Is Gaia Really Conventional Ecology?

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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Is Gaia really conventional ecology?

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The Gaia theory of Lovelock has had a very unequal treatment by conventional ecologists, ranging from being ignored to qualified support. I suggest that the phenomena described by Gaia are really capable of explanation by conventional ecological ideas using a gene/individual unit of selection. This is analogous to the situation in ecology during the 1960's when many apparent 'for the good of the species' adaptations were explained at lower levels of selection.

It is thus that, from principles of natural philosophy, we may arrive at some knowledge of order and system in the oeconomy of this globe. Hutton (1785).

Gaia theory is the suggestion by Lovelock (1979, 1988) that the biosphere functions as a single homeostatic organism, regulating conditions on earth to maintain their suitability for life. If correct this controversial theory is of great importance in ecology; however, it receives very unequal treatment in the ecology textbooks. It is ignored by many of them (Ricklefs 1990, Colinvaux 1993, Krebs 1994, Begon et al. 1996), described as probably no more than a 'charming metaphor' by Brewer (1994) but treated more sympathetically by Odum (1997), Smith and Smith (1998) and the microbial ecology textbook of Atlas and Bartha (1998). The idea appears to have been treated more sympathetically in many 'popular' science books, usually written by non-ecologists (e.g. Margulis and Sagan 1986, 1995, Davies 1987, Leakey and Lewin 1995, Schneider 1996, Smolin 1997, Gribbin 1998).

The greatest problem with Gaia is a theoretical one, 'the idea that homeostatic mechanisms seen in the biosphere evolved with the specific function of maintaining a steady state is to most evolutionary biologists, group selection pushed to an absurd extreme' (Brewer 1994). As Dawkins (1982) has pointed out if one considers oxygen production by plants 'for the good of the biosphere' a mutant plant which did not produce oxygen would have fewer costs and as such be at an advantage. Such a plant 'would outreproduce its more public-spirited colleagues, and genes for public-spiritedness would soon disappear' (Dawkins 1982). This is the classic problem in the evolution of mutualisms, why do cheats not invade the system? (Maynard Smith and Szathmary 1995).

Gaia suggests a number of interesting questions. Firstly is the regulation that Lovelock sees in the biosphere a real phenomenon? If it is, can the apparent modification of the environment by one species for the good of others be explained by conventional theory? This paper concentrates on the second of these questions.

Can natural selection explain Gaia type systems?

The general assumption is that Gaia type behaviour which appears to be for the good of the biosphere cannot easily be explained by natural selection (Dawkins 1982). Is it possible that these apparent 'for the good of the biosphere' adaptations can be explained by gene level selection? Something similar happened during the 1960's when many apparent for the good of the species adaptations were explained at the gene level of selection (Williams 1966, Collins 1986). I will consider three cases that suggest that this may be the case with Gaia; one theoretical and two real examples.

Daisyworld

As a response to criticisms such as those of Dawkins (1982), Lovelock (1988) has developed a simple mathematical model which illustrates the possibility of climatic regulation following from natural selection. In the model Lovelock imagines a world inhabited by different species of plants (daisies). Some being dark coloured, some light coloured and some of intermediate colour, these last being potential 'cheats' in the regulation system. The star around which the planet orbits shows an increase in radiation output over time (typical for a star similar to our sun; Narliker 1977). The daisies are limited by temperature with the lower limit of tolerance at 5°C, optimum conditions at 20°C and the upper limit of tolerance at 40°C. The mean temperature of planet Daisyworld is determined by its albedo; with dark daisies having a lower albedo than bare ground and light daisies a higher albedo than bare ground. The light coloured daisies suffer at low temperatures as they reflect most of the light incident on them; similarly the dark daisies overheat at high temperatures. Lovelock (1988) demonstrated that it was possible to regulate the planet's temperature due to the relative fortunes of daisies with different albedos causing the planet's albedo to increase at higher temperatures, the intermediate grey daisies did not disrupt the system as they only had a selective advantage when solar input was at levels where regulation was not needed (Lenton 1998). In this admittedly simple model, selection between plants leads to climate regulation, as radiation output from the star increases light coloured daisies become more common and reflect more radiation into space, so regulating the planet's temperature. Lenton (1998) has recently extended the model to allow for mutations. This slightly more realistic version of the model gives results similar to the simpler version described above.

Plankton-derived dimethylsulphide (DMS)

One of the classic examples often cited by supporters of Gaia is cloud production due to plankton-derived DMS (Lovelock 1988, Margulis and Sagan 1995). This biogenic cloud formation appears to be on a scale capable of affecting global climate. Interpreting this as a system which has evolved to maintain the earth's temperature at a level suitable for life suffers all the well-known problems of group selection. Why should an alga use resources which it could spend on itself to maintain the long-term stability of the climate, a selfish mutation that did not pay this cost would out-compete its selfless competitors. Recently Hamilton and Lenton (1998) have suggested a self-consistent gene level hypothesis which explains this puzzling behaviour. They argue that algal blooms with high DMS emissions may be attempts to manufacture winds to aid their own dispersal. 'Selection for local induction of wind is likely to be most effective at the level of clonal microbial patches' but such kin selection may not be needed (Hamilton and Lenton 1998). The important point is that *a Gaia type process is capable of a gene level selection explanation.*

Mycorrhizal networks

Lenton (1998) has argued that Gaian feedback concepts may usefully be applied to ecosystem levels. Mycorrhizal networks are an obvious potential example. These have the Gaian property of organisms behaving in a manner which appears to benefit the system as a whole at a net cost to the organisms involved. Over the last two decades it has become apparent that mycorrhizal fungi link together the roots of plants 'like users on a computer network' (Perry et al. 1992). This can allow nutrients to pass between different plant species. This has caused some writers to comment that mycorrhizal fungi are operating for the general good of the whole community (e.g. Leakey and Lewin 1995) an idea with strong connections to Gaia. Plants are apparently giving away resources they could use themselves for the greater good of the community. Can such a system be explained by conventional natural selection? Recently, in this journal, I have provided a potential explanation showing how this could happen (Wilkinson 1998a; see also Perry 1998). I suggested that the fungus benefits by investing resources in plants that can potentially provide it with products of photosynthesis at some point in the future. From the plants' point of view the provision of resources to members of different species could be an accidental effect of providing resources to related individuals growing near by or a side effect of selection for access to a wide genetic diversity of different fungal genotypes.

For the purposes of this paper it hardly matters if the explanation of biogenic cloud formation by Hamilton and Lenton (1998) or mycorrhizal networks by myself (Wilkinson 1998a) are correct. They illustrate that it is possible to produce conventional explanations of these Gaia type phenomena which satisfy the criteria of being consistent with known fact and the theory of evolution by natural selection; the two principal constraints for historical explanations in biology (Greene 1994, Maynard Smith and Szathmary 1995).

Gaia at ecosystem levels

As briefly described above Lenton (1998) has recently pointed out that 'coupling between life and its environment occurs at all scales, beginning with localised niche construction and with ecosystems emerging as integrated systems between the individual and global levels'. He suggests that a Gaian feedback approach can be applied to these systems. This applies Gaian ideas to scales much more familiar to most ecologists. Crucially he argues that 'ecosystems that have stabilising feedbacks will tend to persist and spread' (Lenton 1998: 445). He appears to be considering selection on ecosystems rather than the individuals they are composed of. How realistic is this?

The big problem is that many of these systems are not stable over a time scale of thousands of years. On average species survive for much longer than most communities or ecosystems and are sorted by climate and other changes into novel communities (Bennett 1997, Huntley 1996, Foster et al. 1990). These insights from Quaternary paleoecology may provide an explanation for the observation by Janzen (1985), that few of the species he studied had any specific adaptation to their local environment. Under such conditions it is hard to imagine Gaian selection operating on ecosystems. As a minimum such a model would require a more static ecology, stable over geological time scales. Individual or gene level selection, as in the model outlined for mycorrhizal networks, appears more realistic.

Are biotic effects stabilising to the planet?

As Hamilton and Lenton (1998) have pointed out, showing that large effects on the environment can arise from behaviour which is adaptive at the individual or gene level does not explain why life influences are stabilising to the planet; a key idea of Gaia. Firstly one needs to ask if it is really the case that life has this homeostatic effect. For example, much of the literature on Gaia concerns the regulation of the atmosphere. Clearly on a day-to-day basis the composition of the atmosphere is stable, but over geological time there have been very large changes in the concentration of gases such as oxygen and carbon dioxide (Conway Morris 1995) largely caused by biological processes. Clearly life has huge effects on atmospheric chemistry but on what time scale should we look for regulation? The observation by Smolin (1997) that many of these systems appear to show stability over periods greater than their cycling time may provide a possible solution to this question. It is also very unclear how to recognise changes which benefit life. What is good for a polar species is bad news for a tropical one, conditions which benefit anaerobic microbes would kill the readers of this paper! Part of the problem is caused by a confusion in the literature on Gaia between the relatively uncontroversial claim that 'life affects climate' and the much more heterodox idea that 'life regulates climate'. A similar problem is found in the history of population regulation with the past conflict between density dependent and density independent explanations (McIntosh 1985). The confusion arose because factors which can greatly affect a population size (e.g. climate) cannot regulate it (e.g. the density of a species of mouse is unlikely to affect the probability of a cold mouse killing winter). Regulation requires the 'thermostat' like behaviour of density dependent processes.

If, however, we assume that life does indeed stabilise conditions on the earth, are there conventional mechanisms which could explain this? There appear to be at least two mechanisms which could have this effect.

The weak anthropic principle

There is a very similar problem in cosmology where minor alterations of a few astrophysical constants leads to a universe which would be unable to support life. The weak anthropic principle suggests that this is explained by the fact that only in a universe with the 'correct' values for these constants can astronomers exist and so worry about the problem (Carr and Rees 1979, Penrose 1989; see Smolin 1997 for a critique of these ideas). A similar argument applies to the biosphere, if it had not remained reasonably stable over geological time (even if this is just due to 'luck') then no biologist could evolve to worry about the problem. This suggests that any biosphere that supports intelligent life must at least give the illusion of Gaian type regulation, *even if such processes do not exist on the planet*. Lenton (1998) in his recent review concedes that such an explanation is possible if unimportant in his estimation.

The utilisation of novel resources

Life appears capable of surviving in a wide range of environments. From endolithic micro-organisms in Antarctic dry valleys (Wynn-Williams 1996) to the strange Lake Goang in Indonesia, where in spite of a pH of 2.5 and high concentrations of sulphate, chloride, iron and aluminium a range of organisms from microbes to crabs survive (Green and Kramadibrata 1988). Over geological time life forms evolve to utilise a wide range of novel resources, often biologically produced such as oxygen, lignin, cellulose and petroleum hydrocarbons. If a resource appears in the environment then it seems organisms will evolve to use it. This invasion of vacant niches can have the appearance of Gaian regulation, preventing an excessive build up of the resource (e.g. lignin or oxygen). Consider photosynthesis (i.e. using both photosystems I and II) this can be described conventionally as an adaptation to gain access to a novel energy source (light) or as a Gaian mechanism to provide oxygen supplies for animals (rather like an 18th century argument from final causes). In all these cases the apparent regulation appears to come from selection at the gene or individual level to use a poorly exploited resource. This provides a more conventional explanation of Gaian type systems which has not to my knowledge been properly addressed by pro Gaia authors.

Conclusion

It appears that many (all?) of the phenomena claimed by Gaia are capable of explanation by conventional units of selection (i.e. genes or individuals). Therefore my tentative answer to the question posed in my title, 'Is Gaia really conventional ecology?' is yes.

If I am correct where does this leave Gaia theory. As Thornton (1996) has pointed out in another context 'iconoclasts can stimulate debate, thought, and further research, even if they do not eventually win the day'. Gaia has drawn attention to the role of biology in the 'abiotic' environment (e.g. atmospheric chemistry) and also illustrated the central role of microbes in many global ecological processes, something that is often overlooked by conventional ecologists (Fenchel 1992, Wilkinson 1998b). As such it is a successful scientific theory (albeit probably incorrect) much more than a 'charming metaphor'.

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