis, paleoclimate data now indicate that to the extent that there is such a marine biological thermostat, it is hooked up backwards, making the planet colder when it is cold and warmer when it is warm (Legrand et al., 1988; Kirchner, 1990; Legrand et al., 1991). It now appears that DMS production in the Southern Ocean may be controlled by atmospheric dust, which supplies iron, a limiting nutrient (Watson et al., 2000). The Antarctic ice core record is consistent with this view, showing greater deposition of atmospheric dust during glacial periods, along with higher levels of DMS proxy compounds, lower concentrations of CO₂ and CH₄, and lower temperatures (Figure 1). Watson and Liss (1998) conclude, 'It therefore seems very likely that, both with respect to CO₂ and DMS interactions, the marine biological changes which occurred across the last glacial-interglacial transition were both positive feedbacks'.

This example illustrates how the Gaia hypothesis can motivate interesting and potentially important research, even if, as in this case, the hypothesis itself turns out to be incorrect. But it is one thing to view Gaia as just a stimulus for research, and quite another to view it as 'the essential theoretical basis for the putative profession

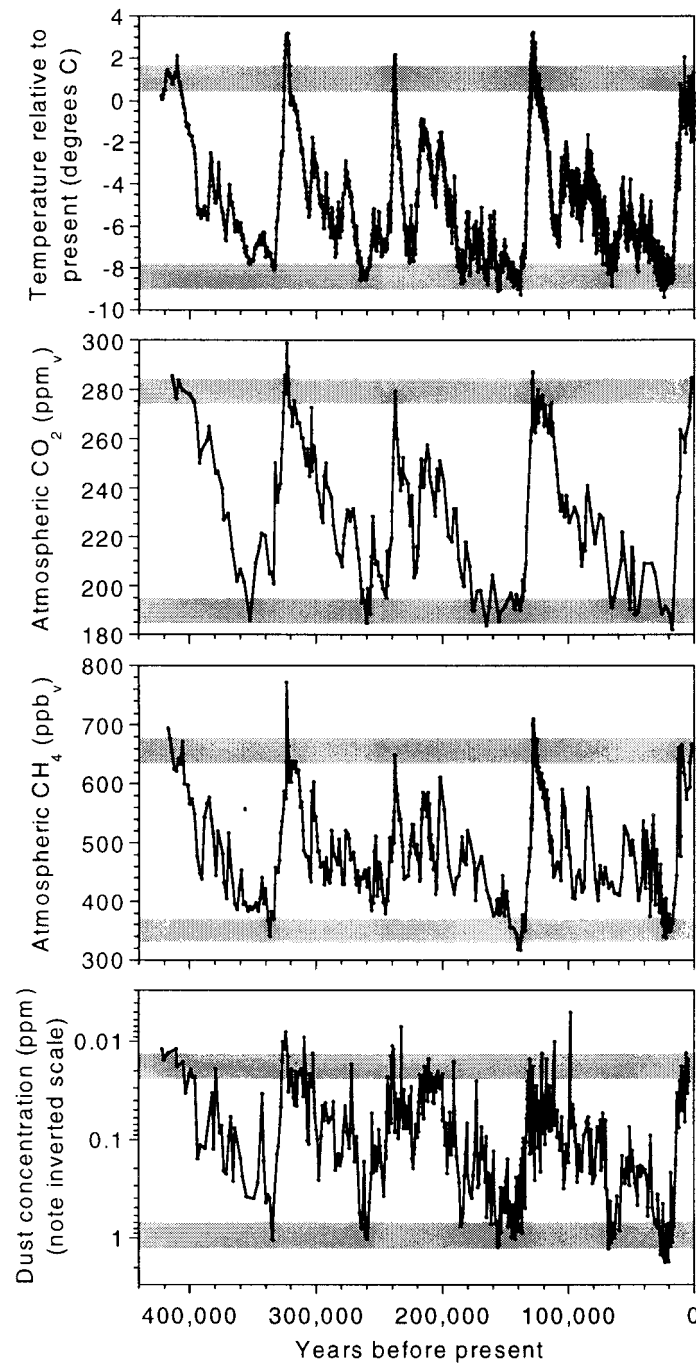


Figure 1. The Vostok ice core record of atmospheric temperature, CO₂, methane, and dust loading (data of Petit et al., 1999). Glacial maxima and interglacials exhibit relatively narrow ranges of characteristic concentrations and temperatures, indicated by the shaded bands. Temperature, CO₂, and methane are strongly correlated. High dust concentrations (note the inverted logarithmic scale) are correlated with low CO₂, methane, and temperature.

of planetary medicine' (Lovelock, 1986). To the extent that the Gaia hypothesis posits that biological feedbacks are typically stabilizing, it is contradicted both by the ice core records and by the great majority of the climate feedback research summarized above. Given the available evidence that biological feedbacks are often destabilizing, it would be scientifically unsound – and unwise as a matter of public policy – to assume that biological feedbacks will limit the impact of anthropogenic climate change. As Woodwell et al. (1998) have put it, 'The biotic feedback issue, critical as it is, has been commonly assumed to reduce the accumulation of heat trapping gases in the atmosphere, not to amplify the trend. The assumption is serious in that the margin of safety in allowing a warming to proceed may be substantially less than has been widely believed'.

3. Gaia and Environmental Enhancement

I now turn to the second major theme in the Gaia hypothesis, namely the claim that the biota alter the physical and chemical environment to their own benefit. We have seen that Gaian claims for biologically mediated homeostasis are inconsistent with much of the available empirical evidence. But by contrast, our day-to-day experience gives the strong impression that our environment is, in fact, very well suited to the organisms that live in it. Given that our environment is partly a biological by-product, it seems reasonable to speculate that biological feedbacks make our environment a better place to live. If we think about how thoroughly our world would be disrupted by the loss of any of the environmental services that its organisms provide, it seems natural to say that biological influences greatly enhance our environment. But it is one thing to say that we benefit from the environmental services that our ecosystem provides, and entirely another to say that our environment is in any sense tailored to our needs.

Organisms can strongly influence their environments. Organisms are also naturally selected to do well in their environments – which means doing well under the conditions that they, and their co-occurring species, have created. Thus it is likely that those particular organisms will be better off under those particular conditions than they would be without the environmental services that they, and their co-occurring species, are responsible for. In any such system, it will be true that 'biotic effects strongly enhance the biogeophysical and biogeochemical conditions for life' (Kleidon, this issue), precisely because the particular life in question is that which has been naturally selected to thrive under the conditions that those particular biotic effects promote.

Let me illustrate this concept with a simple example. Rainforests are wet, in large part because of water recycled by transpiration from the rainforest vegetation itself. Rainforest vegetation is thus spared the heat and drought stress that it would encounter in an arid environment, but instead must cope with other environmental challenges that the rainforest presents, such as light and nutrient stress due to

transpiration = Verdunstung

crowding, or parasitism by pathogens that flourish under damp conditions. Organisms that thrive in the rainforest will be highly evolved to cope with these threats to survival, and to depend on (and exploit, insofar as possible) the prevailing wetness of the rainforest environment. If the recycling of water by transpiration were somehow disrupted, the rainforest would become much drier and its vegetation would suffer. Thus the rainforest's health depends on an environmental service provided by its own organisms.

In cases like this, one might be tempted to say that rainforest vegetation influences its climate to its own benefit, or that the rainforest enhances the physical conditions required for life. These statements 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.

The Gaia literature further compounds this semantic confusion by making claims such as, 'vegetation almost always influences climate *for* its own benefit' (Lenton, 1998, emphasis added), rather than *to* its own benefit. What a difference a word makes! Saying that vegetation influences climate *to* its own benefit implies that vegetation alters its environment in ways that are beneficial. But saying that vegetation influences climate *for* its own benefit advances the much stronger claim that vegetation modifies its environment in order to reap the benefits that will result from doing so. Although Gaia's proponents have tried hard to avoid teleology (Kerr, 1988), it occasionally slips in. This is almost inevitable, given that Gaia's metaphorical models are based on thinking about how the biota could benefit from altering their environment. Thinking mechanistically instead – that is, not thinking about what would be good for the biota, but instead thinking about how the environment will affect natural selection on the biota (and how that, in turn, will further alter the environment) – leads to a more scientifically defensible conclusion: because natural selection will favor organisms that can best exploit their environment, organisms will often be dependent on the environmental services that their ecosystem provides. Thus they will benefit from their environment, even though it has not been constructed to conform to their needs.

The same reasoning holds at global scale. The global environment seems very well suited to the needs of the organisms that inhabit it. Change any major parameter of the global environment (temperature, pH, redox potential, etc.) by very much, and Earth would become a much less hospitable place – at least for the organisms that are now dominant precisely because its conditions suit them. But inferring from this that the environment has been tailored to the needs of the biota is a bit like evaluating the million-dollar lottery by polling only those who have won the jackpot. The life forms that we observe today are descended from a very select subset of evolutionary lineages, namely those for which Earth's conditions have been favorable. The other lineages, for whom Earth's conditions are hostile, have either gone extinct or are found in refugia (such as anaerobic sediments) which

Teleologie: Alle Handlungen, Prozesse und Entwicklungen sind zweckbestimmt und bewegen sich auf diesen Zweck gezielt zu.

protect them from the conditions that prevail elsewhere. As Holland (1984) has put it, ‘We live on an Earth that is the best of all possible worlds only for those who are well adapted to its current state’.

4. Gaia and Natural Selection

Nevertheless, it is striking to observe that Earth’s environment has remained suitable for advanced forms of life for hundreds of millions of years. Before getting too wrapped up in this observation, we should remember that this is also a necessary prerequisite for our being here to observe it, and we are in no position to judge how improbable a circumstance that is. It is therefore possible that the Earth has gotten by on sheer good fortune alone. But although such a hypothesis is logically defensible it is scientifically unsatisfying, since if there is a mechanistic explanation for Earth’s resilience through time, there is a lot to be learned by finding it. Furthermore, paleoclimate records do show patterns that suggest a planetary-scale feedback system. For example, ice core records show that through the last four glacial/interglacial cycles, atmospheric chemistry and temperature have oscillated between the same narrow upper and lower bounds (the shaded bands in Figure 1). What mechanisms set these upper and lower limits, and what processes control how the climate flips from one to the other? The answers are not known at present, but the search for them is a scientific challenge of the highest order (Falkowski et al., 2000).

As an answer to the mystery of how life has persisted, the Gaia hypothesis proposes that the Earth is self-regulated, in a state that is favorable for life, by biologically mediated feedbacks. It further proposes that these stabilizing, environment-enhancing feedbacks should arise naturally as the result of natural selection acting on individual organisms. The primary vehicle through which this theory has been promoted is the Daisyworld model. The Daisyworld model has been modified and elaborated in many different ways (see Lenton, 1998, and references therein), but the original version (Watson and Lovelock, 1983) presents the clearest picture of the underlying mechanisms, and will suffice for the present discussion.

Daisyworld was designed to explain how biologically mediated feedbacks – arising through natural selection alone – could hypothetically stabilize a planet’s temperature in the face of an increase in solar luminosity, similar to that experienced by the Earth on billion-year timescales. Daisyworld is a planet on which the albedo (and thereby temperature) is determined by the black and white daisies growing on its surface. The black daisies and white daisies are assumed to have the same growth response to temperature, but the black daisies are assumed to be warmer than the white daisies. Thus the black daisies thrive in cooler ambient conditions, lower the albedo, and warm the surface, whereas the white daisies thrive

in warmer ambient conditions, raise the albedo, and cool the surface. Schneider (2001) summarizes the climatic evolution of Daisyworld as follows:

As the sun heats up over hundreds of millions of years, black daisies approach their optimum temperatures, become more fit, and thereby increase their numbers, causing the albedo (reflectivity) of the planet's surface to drop. This is a positive feedback, because while more sunlight is absorbed by the dark flowers the planet further warms. Black daisies increase until the temperature passes their fitness peak and moves into the fitness range for the white daisies. These then begin to multiply and replace the black daisies; this shift increases the planet's albedo, which serves as a negative feedback on further warming. The planet's overall temperature is stabilized for eons even though the sun inexorably increases its luminosity. But eventually, the white daisies are heated past their fitness range and can't resist further warming. The biota then collapses and temperatures rise rapidly to the level an inorganic rock would experience.

Schneider (2001) points out that on the real Earth, vegetation albedo has a relatively weak effect on climate because clouds and haze obscure most of the surface. Likewise, vegetation response to temperature is weaker on the real Earth than it is on Daisyworld, where a temperature shift of only 1 °C can expand daisy cover from zero to 45% of the planet's surface (Kirchner, 1989). And on the real Earth, vegetation would actually respond to temperature in the *opposite direction* from what Daisyworld predicts; all else equal, warmer temperatures would expand forests poleward, making the surface darker and thus amplifying the warming (Kirchner, 1989).

But despite the fact that Daisyworld does not apply in any literal sense to the real Earth, it seems to embody a general principle that deserves further exploration. Daisyworld appears to demonstrate that whenever organisms are strongly coupled to their environment, **Darwinian evolution will naturally generate a system that self-regulates near the biological optimum**. What Daisyworld actually demonstrates is that it is **possible for such** a system to arise by natural selection, but only given a **very specific assumption** embedded in the model. Because this assumption may not be true on the real Earth, Daisyworld only demonstrates a theoretical possibility rather than a guiding principle of the natural world. To explain what this assumption is, and why it matters, requires a brief synopsis of evolutionary theory.

Heritable traits become more common over time if the individuals who have those traits have a reproductive advantage over those who lack them. They become more common by virtue of the simple fact that individuals who carry the advantageous trait will have more offspring on average than those who do not (that is what it means for the trait to be 'advantageous'), which implies that in each generation a larger fraction of the population will carry the trait. If a trait were equally beneficial to those who carried it and those who did not, it would not become more widespread in the population, since carriers and non-carriers of the

trait would pass on their genes to the next generation at equal rates. Thus traits that confer a *differential advantage* (for carriers over non-carriers) will become more common via natural selection, but traits that confer a *general benefit* (to carriers and non-carriers alike) will undergo genetic drift; natural selection cannot have any effect on them.

Here, then, is the crux of the matter. The environment is that which is shared among organisms. To the extent that a trait improves the environment for life in general – and thus benefits its carriers and non-carriers alike – natural selection will not have any effect on it. Thus claims that ‘life-enhancing effects would be favored by natural selection’ (Kleidon, 2002) are not generally valid.

Of course, it is always possible that a particular trait could confer both a differential advantage to the individual and a general benefit to the environment. Such a trait would be favored by natural selection, but only because of the differential advantage it confers to the individual, not because of any general benefit that is shared with others who do not carry the trait. Thus environmentally beneficial traits and environmentally detrimental ones will both be favored by natural selection, as long as each confers a differential reproductive advantage to the individuals that carry it. Even if an individual organism benefits from its own environmental good deeds, it will only gain a reproductive advantage (and be favored by natural selection) to the extent that it benefits more than its neighbors do.

Which brings us to Daisyworld. The Daisyworld model assumes that traits that benefit the environment also give an individual a reproductive advantage over its neighbors. Thus Daisyworld gives the impression that traits are favored by natural selection if they are environmentally beneficial, even though natural selection does not – indeed cannot – act on environmental benefits per se, precisely because they are shared between carriers and non-carriers alike. By assuming that individual reproductive success and environmental good deeds are linked, and thus that organisms will do well by doing good, Daisyworld to some extent assumes what it sets out to prove. Environmentally beneficial traits are not favored by natural selection in Daisyworld because they are environmentally beneficial; they are instead favored because they also, coincidentally, confer a reproductive advantage.

When Daisyworld is cool, the black daisies are *not* favored by natural selection because they warm the environment. Instead, they are favored by natural selection because they warm *themselves*, and therefore thrive better in cool temperatures than the white daisies do. To the extent that they also warm the *environment*, and therefore make it better for white daisies and worse for themselves, they *diminish* (not *enhance*) their evolutionary advantage. In competition with white daisies, black daisies would have a greater evolutionary advantage if they had no effect on their environment at all, because the planet would remain cooler and thus more favorable for black daisies. The black daisies could increase their evolutionary advantage still further if, while warming themselves, they *cooled* the environment, thus suppressing competition from the white daisies. If the black daisies only warmed the environment, and thus warmed themselves and the white daisies equally, they

would never be favored by natural selection. Thus the Daisyworld model behaves the way it does specifically because it assumes that a given trait (here, daisy color) will affect the individual and its environment in the same way (Lenton, 1998), with a bigger benefit to the individual than to the environment as a whole.

The numerous elaborations of the Daisyworld model all share this premise. It might be true for the particular case of variations in an organism's albedo, but a moment's reflection will show that it is not universally, or even generally, true in the natural world. For example, all organisms must consume resources, and by doing so they deplete their local environments of those resources. Likewise, all organisms must eliminate wastes, and by doing so they pollute their environments. Traits that enable organisms to better consume resources or eliminate wastes will benefit the individual, and thus will be favored by natural selection, even though they also degrade the environment. Examples of such traits abound. Trees are highly evolved to catch sunlight, and thus shade their neighbors. Plants in arid zones are highly evolved to intercept moisture before it reaches their competitors. Some tree species (such as eucalyptus and black walnut) even conduct a form of chemical warfare against potential competitors, by dropping leaves or fruits that make the surrounding soils toxic for other species.

These evolutionary strategies may offend our human sense of fair play, but they also serve to illustrate an important point about natural selection. Natural selection is a *mechanism*, not a *principle*. It does not seek a goal; it just passes traits from one generation to the next, with the reproductively successful ones becoming more common over time. Thus there is no direction to evolution beyond the fact that whatever works (in a reproductive sense) works, and will be passed on to the next generation. Natural selection will favor both environment-enhancing and environment-degrading traits, as long as those traits confer a reproductive advantage, that is, as long as those who carry them have greater reproductive success than those who don't.

Thus I would agree with Volk (1998, p. 239) that 'What organisms do to help themselves survive may affect the planet in enormous ways that are not at all the reasons those survival skills were favored by evolution'. But if the connection between environmental good deeds and individual reproductive advantage is only coincidental, we should not expect Gaian traits to evolve any more frequently than anti-Gaian ones.

It is still theoretically possible for evolution to systematically favor Gaian traits over anti-Gaian ones, but only if environments and their organisms are jointly subject to some form of natural selection, in competition with other environment/organism assemblages. This would create a kind of metapopulation, and natural selection in metapopulations can produce evolutionary outcomes that would otherwise seem counterintuitive (e.g., Kirchner and Roy, 1999). However, a mechanism needs to be demonstrated by which such natural selection could occur in this context.

→ kommt immer auf den Standpunkt an
Nicht gut für den Umwelt, aber vllt. gut für
eine andere Spezies

! Obviously, no biologically mediated feedback can be too environment-degrading, in the limiting sense that no simple feedback loop can lead to the extinction of the organisms responsible for it. Thus, for example, photosynthetic organisms cannot sequester organic carbon beyond the point at which they starve themselves for CO₂; in this way, the compensation point for photosynthesis (roughly 100–150 ppm CO₂) may set the limit to the glacial deep freeze. Likewise, organisms that consume plants and respire their carbon could not multiply beyond the point at which they either run out of food or poison themselves with waste CO₂. But these are far from the environment-enhancing feedbacks envisioned by the Gaia hypothesis.

One should remember that environment-enhancing feedbacks, if they occur, are intrinsically destabilizing (Kirchner, 1989). Organisms that make their environment more suitable for themselves will grow, and thus affect their environment still more, and thus grow still further. This is positive feedback, not negative feedback. Negative feedback arises when a growing population makes its environment less suitable for itself, and thus limits its growth. Environment-enhancing feedbacks are destabilizing; environment-degrading feedbacks are stabilizing. The Gaian notion of environment-enhancing negative feedbacks is, from the standpoint of control theory, a contradiction in terms.

5. Conclusion

Organisms are not merely passengers, riding passively on spaceship Earth. But to the extent that the biota are piloting the craft, they are flying blind, and the various life forms are probably wrestling over the controls. Earth's surface environment has remained stable enough to allow life in some form to persist for billions of years, but it is not clear whether this has occurred because of biological feedbacks, or in spite of them.

Gaia's proponents have done a great service by championing the need to consider the Earth as a coupled system. We now need to figure out how that system works, and it is crucial that we get it right. As Figure 2 shows, anthropogenic emissions have pushed greenhouse gas concentrations far beyond the limits that they had previously remained within, for over 400,000 years. This indicates that the composition of the atmosphere is not tightly regulated, by either biotic or abiotic feedbacks, on human timescales. Yet both CO₂ and methane are biologically active gases. And at least in the case of CO₂, the anthropogenic fluxes are a tiny fraction of the gross fluxes entering and leaving the biosphere; only a small adjustment to those biological fluxes would have been needed to keep CO₂ concentrations stable. There has been a modest increase in terrestrial photosynthetic uptake of CO₂ (Ciais et al., 1995; Keeling et al., 1996b; Myneni et al., 1997), but not nearly enough to keep CO₂ concentrations within their natural limits. This is an empirical rebuttal

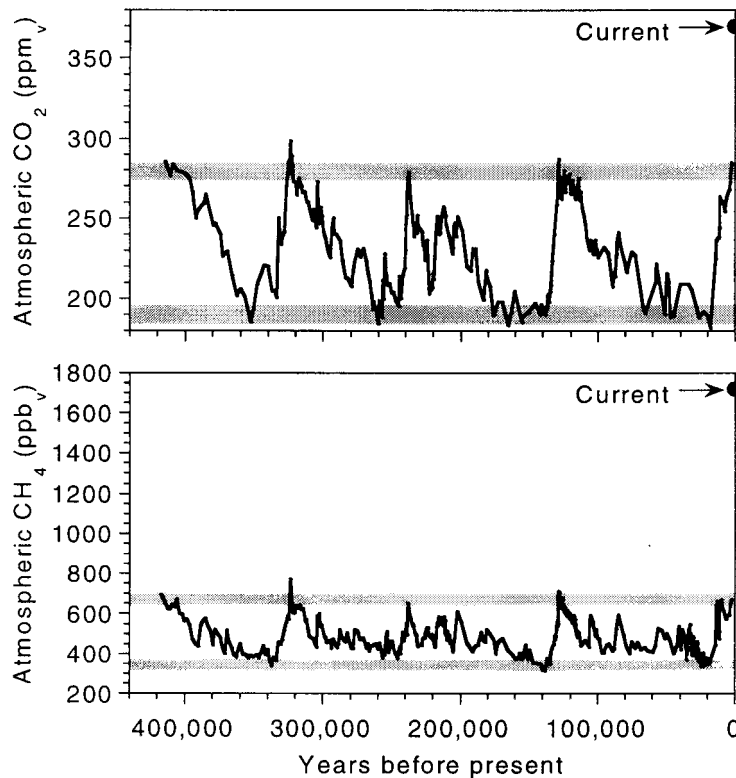


Figure 2. Carbon dioxide and methane concentrations over the last four glacial cycles, from Figure 1, re-scaled to show the current concentrations that have resulted from anthropogenic emissions. The current chemistry of the atmosphere is unprecedented in recent Earth history.

to Gaian notions of homeostasis and optimization, as it indicates that atmospheric CO₂ is not tightly regulated at a biological set point.

This could be the signature of a biological thermostat that has broken down (Lovelock and Kump, 1994), or it could be the signature of a complex system that combines both positive and negative feedbacks. The latter hypothesis is more consistent with what we know about the mechanisms underlying climate feedbacks, and it points to the urgent need to figure out their relative strengths and the timescales over which they operate. In particular, we need to understand why, despite greenhouse gas concentrations that are unprecedented in recent Earth history, global temperatures have not (yet) risen nearly as much as the correlations in the ice core records would indicate that they could. The correlations in the ice core data suggest that, for the current composition of the atmosphere, current temperatures are anomalously cool by many degrees (Figure 3). This might indicate that glacial-interglacial temperature shifts were amplified by ice-albedo feedbacks that are now much less influential (since the ice caps are already nearly gone, relative to ice age conditions). Alternatively, it may indicate that we have not yet

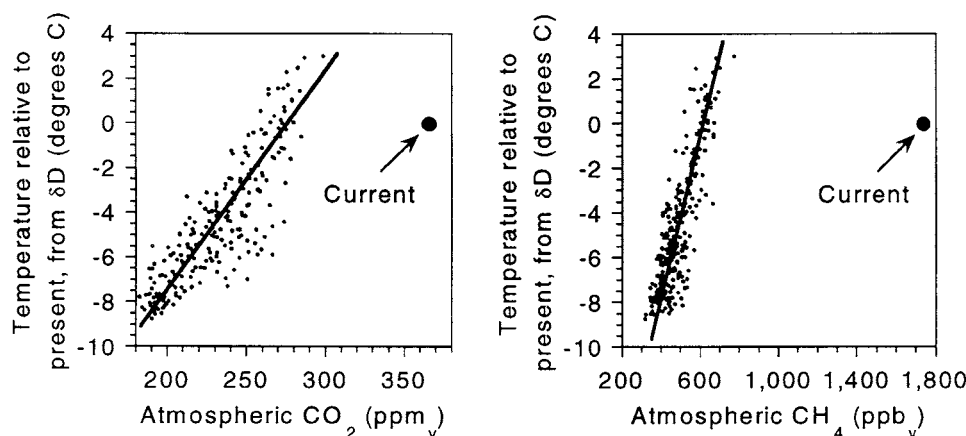


Figure 3. Correlations between atmospheric CO₂, methane, and temperature over the last 400,000 years, from Figure 1, compared to current conditions. Current conditions lie far outside the envelope of the prehistoric data, and far below any extrapolation from them.

fully felt the effects of important positive feedbacks (northward-spreading boreal forests, respiring soils, and so forth) that will amplify the warming experienced to date. If this is the case, it is vitally important that we appreciate it. Believing that biological feedbacks are generally stabilizing and beneficial will not help us unravel this puzzle.

In the human enterprise of science, our most daunting task is to see things as they are, rather than as we wish they were. Gaia's vision of Earth as a harmonious whole, engineered by and for the organisms that live on it, is a deeply evocative notion. It is emotionally very appealing to me. But I suspect that compared to the Gaian vision of global harmony, the actual Earth system – as it comes into clearer focus – will prove to be more complicated, more intriguing, and perhaps more challenging to our notions of the way things should be. Understanding the Earth system, in all of its fascinating complexity, is the most important scientific adventure of our time. We should get on with it, as free as possible from our preconceptions of the way the world ought to work.

References

- Charlson, R. J., Lovelock, J. E., Andreae, M. O., and Warren, S. G.: 1987, 'Oceanic Phytoplankton, Atmospheric Sulphur, Cloud Albedo and Climate', *Nature* **326**, 655–661.
- Ciais, P., Tans, P. P., Trolier, M., White, J. W. C., and Francey, R. J.: 1995, 'A Large Northern Hemisphere Terrestrial CO₂ Sink Indicated by the ¹³C/¹²C ratio of atmospheric CO₂', *Science* **269**, 1098–1102.
- Falkowski, P., Scholes, R. J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Hogberg, P., Linder, S., Mackenzie, F. T., Moore, B., Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V., and Steffen, W.: 2000, 'The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System', *Science* **290**, 291–296.

- Gillon, J.: 2000, 'Feedback on Gaia', *Nature* **406**, 685–686.
- Hamilton, W. D.: 1995, 'Ecology in the Large: Gaia and Ghengis Khan', *J. Appl. Ecol.* **32**, 451–453.
- Harvey, H. W.: 1957, *The Chemistry and Fertility of Sea Waters*, Cambridge University Press, New York.
- Henderson, L. J.: 1913, *The Fitness of the Environment*, MacMillan, New York.
- Holland, H. D.: 1964, 'The Chemical Evolution of the Terrestrial and Cytherian Atmospheres', in Brancazio, P. J. and Cameron, A. G. W. (eds.), *The Origin and Evolution of Atmospheres and Oceans*, Wiley, New York.
- Holland, H. D.: 1984, *The Chemical Evolution of the Atmosphere and Oceans*, Princeton University Press, Princeton, N. J.
- Hutchinson, G. E.: 1954, 'The Biogeochemistry of the Terrestrial Atmosphere', in Kuiper, G. P. (ed.), *The Earth as a Planet*, University of Chicago Press, Chicago, pp. 371–433.
- Huxley, T. H.: 1877, *Physiography*, MacMillan and Co., London.
- Keeling, C. D., Chin, J. F. S., and Whorf, T. P.: 1996a, 'Increased Activity of Northern Vegetation Inferred from Atmospheric CO₂ Measurements', *Nature* **382**, 146–149.
- Keeling, R. F., Piper, S. C., and Heimann, M.: 1996b, 'Global and Hemispheric CO₂ Sinks Deduced from Changes in Atmospheric O₂ Concentration', *Nature* **381**, 218–221.
- Kerr, R. A.: 1988, 'No Longer Willful, Gaia Becomes Respectable', *Science* **240**, 393–395.
- Kirchner, J. W.: 1989, 'The Gaia Hypothesis: Can It Be Tested?', *Rev. Geophys.* **27**, 223–235.
- Kirchner, J. W.: 1990, 'Gaia Metaphor Unfalsifiable', *Nature* **345**, 470.
- Kirchner, J. W.: 1991, 'The Gaia Hypotheses: Are They Testable? Are They Useful?', in Schneider, S. H. and Boston, P. J. (ed.), *Scientists on Gaia*, MIT Press, Cambridge, Massachusetts, pp. 38–46.
- Kirchner, J. W. and Roy, B. A.: 1999, 'The Evolutionary Advantages of Dying Young: Epidemiological Implications of Longevity in Metapopulations', *Amer. Naturalist* **154**, 140–159.
- Kleidon, A.: 2002, 'Testing the Effect of Life on Earth's Functioning: How Gaian Is the Earth System?', *Clim. Change*, this issue.
- Lashof, D. A.: 1989, 'The Dynamic Greenhouse: Feedback Processes That May Influence Future Concentrations of Atmospheric Trace Gases in Climatic Change', *Clim. Change* **14**, 213–242.
- Lashof, D. A., DeAngelo, B. J., Saleska, S. R., and Harte, J.: 1997, 'Terrestrial Ecosystem Feedbacks to Global Climate Change', *Ann. Rev. Energy Environ.* **22**, 75–118.
- Legrand, M., Feniet-Saigne, C., Saltzman, E. S., Germain, C., Barkov, N. I., and Petrov, V. N.: 1991, 'Ice-Core Record of Oceanic Emissions of Dimethylsulphide during the Last Climate Cycle', *Nature* **350**, 144–146.
- Legrand, M. R., Delmas, R. J., and Charlson, R. J.: 1988, 'Climate Forcing Implications from Vostok Ice-Core Sulphate Data', *Nature* **334**, 418–420.
- Lenton, T. M.: 1998, 'Gaia and Natural Selection', *Nature* **394**, 439–447.
- Lovelock, J. E.: 1986, 'Geophysiology: A New Look at Earth Science', in Dickinson, R. E. (ed.), *The Geophysiology of Amazonia: Vegetation and Climate Interactions*, Wiley, New York, pp. 11–23.
- Lovelock, J. E. and Kump, L. R.: 1994, 'Failure of Climate Regulation in a Geophysiological Model', *Nature* **369**, 732–734.
- Lovelock, J. E. and Margulis, L.: 1974a, 'Homeostatic Tendencies of the Earth's Atmosphere', *Origins Life* **5**, 93–103.
- Lovelock, J. E. and Margulis, L.: 1974b, 'Atmospheric Homeostasis by and for the Biosphere: The Gaia Hypothesis', *Tellus* **26**, 2–9.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and Nemani, R. R.: 1997, 'Increased Plant Growth in the Northern High Latitudes from 1981 to 1991', *Nature* **386**, 698–702.
- Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davisk, M., Delaygue, G., Delmotte, M., Kotlyakov, V. M., Legrand, M., Lipenkov, V. Y., Lorius, C., Pepin, L., Ritz, C., Saltzman, E., and Stievenard, M.: 1999, 'Climate and Atmospheric History of the Past 420,000 Years from the Vostok Ice Core, Antarctica', *Nature* **399**, 429–436.

- Redfield, A. C.: 1958, 'The Biological Control of Chemical Factors in the Environment', *Amer. J. Sci.* **46**, 205–221.
- Saleska, S. R., Harte, J., and Torn, M. S.: 1999, 'The Effect of Experimental Ecosystem Warming on CO₂ Fluxes in a Montane Meadow', *Global Change Biol.* **5**, 125–141.
- Schneider, S. H.: 2001, 'A Goddess of Earth or the Imagination of a Man?', *Science* **291**, 1906–1907.
- Schneider, S. H. and Londer, R.: 1984, *The Coevolution of Climate and Life*, San Francisco, Sierra Club Books.
- Schwartzmann, D. W. and Volk, T.: 1989, 'Biotic Enhancement of Weathering and the Habitability of Earth', *Nature* **340**, 457–460.
- Sillen, L. G.: 1966, 'Regulation of O₂, N₂, and CO₂ in the Atmosphere; Thoughts of a Laboratory Chemist', *Tellus* **18**, 198–206.
- Spencer, H.: 1844, 'Remarks upon the Theory of Reciprocal Dependence in the Animal and Vegetable Creations, as Regards its Bearing upon Paleontology', *London Edinburgh Dublin Phil. Magazine and J. Science* **24**, 90–94.
- Tans, P. P., Fung, I. Y., and Takahashi, T.: 1990, 'Observational Constraints on the Global Atmospheric CO₂ Budget', *Science* **247**, 1431–1438.
- Volk, T.: 1998, *Gaia's Body: Toward a Physiology of Earth*, Copernicus, New York.
- Watson, A. J., Bakker, D. C. E., Ridgwell, A. J., Boyd, P. W., and Law, C. S.: 2000, 'Effect of Iron Supply on Southern Ocean CO₂ Uptake and Implications for Glacial Atmospheric CO₂', *Nature* **407**, 730–733.
- Watson, A. J. and Liss, P. S.: 1998, 'Marine Biological Controls on Climate via the Carbon and Sulphur Geochemical Cycles', *Phil. Trans. Roy. Soc. London, Series B* **353**, 41–51.
- Watson, A. J. and Lovelock, J. E.: 1983, 'Biological Homeostasis of the Global Environment: The Parable of Daisyworld', *Tellus, Series B: Chem. Phys. Meteorol.* **35**, 284–289.
- Woodward, F. I., Lomas, M. R., and Betts, R. A.: 1998, 'Vegetation-Climate Feedbacks in a Greenhouse World', *Phil. Trans. Roy. Soc. London, Series B* **353**, 29–39.
- Woodwell, G. M., Mackenzie, F. T., Houghton, R. A., Apps, M., Gorham, E., and Davidson, E.: 1998, 'Biotic Feedbacks in the Warming of the Earth', *Clim. Change* **40**, 495–518.

(Received 16 May 2001; in revised form 9 July 2001)