Review of: "Evidence for the Existence and Early Origin of Genes Making Possible the Darwinian Evolution of Biogeochemical Homeostasis at a Planetary Scale"

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Potential competing interests: No potential competing interests to declare.

Preliminary Comments:

In his original review of Lovelock and Margulis's first Gaia book, Ford Doolittle wrote: (https://www.uvm.edu/~pbierman/classes/gradsem/2008/nature_motherly.pdf)

"Lovelock is not explicit, but he implies that Gaia evolved as life evolved, and if he is to be taken seriously at all, he must mean that she is the product of natural selection operating in the normal way but on a grand scale. And that must mean that organisms (or at least those with important geochemical impact) which behave in such a way as to contribute to the maintenance of Gaia have a greater probability of leaving offspring than those which do not."

This is the essence of the problem of reconciling Gaia and natural selection. There either exists a process to create this bias in Darwinian fitness towards "Gaia-contributing genotypes," or there does not. In response to Doolittle's review, Lovelock emphasized emergent phenomena, and Margulis emphasized how symbiotic interactions blur the boundaries between what biologists categorize as Darwinian units of selection. But neither of them provided a satisfactory response to the above central problem.

In my opinion, the debate about Gaia*in specific relation to natural selection*remained stuck at that point for several decades, not starting to move forward again until Doolittle's own suggestion of process-based persistence-selection for interacting sets of genotypes and geochemical patterns (see "It's-the-song-not-the-singers" theory https://www.pnas.org/doi/full/10.1073/pnas.1722232115).

But this is an ongoing area of research because working out how and whether any such persistence selection might work is a tricky and subtle question, in part because of the fundamental separation of scales between any planetary process and Darwinian dynamics. There remains the fundamental problem that a biological genotype that induces an environmental change that benefits its own fitness (thus triggering a positive feedback by which it will spread) but ultimately destabilizes the climate in some way will nevertheless still spread, potentially undermining habitability completely if not checked by some mitigating factor (e.g., a white daisy with an anomalously cold optimum growth temperature, in terms of the original Daisyworld model https://en.wikipedia.org/wiki/Daisyworld).

It may be that there is some additional factor, which is outside the scope of traditional Darwinian thought, that has the effect that Gaia can nevertheless still appear despite the above issues. Each suggestion for the nature of any such factor

has its own problems. Lovelock himself emphasized the importance of emergent climatic patterns with homeostatic properties. But Gaia explicitly compares Earth with comparable lifeless planets. Therefore, if it is simply a matter of "emergent homeostasis over-rides Darwinian tendencies," why does homeostasis not emerge from abiotic processes on (say) Mars and Venus? (The relationship between Darwinian selection and geochemical/climatic feedback is reviewed by Tim Lenton here https://www.nature.com/articles/28792.)

It might be the case that the byproducts of life tend to give rise to the emergence of homeostasis (see Tyler Volk, "Gaia's Body" https://mitpress.mit.edu/9780262720427/gaias-body/), in a way that, presumably, the products of abiotic reactions do not. This would avoid any specific need for natural selection, but exactly how might the emergence of byproduct-driven homeostasis work?

It might be the case that physical constraints on growth and adaptation mitigate the destabilizing influence of any Darwinian "anti-Gaian" genotype by causing its growth to self-limit at the edge of the habitable range (Lenton and Lovelock, 2000 https://www.sciencedirect.com/science/article/abs/pii/S0022519300921052), but again, what is the precise source of any climatic homeostasis relative to lifeless planets?

It might be that our interpretation of the habitability of the Earth must be weighted by an awareness of anthropic observer bias (Andy Watson is of this view https://doi.org/10.7551/mitpress/9780262194983.003.0019). But this does not address how our situation differs from the norm (relative to observer likelihood) for the universe as a whole; it simply notes that it must so differ, given that we observe it.

Finally, it might be the case that the evidence for climatic homeostasis by life is largely misinterpreted or unwarranted, and that a close look at the evidence leaves Gaia as an interesting idea now falsified in the negative (Toby Tyrell, On Gaia https://press.princeton.edu/books/hardcover/9780691121581/on-gaia). On this critical view, there are byproducts, constraints on life from abiotic variables, and in some cases what biologists call niche construction (https://en.wikipedia.org/wiki/Niche_construction), but no need to invoke regulation. But this view does not so much explain the difference between Earth and comparable lifeless planets as challenge the premise that a unique explanation is required.

Thus, there exists a range of views articulated in a significant secondary literature on the subject. For each of the above perspectives, there is a distinguished scholar defending that view, and there are valid counterarguments that make it possible to argue the point at length. In my opinion, this debate will remain at least somewhat ambiguous until there is data from extraterrestrial biospheres capable of resolving the sample-size-of-one issue, which is (!) obviously quite a tall order.

With this context noted, I come to my specific response to this paper:

A. Leggett and Ball's previous work suggests that various global-scale climatic time series datasets exhibit properties that suggest the operation of a sophisticated control system, which is sensitive to both the integral and derivative of the controlled variable, as well as the value of this variable itself. This is a very interesting claim, and if correct, is very

important. It is good to have the relevant ideas summarized in an accessible form in this paper. This is evidence supporting the existence of some stabilizing negative feedback connected to the presence of life, which again is interesting and important, but not “clear evidence that Gaia does exist.”

B. The review here of the biological evidence is, I am afraid, of questionable relevance to Gaia. This evidence demonstrates that:

- Prokaryotes form biofilms.
- The genetic machinery for bacterial chemotaxis is ancient and widespread, particularly in regard to interaction with the flagellum.
- Bacteria engage in quorum sensing to express various collective phenotypes when the population density is appropriate.
- Plants release airborne compounds in response to herbivory stress, to which adjacent plants may respond in a way that benefits the collective. Some of these compounds may be involved in aerosol formation and potentially relevant to clouds, connected to some of the feedback mentioned in previous work.

Imagine, for example, a mutant plant genotype that failed to produce the herbivory warning signal and thus did not benefit its neighbours. Its immediate short-term fitness might increase due to a reduced metabolic cost. The equilibrium reached would depend on the details of what biologists term multi-level selection. Now, for the sake of argument, imagine there definitively is a “cloud condensation nuclei formation gene” and its presence definitively has a “Gaian” effect. Now imagine an analogous mutant genotype in the same species that switches off the emission of the relevant biochemical, thus saving itself a metabolic cost and increasing its local fitness. The neighbouring original genotype would still maintain the “Gaian” effect by producing the relevant substance. And again, biologists would speak in terms of multi-level selection, freeloaders, cheaters, fitness payoffs, etc. Why should this mutant not displace the original? This is the starting point of the problem, at least if the objective is to reconcile Dawkins’s original criticism.

Scaling up from the local to the global is another issue. It is not clear to me how the aspects of this paper referring to these two different categories fit together. Specifically, the idea of “non-planetary core attributes” of Gaia seems to presuppose that organism-level homeostasis can straightforwardly spread, through population-level “mass action,” to planetary climatic/geochemical regulation, without lower-level Darwinian selection (or other constraints), breaking the process or undermining habitability. Whether and how this can happen is precisely the question under investigation. Biological organisms, even when they construct their own niches to some degree, do not, in general, regulate their environments in a homeostatic sense. (Beavers build dams because this benefits beaver genes, but this is not good for the felled trees or the flooded microcosms, etc.). Therefore, I’m not sure that the first two Gaian attributes are necessary or even particularly relevant. Mass action in one locale could just as easily have an anti-regulatory effect on the global climate. There are various permutations for the difference between the change in global average habitability and the local change experienced by the genotype that induces this global change. These and similar issues are reviewed in the context of Daisyworld here:
https://eprints.soton.ac.uk/272881/1/Reviews%2520of%2520%25E2%2580%25A6%25202008%2520Wood.pdf

The general point is that a genotype can trigger a global collapse in habitability but not experience negative feedback on its own growth until it's too late to mitigate this collapse, due to some discontinuity between the local and global scales. The assumption here that "mass action" will simply spread into global regulation ignores this central problem.

I find it convenient to define Gaia as the general idea that "life tends to keep the earth in a state that's good for life," i.e., life (as a planetary-scale entity) tends, on average, to exert an influence on climate/geochemistry that is conducive to the continued persistence of life (as a planetary-scale entity). If this is true, obviously various genes are necessary for any such planetary-scale influence but are only going to be sufficient in the context of a wider life-environment interaction. But this interaction must be stable despite an inherent "incentive" for Darwinian units of selection to break it, to the benefit of their own immediate fitness. It is non-trivial to work out how. This brings the whole discussion back to Doolittle's articulation of the central problem above. Consequently, whilst I welcome Leggett and Ball's summary of their previous interesting work, I cannot agree with their claim to have resolved the issues raised by Dawkins's original critique of Lovelock's ideas.

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