

Commentary

Does Gaia Need to Be Darwinized?

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We discuss W. Ford Doolittle's proposal for 'Darwinizing Gaia'. While we agree with the importance of having a sound theoretical basis for Gaia and that evolutionary theory plays an important role in this, we identify several critical missing pieces in the Darwinizing programme. We argue that Doolittle's work (especially as summarised in his recent book) helps clarify what is required for a fuller Gaia theory, and use our critiques to offer some suggestions for what a modern Gaia theory should include.

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Introduction

In recent work^{[1][2][3][4][5][6]}, W. Ford Doolittle and others have been trying to, 'legitimize the Gaia hypothesis'^[6]. Central to this is the idea of persistence based selection, of which there are two main types **Selection by survival (SBS)**^{[7][8][9]} and **Sequential Selection (SS)**^{[10][11]}. While the latter considers persistent states of a single system over time, and so may be more directly applicable to Gaia^[12], the former is what is mostly considered by Doolittle and collaborators.

Selection by survival is an, almost, tautological observation: entities that survive have properties that enable them to survive. In its most straightforward interpretation applied to Gaia, SBS is little more than the anthropic principle – Gaia has the properties it does because otherwise we wouldn't be here. While not predictive, this version can serve as a useful null model^[12]. If the persisting entities also change in some way, as suggested by Bouchard, Doolittle and others, there are non-trivial consequences which move the idea beyond merely being a restatement of the anthropic principle and having real explanatory power.

In this commentary we reflect on Doolittle's programme as proponents of Gaia rather than critics, to whom much of his writing is addressed. We believe that the core idea of persistence based selection is important, however we highlight a number of issues:

1. It is irrelevant if an explanation can be called ‘Darwinian’ or not, and the contortions required to do so obscure rather than illuminate.
2. Gaia is considered purely as a problem in evolutionary biology, missing her other half, the environment.
3. There is a lack of engagement with prior research in Gaia Theory, especially modelling studies.

We expand on each of these points below after a brief historical introduction, which puts Doolittle’s et al.’s contributions into context and conclude with some thoughts about the future of Gaia Theory.

The Darwinizing Programme

Doolittle^[13], along with Richard Dawkins^[14], George Williams^[15] and others^{[16][17][18]}, was one of the more prominent early evolutionary critics of Gaia who were responding to what they saw as the unacceptably teleological reasoning used by Lovelock and Margulis to argue for ‘*atmospheric homeostasis by and for the biosphere*’^[19]. These critics saw Gaia as the ultimate example of group selection^[20], a perpetual source of controversy in evolutionary biology, but even worse, as in the case of Gaia there is only one group!

In the intervening forty years, as discussed in^[6], Doolittle’s own position has become more sympathetic to Gaia. To clarify what we see as Doolittle’s aim, we first define Gaia to be the interacting system consisting of all life and the abiotic processes with which it interacts. This system has emergent behaviours, like temperature regulation, which are only apparent when viewing the system as a whole. The Gaia hypothesis is that these emergent behaviours are generally beneficial for life. Much of the work on Gaia aims to determine to what extent this is true and, especially for Lovelock, to derive novel insights into planetary scale processes from this shift in perspective.

The conflict that concerns Doolittle and others is between ‘downward’ and ‘upward’ causal explanations. In other fields both explanations have their place. An economist may make the (upwards) claim that “Mass unemployment caused the current recession”, or the (downwards) one “The recession caused mass unemployment”. Generally there is no issue with ascribing causal agency to an entity called The Economy. Lovelock’s Geophysiology^[21] makes a similar sort of analogy, since in physiology we accept that biochemical changes within an organism cause *and are caused by* its behaviour.

In evolutionary biology, Doolittle argues, the upward direction is the only one with legitimacy and ‘Darwinization’ is his attempt to put the downwards direction on firmer footing, to show Gaia is ‘possible

in theory' ^[6]. For Doolittle, the only acceptable theoretical framework is a Darwinian one: *'For Darwinians ... to accept the Gaia hypothesis as legitimate and in their purview, it has to be ENS [Evolution by Natural Selection] that was the basic principle making Gaia probable'* ^[6]. His recent work, culminating in the book *Darwinizing Gaia*, is his attempt to show *'that there are ENS formulations in which the Gaia hypothesis is a legitimate Darwinian claim, not that the hypothesis is necessarily true.'* ^[6].

This effort is mostly centred around clarifying and synthesising different frameworks for defining evolution by natural selection of which he identifies two mainstream approaches: Lewontin's recipe ^[22] and Hull's interactor/replicator concept ^[23]. In ^[6] he discusses how they apply to more complex evolutionary problems like multilevel selection or holobiosis. Gaia only appears relatively late in the book, when the discussion comes together to argue for, basically, expanding the definition of evolution by natural selection to incorporate the notion of persistence and soften the requirement of reproduction, thereby allowing entities other than genes or individuals to be subject to this new, more expansive version of ENS.

Consequence and Compatibility

It is essential that the environmental part of Gaia is consistent with known laws of chemistry and physics. The living part also has to be consistent with the key principles of biology, especially evolution by natural selection. Gaia should 'emerge' as a distinct entity, more than the sum of those parts. The idea of emergence implies that the description of Gaia may use a different theoretical framework than the ones that describe its components. This is standard across the sciences, one does not use the equations of quantum mechanics to predict the weather. From the first work by Lovelock, Gaia has usually been discussed in the cybernetic language of coupled feedback mechanisms within and between biogeochemical cycles ^[24].

For Doolittle, a molecular biologist and more recently a philosopher of biology, the only way Gaia can be legitimised is by deriving it as a consequence of ENS. By trying to Darwinize Gaia, Doolittle elevates the requirement of 'consistency with' evolutionary theory to the requirement of being 'explained by' evolutionary theory. This is akin to demanding an explanation of evolution by chemistry or elementary particle physics in order to convince chemists or particle physicists of its truth. Obviously, these frameworks do not operate at the appropriate level to describe a peacock's tail, a finch's beak or their

interactions with other peacocks, finches and the environment. Expanding them to do so would be a difficult endeavour, to say the least.

For similar reasons, the attempt to Darwinize Gaia seems unlikely to succeed in describing emergent properties of life-environment interaction, unless Darwin is stretched so far as to be unrecognisable, a criticism already made by others^[25]. It is also quite optimistic to believe that evolutionary biologists, traditionally Gaia sceptics, would be convinced by changing Darwin to fit Gaia, as Doolittle proposes, rather than vice versa^[26].

The Environment

Like another (relatively) recent Gaia book by Ruse^[20] the terrain of discussion in^[6] is entirely biological, perhaps not surprising given Doolittle's background and professed interest. However, echoing the comments of Dutreuil^[27] about Ruse's book, Gaia was intended as, and has mostly been, a theory of planetary scale processes due to life-environment interaction. The primary scientific audience for it was atmospheric scientists, geologists, chemists, ecologists and others working in what would now be called Earth Systems Science^[28]^[29] made a similar point about the biological focus of some of Doolittle's ideas (especially clade selection) in the past.

While evolutionary biologists like Dawkins, Doolittle, Williams, Gould and others didn't like Gaia Theory, they largely ignored it. Dawkins' much discussed critique of Gaia took up only three pages in *The Extended Phenotype*^[14]. Despite Gould's own interest in evolutionary patterns over geologic time, Gaia merits only one paragraph in the 1400 page tome *The Structure of Evolutionary Theory*^[17], which largely echoes Dawkins. Evolutionary biologists had much bigger fish to fry than Lovelock and Gaia, from group selectionists in their own field to young Earth creationists outside of it. They also had seemingly little interest in the primary questions of Gaia Theory, like the past and future habitability of Earth and other worlds.

Gaia theorists on the other hand were, from the beginning, chiefly concerned with the interaction of life and the environment on a planetary scale^[30]. While biogeochemical cycles are sometimes mentioned^[1], the Darwinized Gaia of^[6] has little if anything to say about the environment, compared to other frameworks like cybernetic rein-control^[31], niche-construction theory^[32] or even basic ecological theory^[29] and so is fundamentally incomplete as a theory of Gaia.

Models of Gaia

Questions of ENS raised by evolutionary biologists needed to be taken seriously – a quarter of a century ago this was the problem that first attracted one of us to theoretical work on Gaia^[33]. Responding to criticisms, Gaia theorists sharpened their use of evolutionary concepts, mostly through models of life–environment interaction like the famous Daisyworld^[34]. Doolittle remains unconvinced by such efforts, stating that the regulation which emerges in Daisyworld is ‘baked in’^[6].

The original Daisyworld was intended to show that regulation can emerge in a coupled life–environment system (which was in doubt) and was explicitly referred to as a ‘parable’. Not discussed by Doolittle is the voluminous work done since the original Daisyworld, showing that in Darwinian Daisyworlds and other, completely different models, Gaian life–environment interactions arise in systems of evolving agents.^[31] ^{[35][36][37][38][39][40][41][42][43]} is a small sample of this. Taken together this work demonstrates the compatibility of Gaia with ENS and permits detailed study of questions like evolutionary ‘cheating’^[37] or the interplay between ENS and weaker forms of selection^[40].

Doolittle in^[6] and elsewhere does not refer to much if any of this work and makes no use of mathematical models (he refers to his ‘mathphobia’^[6]). Evolutionary theorists like Doolittle, Dawkins, Williams and others often rely on rigorous verbal argumentation, while the Gaia theorists’ engagement with evolution has been largely through mathematics and computational models. Again, this reflects the scientific audience of Gaia – chemists, climate scientists and ecologists who are accustomed to testing theories in this way. An illuminating example is^[4] which describes a verbal model of a chemostat and does not refer to the very similar, computational, flask model^[36] or the body of work about it, even papers using this model *specifically addressing persistence based selection*^[44].

Doolittle’s citation practices reflect his background and interests, however what is missing is important. In particular we want to highlight two key points. The first is that Gaia theorists have not ignored evolution or evolutionary critics, despite^[6] characterising the debate as frozen in 1982. Rather, prominent evolutionary theorists have largely ignored the responses to their critiques (with the notable exception of W. D. Hamilton^{[45][46]}, also not discussed by Doolittle). We speculate this is due to a combination of their lack of interest in the core questions of Gaia theory together with the difference in scientific language.

Our second point, is that while the model of^[4] may suffice to illuminate some aspect of clade selection, the simulation model of^[36] is far more precise, far richer and considers multi-species–environment

interactions which are the core of the Gaia concept. The description of this model consists of simple rules for microbe reproduction and mutation. Nutrient recycling within punctuated equilibria *emerges* by following these rules, rather than being ‘*baked in*’. Models of this sort allow one to study the robustness of system behaviours and trace explanations from the individual to the global level (and for the mathphobic Doolittle, such explanations are often verbal). We contend that the model in^[4], or indeed, the models in^[1] would be far more interesting and convincing if they were precisely formulated and solved or simulated, similarly to^[36] or any of the other Gaia modelling literature. Also, speaking from our experience, doing so for a model of even moderate complexity often leads to unexpected findings which are only apparent after seeing the model dynamics unfold.

Alternative Selection Principles

Much more aligned with Doolittle’s interest, his book gives a thoughtful and thorough summary of ongoing debates about multilevel selection. Doolittle has made important contributions to these debates^{[1][2][3]}. It is these concepts, particularly persistence as an explanatory mechanism in biological systems, that motivates much of Doolittle’s proposed modifications to established Darwinian frameworks.

We agree with Doolittle that persistence is a subtle, potent and understudied mechanism, and is especially relevant for Gaia. Differential survival among large populations, the primary concern of Doolittle, or repeated ‘trials’ within a single system, sequential selection, can lead to surprisingly complex outcomes. The Gaia that emerges from these considerations (called ‘entropic Gaia’ in^[12]) is perhaps more limited than Lovelock’s original, but is grounded in rigorous argumentation, with mathematics and modelling playing a key role, and depends crucially on this type of selection.

This is an active research subject encompassing evolutionary biology, Earth history and astrobiology^{[12][44][47][48][49][50][51][52][53][54][55][56][57]}. Importantly, the success or failure of persistence as an explanation for any phenomenon in nature is independent of whether evolutionary biologists agree that persistence based selection can be called Darwinian or not.

Gaia in the Anthropocene

We also agree with Doolittle that ‘*We face an existential crisis (possibly several at once), and seeing the biosphere as a single entity that includes us might be part of the solution*’^[6]. A view also developed by other

philosophers, such as Mary Midgley^[58] and Bruno Latour^[59]. Today, with desperate pleas from scientists to the public to recognise and react to the imminent dangers of climate change and biodiversity loss, an engaging and resonant concept like Gaia is called for and we too hope for a resurgence in Gaian thinking among scientists and the general public. Gaia can be both a scientific explanation of the Earth system and an approach to environmental philosophy underpinned by this science.

One of the unique aspects of Gaia theory is that it was largely developed through the popular writing of Lovelock and Margulis. As discussed by Ruse^[20], many of the Gaia critics in the 80s and 90s were repelled by the popularity of Gaia, particularly within the ‘new age’ movement. If popularity with an enthusiastic, but scientifically illiterate public is enough to fatally tarnish an idea, we can also say farewell to quantum mechanics, relativity and, if we consider the social Darwinists, evolutionary theory too.

^[6] reviews some of the suggestions from prominent Gaia theorists about recent Gaia inspired approaches to addressing climate change, from the managed Gaia of Lenton and Latour^[60] to the apocalyptic sci-fi of Lovelock’s last work^[61]. Rather than either of these, we believe that a renewed Gaia could productively engage with both scholarship and a receptive public seeking to connect an intrinsic wonder and appreciation for nature to modern scientific developments^{[62][63]}. This Gaia might once again capture people’s imagination in ways that respectable but dour climate and Earth Systems Sciences have failed to. See^[64] for a recent example.

Conclusions

The early criticisms by Doolittle and others were helpful for forcing clarification of the nuanced and complex problem of life adapting the environment versus adapting **to** the environment. We argue this has more or less been achieved through computational and mathematical modelling, with many examples of evolutionary systems, not just Daisyworlds, showing Gaian behaviour and Doolittle’s favoured idea of persistence based selection playing a large role. Further, as summarised in^[6], today evolutionary arguments beyond the gene or individual are quite mainstream. From a biological perspective, Gaia is multilevel selection^[65] or niche construction^[32] taken to its logical extreme. Thus Gaia already fits nicely into a number of scientific and evolutionary frameworks, even one as mainstream as the Price equation^[51], so that bending classical Darwinism to fit it seems superfluous.

There is also much more to Gaia than just ENS, and Doolittle’s presentation helps clarify thoughts on what is missing and what would be required in a fuller theoretical basis for Gaia Theory. Much of what

Lovelock intended as the domain of Gaia theory is nowadays studied under the banner of Earth Systems Science, by people only vaguely aware of Gaia^[28]. Lovelock^[66] and Margulis^[67] argued that Earth Systems Science is just a more palatable name for what they intended as Gaia. Twenty years later, as Earth Systems Science waxed and Gaia waned, Lenton, Latour and Dutreuil argued convincingly^[68]^[69] that there is a useful distinction to be made between the Earth system and Gaia, primarily concerning the importance of Life's role. We would also add that there is a much stronger emphasis in the Gaia literature on holistic properties and emergent behaviour.

The chemical history of Earth, the search for other inhabited worlds and the multiple crises of climate change motivate our continued interest in Gaia. These are largely about the interactions of life with the environment at planetary scale and are the domain of Gaia Theory. This theory must be consistent with Darwinian principles, as much as with thermodynamics and gravity, but it does not have to be Darwinized, Kelvinated or Einsteinified! Doolittle's insistence on explaining Gaia with something that can be called 'Darwinian' is likely only to increase confusion among evolutionary biologists and obscure the importance of persistence based selection. The Darwinization models are less convincing than the many, much more precisely formulated and thoroughly investigated models which Doolittle ignores. Given Doolittle's stature and the prominence of his ideas in modern discussions of Gaia Theory^[70] we think it is important to provide this counterpoint to emphasise that there is more to Gaia research than the project of Darwinization.

There are now multiple approaches to understanding Gaia, which tend to draw on their author's area of expertise, evolutionary biology in Dolittle's case or thermodynamics in others^{[71][72]}. Just as Doolittle neglects thermodynamics, the thermodynamic approaches largely neglect evolution. If Gaia theory is to move forward, rather than 'Darwinizing Gaia' or 'Gaianizing Darwin'^[73] what is needed are ways to combine these various partial answers, building on and integrating the decades of progress in evolutionary biology, Earth Systems Science and complexity theory since Lovelock's original hypothesis.

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