James Lovelock was awarded Honorary Membership of the BES in 2005. The following articles discuss his most significant contribution to ecology, Gaia theory.

Thank you for Gaia!

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'Gaia' has made many people think. I suggest James Lovelock has contributed greatly to ecology with the observation that the Earth shows an improbable stability. Whilst such stability is increasingly accepted, the mechanism promoting it remains controversial. I hope to illustrate why parts of Gaia theory should be endorsed by ecologists, but note that there are educational risks-unless evolutionary criticisms are incorporated.

Biologists have discussed facets of the stability for hundreds of years: for example the 'balance of nature' was considered by Linnaeus and others. Lovelock and ecologists are of course also aware of previous massive changes in the atmospheric composition. However, Lovelock's background includes a range of sciences, which may have enabled him to spot how remarkable the general stability of Earth is. The stability of atmospheric oxygen is extraordinary, given abundant abiotic materials (such as iron and sulphur) and biotic materials (such as methane and wood) which can be oxidised. Then there is the surface water on which life as we know it depends - Earth has it, Mars and Venus had it. Did Earth keep its liquid water simply because of its distance from the sun, in a "Goldilocks zone"? Some consider it more likely that water would have been stripped off the Earth through photo-dissociation, with the resultant hydrogen bleeding off into space. Why did this not happen? Gaian theorists have suggested that oxygen helps retain the hydrogen.

So we have the planetary oddities including alkalinity of the surface in water-clouds and rainfall, and to some extent in temperature through the day and millennia. Lovelock noted that life is not only involved with some of these processes – such as producing oxygen and binding carbon dioxide as carbonate rocks – but that stability favours life as we know it. One can see how tempting it was to draw the conclusion that life is "regulating" the environment for its own benefit, or to put is as Lovelock did, "homeostatic" processes keep the

"living" planet "comfortable" for life. Evolutionary biologists (e.g., Dawkins, 1982; Hamilton, 1995) have pointed out why that would not work. Why should one living thing, such as a coccolithophore, act to stabilise the planet for the benefit of other individuals and species – even if there is no cost to doing so? However, Lovelock (2006) continues to suggest such mechanisms, for example in proposing that animals excrete nitrogenous waste as urea rather than nitrogen to help other species use the waste product, or for the long-term benefit of animals using it to feed their food plants.

As another example, phytoplankton in the oceans secrete DMS – a costly gas which tends to condense water into clouds. This massively influences planetary rainfall and albedo, and benefits many species. Hamilton and Lenton (1998) looked for a 'selfish' explanation. They proposed that heat is released when clouds condense – and the rising warm air lifts clones of individuals secreting DMS into the sky, helping their dispersal. Forest microbes may use a similar method to fly. This controversial theory makes testable predictions, and may provide a breakthrough typical of Hamilton. Hamilton, Sutherland (1997) and I have stressed that we must look for conventional mechanisms: we should not rely on altruism, group-selection, long-term benefits and widespread interspecies mutualism to make Gaia work (Hambler, 1997).

Hamilton, Henderson and I also rejected Lovelock's Daisyworld model of Gaia. In this model, daisies with preprogrammed constraints in their optimal growth temperature and colours "regulate" the temperature of a planet: black daisies thrive when it is cold, and white ones when it is hot. The sun gets hotter through time (as in reality), and the planet eventually becomes lifeless when even a world full of white daisies does not reflect enough heat. But Hamilton (1995) pointed out the interim period of stability is an artefact of the genetic bias in the daisies introduced by the modeller. I suggested that in a more realistic world the optimal temperature of the daisies would adapt upwards with the increasing solar output, and that increasingly pale daisies



would evolve before life dies out at extreme temperatures. This failure to stabilise is indicated by new models (e.g., Lenton & Lovelock, 2000). What such models show again is that Daisyworld relies on massive evolutionary constraints on perfection

Feature: Gaia

(Dawkins, 1982). These constraints include insufficient polymorphism in colour, or constraints on the thermal stability of organic molecules from which life is composed. Lovelock (2006) suggests there are also abiotic constraints due to thermoclines in the oceans, which at high temperatures isolate plankton from nutrients. The more constraints (i.e., bias) in the models, the better the "self-regulation". Considering even the known and present thermal range of life on Earth, I suggest that global temperature and evolution have a long way to go before such constraints should make much difference.

So what can explain the planetary stability? Peter Henderson and Bill Hamilton were working on this problem when Hamilton died, and were just about to submit a radically new model - which Henderson called Dam World. This model includes numerous density-dependent interactions between species in a pool behind a dam. The dam is created by the rocky secretions of some organisms. If the abundance of some other species becomes high, they bore through the dam and burst it. This model suggests high species richness is associated with higher water levels in the dam - analogous perhaps to high oxygen levels in the atmosphere. Considering this and other studies, Hamilton was increasingly confident that richer ecosystems are more stable. This is still controversial, considering R.M. May's models of ecosystem stability. An example of an output from Dam World is given in Hambler, 2004, and Henderson intends to publish the model much as it was when Hamilton died.

Both Dam World and Daisyworld share an essential feature of Lovelock's vision: that life and the abiotic parts of the planet are "tightly coupled". Of course, this is what the term "ecosystem" was coined in the 1930s to convey, and the importance of life in retaining soil and clouds has been discussed for hundreds or even thousands of years (Hambler, 2004). However, Lovelock has looked at coupling on larger spatial and temporal scales than many. He stresses the feedbacks between changes in life forms and changes in abiotic features, fostering further evolutionary pressures on life, as with extended phenotypes and niche construction (Dawkins, 1982; Odling-Smee et al., 2003).

Where might Gaia theory take us next? I suggest that while 'earth-system scientists' clarify the mechanism(s), environmentalists can already draw important conclusions. Life has massive relevance to the stability of the planet. The gas balance and other features have proven resilient even to some mass extinctions, yet there may be limits before stability breaks down – analogous to a dam burst in Dam World. Some species might trigger shifts between metastable

states (attractors in a complex system). We know that life is perfectly capable of being enormously destructive to other life – indeed, this is the expected evolutionary norm. The advent of excretion of oxygen illustrates that successful genes can drive massive planetary change and extinctions. One concern about climate change (a disaster emphasised in Lovelock's *The revenge of Gaia*) is that the present stable state will indeed break down (perhaps temporarily) in the face of the evolutionary success of humans: we are the sort of 'Genghis Khan' of which Hamilton (1995) warned.

There is a massive risk to humans if ecosystem services are lost, and this is an acid test of the precautionary Principle 15 of the 1992 Rio Declaration. In the face of such risk, should we wait to gain advanced understanding of the mechanism of Gaia, or should we act as if irreversible deletion of species and habitats might destabilise the planet? This is not a new message, but is one the Gaian perspective reinforces.

Gaia could cause confusion if flawed mechanisms or misleading metaphors are promoted without criticism. Yet the baby should not be thrown out with the bathwater: the general idea of Gaia, a science of planet-level ecology, can progress despite and because of the controversies. Gaia encourages people to look at the big picture, the state of the planet and the long term. It has policy implications ranging from promoting nuclear power to protection of biodiversity (both long-advocated by a number of ecologists). Gaia has existed, despite humans, for millennia. Gaia has not just made us think – it has permitted us to do so.

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