Journal of Theoretical Biology 434 (2017) 11–19

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtbi

Darwinizing Gaia

W. Ford Doolittle

Department of Biochemistry and Molecular Biology, Dalhousie University, Halifax, Nova Scotia, Canada

ARTICLE INFO

Article history:
Received 9 December 2016
Revised 6 February 2017
Accepted 13 February 2017
Available online 22 February 2017

Keywords:
Global homeostasis
Evolution by natural selection
Persistence
Biogeochemical cycle

ABSTRACT

The Gaia hypothesis of James Lovelock was co-developed with and vigorously promoted by Lynn Margulis, but most mainstream Darwinists scorned and still do not accept the notion. They cannot imagine selection for global stability being realized at the level of the individuals or species that make up the biosphere. Here I suggest that we look at the biogeochemical cycles and other homeostatic processes that might confer stability – rather than the taxa (mostly microbial) that implement them – as the relevant units of selection. By thus focusing our attentions on the "song", not the "singers", a Darwinized Gaia might be developed. Our understanding of evolution by natural selection would however need to be stretched to accommodate differential persistence as well as differential reproduction.

1. Introduction: Gaia and why Darwinists scorned her

In the prologue for her 1998 book *Symbiotic Planet* (Margulis, 1998), Lynn Margulis recounts how a former student, in remarking that "Gaia is just symbiosis seen from space", established a previously unrecognized (or so she claims) connection between her two principle theoretical preoccupations, serial endosymbiosis at the cellular level and Gaia as an evolved global homeostatic system. This essay is about that second preoccupation. Margulis' thinking in this area, as in several others, went against the main current of evolutionary thought.

What I hope to accomplish here is a sort of reconciliation. I attempt to recast Gaia theory in a conceptually stretched neoDarwinian framework. Many may think this a stretch too far, but *if* Gaia is to be Darwinized, what I propose seems a good way to start. I dedicate the exercise to Lynn, who would no doubt have thought it superfluous.

In this section, I introduce the Gaia hypothesis of Lovelock and Margulis (1974); see also Margulis and Lovelock (1974); Lovelock, (1972, 1979) and explain why Darwinists found it so difficult to accept. In Section 2, I discuss the (in my opinion) unsatisfactory attempts of Gaia's defenders to "Darwinize" the notion by assuming that it is organismal lineages or communities that natural selection must address. In Section 3, I develop a novel Darwinizing tactic, holding that for biogeochemical cycles or other Gaian homeostatic systems, it is the cycles or systems themselves – not the organismal lineages or communities that implement them – that are best viewed as *units of selection*. I take that term to mean membership in something like a "Darwinian population", as conceived by Godfrey-Smith (2009) but necessarily expanded to accommodate the fact that differential persistence as well as differential reproduction can define *fitness*. In the fourth section, I argue that Lewontin's three-part formulation for evolution by natural selection (ENS) could fruitfully be relaxed or expanded to accommodate both persistence and reproduction. In the penultimate, fifth section, I discuss some attempts to cast entire planetary biospheres – assemblages of homeostatic systems – as units of selection. In the final paragraph I remind the reader of my purpose.

Gaia was the brainchild of James E. Lovelock, a successful inventor of delicate and sensitive machines: the name was suggested by his neighbor William Golding (of *Lord of the Flies*). Lovelock was soon joined in his efforts to promote the idea by Margulis, and together and separately they wrote many papers, popular articles and books on Gaia, showing varying degrees of adherence to the idea that she is like, or indeed *is*, a single organism. Their 1974 *Tellus* article (Lovelock and Margulis, 1974) offers this overview of their hypothesis ….

> … the total ensemble of living organisms which constitute the biosphere can act as a single entity to regulate chemical compositions, surface pH and possibly also climate. The notion of the biosphere as *an active adaptive control system able to maintain the Earth in homeostasis* we are calling the Gaia hypothesis. (Lovelock and Margulis, 1974, 3, emphasis mine)

Thus one might consider Gaia to represent the mother of all "major transitions in evolution", to borrow the title of Maynard Smith and Száthmáry's well-known monograph (Maynard Smith and Száthmáry, 1997). That is, she is expected to combine the evolutionary interests of her constituent parts (organisms or species) as units of selection into one more-inclusive or higher-order entity, to whose evolutionary interests those of the constituents are at least partly subordinated. Although Margulis and Lovelock did

http://dx.doi.org/10.1016/j.jtbi.2017.02.015
0022-5193/

not necessarily think along such fundamentally Darwinian and selection-focused lines (and *Major Transition in Evolution* was not to appear for another two decades), something like this was at stake. Indeed, Margulis and her son Dorion Sagan (Margulis and Sagan, 1997, p. 66) wrote ….

> Life at the surface of the Earth seems to regulate itself in the face of external perturbation, and does so without regard for the individuals and species that compose it …

Ruse (2013), in his recent book *The Gaia Hypothesis*, nicely positions the concept within the long history of Western philosophical thought on the nature and extent of life processes and superorganismality, although it is unclear whether this tradition informed Lovelock and Margulis any more than did Darwinism. Ruse extensively documents Gaia's obvious appeal to and rapid embrace by New Age holists, feminists and many of a teleological bent. But, as he also notes, the idea appeared at a time when mainstream biologists were moving in the opposite direction. Richard Dawkins was very soon to publish *The Selfish Gene* (1976), and most of us were busily schooling ourselves that the "for the good of the species" language of Konrad Lorenz and V.C. Wynne Edwards was to be assiduously avoided. So although Gaia found favor in the public, most self-respecting Darwinists reacted strongly against her. My own critique (Doolittle, 1981) focused on the unlikeliness of natural selection favoring the fixation in any species of a Gaia-serving altruistic trait that would not specifically benefit any of that species' own members for many, many generations – and conversely on the likeliness of "cheaters" that default on any such trait taking over, if contributing to it incurs any cost.

I did not of course deny the existence of co-evolved symbioses. Co-evolution, as defined long ago by Janzen (1980), 611), entails "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first." A more relaxed view would be that each of two species has selfishly selected-for traits that affect its interaction with the other, without any necessary trait-for-trait correspondence. Interaction need not be mutually beneficial: arms races between hosts and parasites or predators and prey are quintessentially coevolutionary.

Co-evolution admitted, there is uncertainty as to how all-embracing the process might be. Wade (2007) notes that a still active question in ecological genetics is: "Does co-evolution lead to highly specialized adaptations with particular partners, or is it diffuse, involving general adaptations for successful interaction with many other community members?" (2007, 185), while Nuismer et al. (2012) more recently conclude from multi-species modeling studies that " … coevolution can have important consequences for the structure and function of highly diverse and species-rich communities of mutualists (2012, 349)". Nevertheless, it is very hard to see an entire biosphere functioning as such a community, without some sort of global sanctioning force capable of targeting cheaters. And the fact that global parameters such as ocean salinity or atmospheric oxygen level change so slowly compared to the lifetimes of organisms within populations – and depend on the behaviors of so many species – rules out positive selection for any contributions to planet-wide homeostatic stability that are not in the first place selfish.

In the early 1980s, Dawkins, Gould, Maynard Smith and others voiced Darwinian objections to Gaia similar to mine (Ruse, 2013). A bottom-line argument that Gaia cannot be a product of evolution by natural selection (ENS) because there is only one of her was also advanced early and is often heard. Dawkins, in *The Extended Phenotype* (1982) elaborated on this notion, which was for him a *reductio ad absurdum*.

> The Universe would have to be full of dead planets whose homeostatic regulation systems had failed, with, dotted around, a handful of successful, well-regulated planets, of which the Earth is one. Even this *improbable scenario* is not sufficient to lead to the evolution of planetary adaptations of the kind Lovelock proposes. In addition we would have to postulate some kind of reproduction, whereby successful planets spawned copies of their life forms on new planets (emphasis mine, Dawkins, 1982, 236).

More than three decades later, philosopher Peter Godfrey-Smith (2015a), in a review of a new book by Lovelock, continues the general Darwinian line of critique. That is, he does not deny the *possibility* of global homeostases, only that the existence of any such mechanisms can be construed as the product of *natural selection specifically favoring them.*

> The fact that the Earth is not like an organism doesn't make it *impossible* for some of those relationships to be present. If they arise, they arise as *fortuitous byproducts* of the evolution of particular living things (Godfrey-Smith, 2015a, 19, emphasis mine).

Godfrey-Smith sees the biosphere as a complex system, to be sure, and seems to endorse something close to an anthropic explanation for why this system has not (yet) crashed. But he stops far short of allowing that there are systems-level functions evolved by natural selection (or that anthropism is itself some sort of cause).

> The interactions between species are consequences of the traits and behaviors that evolutionary processes within those species give rise to, and those processes are driven by reproductive competition within each species. The upshot of all these evolved behaviors and chemical reactions may be helpful to life as a whole, or not helpful, as the case may be. If a new behavior, or new chemical product, that was advantageous within some particular species would doom life on Earth if it became common, that fact won't stop its becoming common. From the fact that life still exists, we can tell that traits too antagonistic to life itself, however beneficial to the organisms that bear them, must not have arisen. If they had, we wouldn't be around to discuss the matter. But that isn't what kept those traits at bay. (Godfrey-Smith, 2015a, 19)

2. Defending Gaia

Lovelock has tried to take account of Darwinists' objections, and show how global homeostases might arise by natural selection. In a series of papers, he and Gaia's supporters presented increasingly elaborate versions of a model planet they called Daisyworld (see Lenton, 1998). In its simplest form, we are to imagine an otherwise gray planet under a slowly warming sun, boasting two kinds of daisies, black and white. Both have the same optimum growth temperature. When the planet is cooler than the optimum, black daisies grow faster, because they absorb more light and heat themselves and their surroundings up. When the global temperature exceeds the optimum, there is selection for white daisies, which do better than black because they reflect the light, cooling themselves individually and collectively the planet down. An equilibrium between the two forms of daisy, and around the optimal temperature for both, results. Natural selection for color is all that operates on the daisies, but – as if by magic – a daisy-mediated homeostatic regulatory mechanism is established and will, over a certain range, keep the planet suitable for all daisies, even as the sun warms.

Darwinists would have two problems with this. First, Daisyworld is *designed* to exhibit negative feedback: the magic is contrived. Destabilizing positive feedbacks can as easily arise, as Lenton (1998) admits, while adding ever more complexity to