

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.

Keywords

Gaia • Selection • Darwinizing

1. Introduction

In recent work (Doolittle 2014, 2017, 2019; Neto and Doolittle 2023; Papale and Doolittle 2024; Doolittle 2024), W. Ford Doolittle and others have been trying to, “legitimize the Gaia hypothesis” (Doolittle 2024, xi). Central to this is the idea of persistence-based selection, of which there are two main types: *selection by survival (SBS)* (Bouchard 2008, 2011; Charbonneau 2014) and *sequential selection (SS)* (Betts and Lenton 2007; Lenton et al. 2018). While the latter considers persistent states of a single system over time, and so may be more directly applicable to Gaia (Arthur and Nicholson 2022), the former is what is mostly considered by Doolittle and collaborators.

Selection by survival is (almost) a tautological observation: entities that survive have properties that enable them to survive. In its most straightforward interpretation as 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 (Arthur and Nicholson 2022). 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 give it 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:

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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 et al.’s contributions into context, and conclude with some thoughts about the future of Gaia theory.

2. The Darwinizing Programme

Doolittle (1981), along with Richard Dawkins (1982), George Williams (1992) and others (Postgate 1988; Gould 2002; Hamilton 1995), 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” (Lovelock and Margulis 1974). These critics saw Gaia as the ultimate example of group selection (Ruse 2013) – a perpetual source of controversy in evolutionary biology – but even worse, as in the case of Gaia there is only one group!

As Doolittle (2024) has discussed, in the intervening forty years, his own position has become much more sympathetic towards 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 (upward) claim that “mass unemployment caused the current recession,” or the (downward) one that “the recession caused mass unemployment.” Generally, there is no issue with ascribing causal agency to an entity called “the economy.” Lovelock’s geophysiology (1986) 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” (Doolittle 2024, 170). 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” (Doolittle 2024, 9). 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” (Doolittle 2024, xii).

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 (Lewontin 1970) and Hull’s interactor/replicator concept (Hull 1980). In the book, he discusses how these frameworks apply to more complex evolutionary problems, like multi-level selection or holobiosis (Doolittle 2024). Gaia only appears relatively late in the work, when

the discussion comes together to argue for, basically, expanding the definition of evolution by natural selection to incorporate the notion of persistence and to soften the requirement of reproduction, thereby allowing entities other than genes or individuals to be subject to this new, more expansive version of ENS.

3. 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 (Lenton 1998).

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 (Hermida and Okasha 2025). 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 (Zhang and Li 2025).

4. The Environment

Like another (relatively) recent Gaia book by Ruse (2013) the terrain of discussion in Doolittle’s work is entirely biological – perhaps not surprising given Doolittle’s background and professed interest. However, echoing the comments of Dutreuil (2014) 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 (Steffen et al. 2020). One of us made a similar point about the biological focus of some of Doolittle’s ideas (especially clade selection) in the past (Wilkinson 2023, 118).

While evolutionary biologists like Dawkins, Doolittle, Williams, Gould and others didn’t like Gaia Theory, they largely ignored it. Dawkins’s much-discussed critique of Gaia took up only three pages in *The Extended Phenotype* (Dawkins 1982, 234–37). Despite Gould’s own interest in evolutionary patterns over geologic time, Gaia merits only one paragraph in the 1,400 page tome *The Structure of Evolutionary Theory* (Gould 2002, 612), 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 (Hitchcock and Lovelock 1967). While biogeochemical cycles are sometimes mentioned (Doolittle 2014), the Darwinized Gaia of Doolittle's recent book has little, if anything, to say about the environment, compared to other frameworks like cybernetic rein-control (Wood et al. 2008), niche-construction theory (Odling-Smee, Laland, and Feldman 1996) or even basic ecological theory (Wilkinson 2023), and so is fundamentally incomplete as a theory of Gaia.

5. 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 (Wilkinson 1999). Responding to criticisms, Gaia theorists sharpened their use of evolutionary concepts, mostly through models of life-environment interaction like the famous Daisyworld (Watson and Lovelock 1983). Doolittle remains unconvinced by such efforts, stating that the regulation which emerges in Daisyworld is “baked in” (Doolittle 2024, 13).

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 (e.g., Downing and Zvirinsky 1999; Wood et al. 2008; Williams and Lenton 2007; Worden 2010; Dyke and Weaver 2013; Harvey 2015; Arthur and Nicholson 2017; Nicholson et al. 2018b; Pastor et al. 2020; Vakulenko et al. 2021). Taken together, this work demonstrates the compatibility of Gaia with ENS and permits detailed study of questions like evolutionary ‘cheating’ (Worden 2010) or the interplay between ENS and weaker forms of selection (Arthur and Nicholson 2017).

Doolittle, in his recent book and elsewhere, does not refer to much, if any, of this work, and makes no use of mathematical models (he refers to his “mathphobia;” Doolittle 2024, xviii). 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 offered by Neto and Doolittle (2023), which describes a verbal model of a chemostat and does not refer to the *very* similar, computational, flask model (Williams and Lenton 2007) or the body of work about it, even papers using this model *specifically addressing persistence-based selection* (Nicholson et al. 2018a).

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 Doolittle (2024) having characterised 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, also not discussed by Doolittle; Hamilton and Lenton 1998; Lenton 2005). 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 Neto and Doolittle (2023) may suffice to illuminate some aspect of clade selection, the simulation model of Williams and Lenton (2007) 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 Neto and Doolittle (2023), or indeed, the models in Doolittle (2014), would be far more interesting and convincing if they were precisely formulated and solved or simulated, similarly to Williams and Lenton (2007) 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.

6. 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 (Doolittle 2014, 2017, 2019). These concepts, particularly persistence as an explanatory mechanism in biological systems, motivate 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 Arthur and Nicholson 2022) 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 (Toman and Flegr 2017; Nicholson et al. 2018a; Lenton et al. 2021; Arthur and Nicholson 2022; Boyle and Lenton 2022; Nicholson et al. 2022; Bourrat 2023; Arthur and Nicholson 2023a; Nicholson and Mayne 2023; Arthur and Nicholson 2023b; Arthur, Nicholson, and Mayne 2024; Tamre and Parsons 2024; Boyle et al. 2025). 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.

7. 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” (Doolittle 2024, xii). This view is also developed by other philosophers, such as Mary Midgley (2013) and Bruno Latour (2017). 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 (2013), many of the Gaia critics in the 1980s and 1990s 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.

Doolittle (2024) 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 (2018) to the apocalyptic sci-fi of Lovelock’s last work (2019). 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 (Harding 2009; Kimmerer 2013). This Gaia might once again capture people’s imagination in ways that respectable but dour climate and Earth Systems Sciences have failed to (see, for a recent example, Nicholson and Haywood 2023).

8. 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 by Doolittle (2024), today, evolutionary arguments beyond the gene or individual are quite mainstream. From a biological perspective, Gaia is multilevel selection (Okasha 2006) or niche construction (Odling-Smee, Laland, and Feldman 1996) taken to its logical extreme. Thus Gaia already fits nicely into a number of scientific and evolutionary frameworks, even ones as mainstream as the Price equation (Bourrat 2023), 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 (Steffen et al. 2020). Lovelock (2004) and Margulis (2004) 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 (Lenton and Dutreuil 2020; Lenton, Dutreuil, and Latour 2020) 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 (Philosophical Transactions of the Royal Society B 2025) 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 Doolittle's case or thermodynamics in others (Kleidon 2004; Rubin et al. 2020). 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” (Rubin and Castro 2021), 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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