Gaia – The Earth is an Organism (Not a Darwinian Individual)

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Abstract

The Gaia hypothesis has been roundly criticized by a number of evolutionary biologists, who maintain that no plausible evolutionary account is compatible with the idea that the Earth is an organism. These criticisms focus on the observation that Gaia is not the kind of entity that can be explained through evolutionary models. After all, Gaia does not belong to a population of Gaias and does not reproduce, and thus cannot evolve through natural selection. In this paper, we hope to deflate the force of such criticisms by showing that they have the wrong target. By clearly distinguishing Darwinian individuals from organisms and identifying the distinctive features of organismality, we show that the claim that Gaia is an organism does not fall prey to the criticisms commonly made. Drawing from theoretical work on holobionts we clarify how, despite not being a Darwinian individual, it is plausible to think that Gaia has features that have been shaped by natural selection.

Keywords: Darwinian individuals; Gaia hypothesis; holobionts; organismality; Richard Dawkins

1. Introduction

When Lynn Margulis and James Lovelock first suggested the Gaia hypothesis (Lovelock, 1979/2000; Lovelock & Margulis, 1974) they were roundly criticized by a number of evolutionary biologists, who maintained that no plausible evolutionary account was compatible with the idea that the Earth is an organism (Dawkins, 1982/2016, pp. 357-63; Doolittle, 1981). Central to this critique was the observation that Gaia constitutes a population of one and, relatedly, does not reproduce. Without a population and reproduction, critics maintained, there was no viable way to explain how Earth could possibly have been shaped by natural selection, which was, not unreasonably, taken to be characteristic of organisms.

The Gaia hypothesis is currently undergoing something of a revival (e.g., Bourrat, 2023; Doolittle, 2017, 2024; Inkpen & Doolittle, 2022; Lenton & Latour, 2018; Steffen et al., 2020) but the old critique is still around and has been resurrected (Pigliucci, 2021; Godfrey-Smith 2015). In what follows, we hope to deflate its force by showing that it has the wrong target. This critique mostly depends on the impossibility of natural selection operating on the planet as a whole because the planet is not a Darwinian individual (i.e., a member of a population that can undergo natural selection) (Godfrey-Smith, 2009). If the Gaia hypothesis maintains that the planet is an organism, rather than a Darwinian individual, the criticism may not apply. It may be objected that, for the Gaia hypothesis to be scientifically plausible, Gaia must in some sense be a product of Darwinian evolution, even if they[1] are not themselves a Darwinian individual. Happily, contemporary efforts to Darwinize Gaia are exactly aimed at sorting out this problem. Moreover, contemporary work on the holobiont, which has been useful for teasing out the distinction between organisms and Darwinian individuals (e.g., Smith 2017), has also produced useful analyses of the ontology of Darwinian processes that can be put to work in addressing this objection.

In what follows, we begin with a brief overview of the Gaia hypothesis as Margulis and Lovelock articulated it, before moving on to the criticisms. After that, we introduce the distinction between Darwinian individuals and organisms, as articulated by Peter Godfrey-Smith

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[1] We use the singular "they" as Gaia's personal pronoun. Some of the same people who were annoyed by the feminine characteristics and Earth Mother implications of "Gaia" may be annoyed by our use of the singular "they," but there is much to recommend it. (i) Gaia is asexual (obviously). (ii) The gendered ideas of God the father and the Earth mother problematically echo various troubling sexist dichotomies, such as form versus matter, mind versus body (Warren, 1990), as well as hetero- and cis-sexist norms. Referring to Gaia as a singular "they" goes some way to avoiding these connotations. (iii) The ambiguity of "they" between one and many is productive. Words drag their secondary meanings along with them, regardless of what we try to stipulate (witness the way the word "selfish" applied to genes has warped evolutionary discussions). Here we stipulate that when we refer to Gaia as "they" we mean the singular "they" and acknowledge that the third-person plural may nonetheless echo in people's minds—and that's a good thing. Who knows what individuality is, anyway? As Peter Godfrey-Smith points out, "[t]here are no fundamental or most-real individuals in biology" (2013, p. 19).

(2013) and Subrena Smith (2017). Usefully, Smith's work engages recent research into the ontology of holobionts understood as organisms, which has interesting intersections with discussions of Gaia. Holobionts are more plausibly Darwinian individuals than Gaia, but there are reasons to think that they do not qualify either. Recent attempts to prove their Darwinian character are, however, instructive, and similarities between the two cases reveal how holobionts and Gaia might be both organisms and products of Darwinian processes while not being proper Darwinian individuals. This will bring us to consider Ford Doolittle's efforts to "Darwinize Gaia" (2017; 2024) and Earth Systems Science, which, as has been noted by some—but by no means all—of its practitioners, is Gaia theory by another name (Dutreuil, 2018; Steffen et al., 2020).[2]

We will conclude with some reflections on the upshot of this discussion. Thinking of the Earth as an organism reframes how we think of biological processes on the planet and foregrounds different questions. Just as the holobiont concept has changed medicine by reframing how we think of the relationship of human cells with the many other species that inhabit us (Douglas, 2022; Dryden, 2023), an organismal view of Earth may reframe how we think of, investigate, and protect the planet's ecological health. While a thoroughgoing discussion is far beyond the scope of this paper, we hope to suggest some important avenues for future investigation as well as some risks.

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[2] Barton (2022) suggests the link is "more philosophical than historical"; while various Earth System scientists acknowledge the influence of the Gaia hypothesis on their thinking, there is no archival evidence to suggest that it informed the institutional work of NASA's Earth Systems Sciences Committee and its attempt to develop Earth Systems Science (2022, p. 52, n. 2).

2. The Gaia Hypothesis and Its Detractors

In some ways, the Gaia hypothesis is not particularly controversial. As Lovelock put it in his 2000 preface to the reprint of his 1979 classic, *Gaia: A New Look at Life on Earth*, "[n]ow most scientists appear to accept Gaia theory and apply it to their research, but they still reject the name Gaia and prefer to talk of Earth System Science, or Geophysiology, instead" (1979/2000, p. xiii). Margulis makes much the same point, albeit rather more colourfully, in her "Another Four Letter Word: Gaia" (1998). She writes,

> …the evolutionist establishment… denigrated, derided, and ignored Gaia as if she were an old witch. In the end, the scientific community of scholars co-opted our scientific ideas (to our delight). Still railing against the G-word (Gaia) they infiltrated their research with G-concepts. Atmospheric chemists, environmental scientists, planetary astronomers, geophysicists, geomorphologists, geographers, ecologists, and the public called this new view of our living planet 'Earth System Science.' (1998, p. 4)

These are not simply self-aggrandizing rationalizations; Earth systems scientists seem to acknowledge their Gaian origins, often citing work by Lovelock and Margulis, with some even using the forbidden word (see especially Tim Lenton's work [1998; Lenton et al., 2018; Lenton, Dutreuil and Latour 2020]).

So, what is the content of this both widely rejected and (by another name) widely accepted theory? In their groundbreaking 1974 paper, "Atmospheric Homeostasis By and For the Biosphere: The Gaia Hypothesis," Lovelock and Margulis identify Gaia in three different, complimentary ways:

> …the total ensemble of living organisms which constitute the biosphere [that] can act as *a single entity* to regulate chemical composition, surface pH and possibly also climate
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> an active *adaptive* control system able to maintain the Earth in homeostasis
>
> the hypothetical new entity with properties that *could not be predicted from the sum of its parts* (Lovelock & Margulis, 1974, p. 3, emphasis added)

While these are presented as three ways of saying much the same thing, they each have a different emphasis that will help to guide the discussion below.

The first point is the idea that the Earth, understood as all living organisms, is in a sense a whole. While Lovelock later admitted that in early work he sometimes equivocated between the biosphere understood as organic matter alone and the biosphere understood as that in addition to the "entire surface of the Earth" (Lovelock, 1979/2000, p. ix), he and Margulis are clear that it is the homeostatic integration of both living and non-living systems on the surface of the Earth (understood inclusively) that form this hypothetical entity. Second, like other living things, this entity is "an active adaptive control system," though the sense in which we are meant to understand "adaptive" is not clear. Adaptations are at once of singular interest to evolutionary biologists, often identified as the very target of natural selection explanations (see Dawkins, 1983/1998; Mayr, 1983), while at the same time being notoriously difficult to identify (see Amundson & Lauder, 1994; Gould & Lewontin, 1979; West-Eberhard, 1992). Provocatively, Lovelock quips that "the idea of Gaia…is the story of a planet that is alive in the same way that a gene is selfish" (Lovelock, 1979/2000, pp. viii–ix), acknowledging the metaphorical character of Gaia while accusing central concepts in evolutionary theory, like selfishness, of having similarly suggestive but slippery meanings. The third point is that Gaia is an emergent being. Gaia cannot be entirely explained by their parts any more than any other life form.

Importantly, there is a certain vagueness around what exactly is the *explanans* and what is the *explanandum* with the Gaia hypothesis. Perhaps the most natural way to understand the program is that the comparative stability of global biological, chemical, geological, and climatic systems is an empirical fact in need of both better description and explanation. Why is Earth stable enough so that life could continuously evolve on it? That this could simply be a happy accident is certainly a possibility, but to glibly accept chance as an explanation is to give up on scientific explanation altogether, as Ernst Mayr pointed out in a rather different context (1983, p. 326). The Gaia hypothesis seeks to explain the manifest stability of various biogeochemical systems on Earth through treating the planet as an emergent entity with its own self-maintaining internal systems. But what kind of entity is it?

3. Gaia's detractors—featuring Richard Dawkins

While Gaia's Darwinian critics were numerous (see Ruse 2013, chapter 2 for an overview), even including figures who might be expected to be sympathetic, like Stephen Jay Gould (1988), Richard Dawkins stands out both because of his remarkable success as a popularizer of neo-Darwinism and because of his distinctive style. His criticisms were representative of what might be considered the received view among evolutionary biologists (Ruse 2013, p. 30) (and philosophers of biology). Interestingly, Dawkins is eager to dissociate his own expansive and controversial idea of the selfish gene and its extended phenotype from "talk of adaptation at the global scale…[—] the fashionable image of the ecological 'web', of which the most extreme manifestation is the ‘Gaia’ hypothesis” (1982/2016, p. 357). Tellingly for our purposes, he writes,

> Lovelock rightly regards homeostatic self-regulation as one of the characteristic activities of living *organisms*, and this leads him to the daring hypothesis that the whole *Earth is equivalent to a living organism*. Whereas Thomas’s (1974) likening of the world to a living cell can be accepted as a throwaway poetic line, Lovelock clearly takes his *Earth/organism* comparison seriously enough to devote a whole book to it. He really means it. (1982/2016, p. 358, emphasis added)

The evidence Dawkins presents is equally telling. He points to Lovelock’s application of the terms “adaptation,” “purpose,” and “function” to the production of various gases (and, presumably, other Earth systems). So, for instance, “plants produce oxygen *because* it benefits life as a whole” (1982/2016, p. 358, emphasis his). Equally, methane, nitrous oxide, and ammonia are identified as fulfilling useful global functions, such as maintaining anerobic zones and controlling acidity in the environment (1982/2016, p. 358).

Dawkins suggests that such function talk is effectively meaningless except when grounded in Darwinian theory. For a feature to have a function implies that it is an adaptation produced through evolution by natural selection. He explains,

> Homeostatic adaptations in individual bodies evolve because individuals with improved homeostatic apparatus [sic] pass on their genes more effectively than individuals with inferior homeostatic apparatuses. For the analogy to apply strictly, there would have to have been a set of rival Gaias, presumably on different planets. Biospheres which did not develop efficient homeostatic

> regulation of their planetary atmospheres tended to go extinct. 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 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….
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> [Lovelock] might dispute that it does entail those assumptions and maintain that Gaia could evolve her global adaptations by the ordinary processes of Darwinian selection acting within the one planet. I very much doubt that a model of such a selection process could be made to work: it would have all the notorious difficulties of 'group selection.' (1982/2016, p. 359)

Finally, Dawkins goes after "The BBC Theorem". While lauding the "excellence of its nature photography" and "serious commentary," Dawkins complains that the dominant message of the British Broadcasting Corporation's nature programming was the "balance of nature, an exquisitely fashioned machine in which plants, herbivores, carnivores, parasites, and scavengers each played their appointed role for the good of all" (1982/2016, p. 360). He continues:

> The only thing that threatened this delicate ecological china shop was the insensitive bull of human progress, the bulldozer of…, etc. The world needs the patient, toiling dung beetles and other scavengers, but for those selfless efforts as the sanitary workers of the world…, etc….

> There is, no doubt, much merit in the moralistic exhortations that seem to flow from the BBC Theorem, but that does not mean its theoretical basis is sound…A network of relationships there may be, but it is made up of small, self-interested components. Entities that pay the costs of furthering the well-being of the ecosystems as a whole will tend to reproduce themselves less successfully than rivals that exploit their public-spirited colleagues and contribute nothing to the general welfare. Hardin (1968) summed up the problem in his memorable phrase 'The tragedy of the commons', and more recently (Hardin 1978) in the aphorism, 'Nice guys finish last'. (1982/2016, pp. 360–361)

To summarize, Dawkins assumes that Gaian function and adaptation talk must refer to functions that are selected effects, the traits that fulfill them having been shaped by natural selection. Just as evolution by natural selection produces adaptive traits in organisms by selecting more fit individuals generation after generation, if there are to be planetary adaptations there must be (i) a population of planets, (ii) the planets (or at least their biospheres) must reproduce and (iii) there must be differential fitness. As these criticisms are particularly pertinent to the organism-Darwinian individual distinction addressed in the next section, we will put them aside for now and briefly address the last two criticisms, one of which is, we believe, off-base and the other being rather more compelling.

First, let us address the BBC Theorem. What is perhaps most striking is that Dawkins fails to recognize that this isn't a hypothetical theory but is in fact the *explanandum* of the theory. Lovelock seeks to explain why "Earth was different from Mars and Venus…[having] apparently the strange property of keeping itself always a fit and comfortable place for living things to inhabit" (1979/2000, p. vii). Moreover, his characterization of the balance of nature is seriously off the mark, at least as far as Gaia goes. The interactions between macroorganisms that most feature in BBC programming and Dawkins' description are mostly irrelevant to Gaian systems. Single eukaryotic species or geographically located ecologies are typically of little interest; that is, until one particular ape threatens this generally relatively robust balance. The vast majority of macroorganisms in their particularity are merely decorative spandrels that do little work in the Gaian system other than, say, transforming chemicals—for instance, fulfilling a step in the nitrogen cycle by converting organic nitrogen into ammonium. Of course, Dawkins himself is happy to accept that there are expansive webs that are stably reproduced generation after generation, but these, he suggests, are driven by selfish genes manipulating their environments to forward their potential immortality. How an extended phenotype is to be maintained given that the components of these networks are *ex hypothesi* entirely shaped and maintained by selfish genes looking for any opportunity to cheat on each other is unclear. No wonder Dawkins is concerned about people confusing his own view with Gaia.

The second problem is obliquely alluded to by Dawkins as "the notorious difficulties with 'group selection'." This appears to refer to the problem of evolutionary altruism.[3] In brief, given not just the causal but the logical structure of natural selection, even if an altruistic trait—suitably defined (Sober, 1988)—evolves that makes all members of a group better off fitness-wise, eventually a cheater will appear, who reaps the fitness benefit but pays none of the fitness cost. By the very logic of natural selection, the cheater and its cheating progeny will eventually take over the population, selecting out the altruistic trait. This "subversion from within" stands as the

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[3] It has been suggested to us by an anonymous reviewer that Dawkins' target wasn't group selection simpliciter but Wynn-Edward's particular version of it, which was roundly rejected by biologists. However, we think that the history of this is somewhat more nuanced (see Collins 1986). Moreover, Elisabeth Lloyd argues that in his criticisms of group selection Dawkins fails to distinguish Wynne-Edward's approach from that of other group selectionists (1988, 143).

major theoretical barrier to the evolution of cooperation. Ford Doolittle, an early critic but current proponent of Gaia, also made this argument in the early 1980s:

> Gaia is a symbiosis…of global dimensions….For each member of the partnership to behave responsibly, there must be selective pressure against irresponsible behavior [that] will not be felt for thousands or millions of years, during which time irresponsible mutants, which may well have a temporary selective advantage, would have replaced all responsible members of the species. (1981, p. 61)

Although in the 1970s and 1980s group selection was as disreputable as the Gaia hypothesis, its status has changed in the subsequent decades. Group selection has been folded into the more general multilevel selection theory (MLST), which recognizes that selection can work at the level of genes, organisms, groups of organisms, or other levels. So long as the level in question can be accurately described as having populations of Darwinian individuals in such a way that their dynamics can follow Lewontin's recipe (described below), then natural selection will work there. So, it seems that this concern about groups is really about Darwinian individuals after all and, along with the three points above, is better addressed below.[4]

One final consideration is the apparent forward-looking character of Gaia (also apparent in the quotation from Doolittle above). This kind of teleological thinking is generally considered antithetical to evolution by natural selection, which is necessarily historical, as it explains how current features are a result of past processes, but is more or less silent on what the future holds

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[4] Some recent work by Chris Jones and colleagues (2023) suggests that certain ecological scaffolds may significantly weaken the strength of this subversion from within. This would mean that the evolution of cooperation and even major transitions like multicellularity, might be considerably more probable than was previously thought, assuming that the conditions comprising the relevant scaffolds are themselves relatively frequent.

(*pace* the limits of evolvability from the current state of things). However, we will find that this future orientation it is rather differently positioned in accounts of organismality. Again, this depends on distinguishing Darwinian individuals—the targets of evolutionary processes—from organisms, the subject to which we now turn.

4. Darwinian Individuals

While "organism" is, of course, the prior concept historically, the "Darwinian individual" (sometimes called the "biological individual," a moniker not to be confused with "biological entity") currently takes centre stage, at least, in evolutionary biology (Smith, 2017, p. 1). It is, in fact, the easier concept to define and apply, so we shall begin there and then describe organismality through comparison, before looking at the case of the holobiont.

Darwinian individuals are defined by the process of natural selection, and although the empirical question of what biological entities meet the defining criteria is a thorny one (Godfrey-Smith, 2009, pp. 70–81), the *basic* theoretical content is both reasonably clear and relatively uncontroversial. There is no doubt that there are numerous different devils in the details, but the received view is that natural selection roughly boils down to what is called 'Lewontin's recipe.' That this is a recipe and not a law or a formula should be noted. Like any classic recipe, it admits of umpteen slightly different versions, which, though recognizably much the same thing, have rather different flavors (see Godfrey-Smith, 2009, ch. 2). Everyone seems to have their favorite; Lewontin has at least two, of which the following is one:

> Darwin's scheme embodies three principles…

> 1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
> 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness)
> 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable). (Lewontin, 1970, p. 1)

When a population has phenotypic variation, differential fitness, and this fitness is heritable, the eventual outcome — assuming a sufficiently stable environment — will be that later generations will have traits that are increasingly better adapted to that environment. The logic is unassailable. Natural selection shapes any population of reproducers with heritable traits which have differential fitness as a result of phenotypic variation of those traits. Evolution by natural selection explains why organisms have traits that help them flourish in their environments and how biological traits can have functions despite not being designed by anyone. Adaptations and the functions they fulfill are the result of natural selection working (typically) by tiny incremental tweaks, generation after generation.

Although Darwin and Wallace formulated the basic recipe in the 19th century, the theory became central to evolution when it was given mathematical representation in the mid-20th century to form population genetics (Okasha 2024). The mathematical formulas subsequently developed have not only driven empirical investigations in the field, the lab, and increasingly *in silico*, but have—through the operationalization of key terms (like fitness and inheritance [Gardner 2008 and see e.g., Jones et al. 2023])—come to define those terms in the minds of many biologists. Of course, the data needed for such projects requires populations of countable objects with features that vary. Tamed by Mendel's laws and paradigmatically embodied by Mendel's peas (making genes 'visible' and thus countable long before DNA was identified with genes), the gene and its allelic variants dislodged organisms as the paradigm Darwinian individual (Okasha 2024, §1). That the neat genetic expression associated with Mendel's peas is far more the exception than the rule[5] has done little to dislodge gene-centrism in evolutionary biology, even as MLST has been widely accepted.

Now, at the risk of belabouring what we hope is obvious, the three key points of Dawkins' critique of the Gaia hypothesis are clearly aimed at the impossibility of Gaia being a Darwinian individual. As he maintains, for the analogy with organisms to "apply strictly" there needs to be (i) a population of planets, (ii) the planets (or at least their biosphere) must reproduce and (iii) there must be competition. These align quite clearly with the three ingredients of Lewontin's recipe. (i) is implied by phenotypic variation, as *variation* implies a *population* of variants. (ii) is implied by heritable fitness, as heritability is typically associated with inheritance, which is a relationship between ancestor and descendant—an essentially reproductive relation. And (iii) is implied by differential fitness, as competition is nothing other than one member of a population doing better—being fitter—than another. So, Dawkins' three complaints squarely come down to objecting that Gaia cannot be a Darwinian individual.

Of course, even if this is the core of his critique, there is more to Dawkins' argument against Gaia than just this. After all, if Gaia is not a Darwinian individual, then what are we to make of Lovelock's claims about various chemicals having *functions* or Gaia being "an *adaptive* control

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[5] It is worth noting that even Mendel's peas appear not to have perfectly exemplified Mendel's Laws (Radick 2022).

system"? Also, even if Gaia is not a Darwinian individual, given that natural selection had an essential role in shaping their parts, there must be some evolutionary story to tell here. Perhaps this is where the group selection objection has some teeth. Just as the problem of cheaters threatens to undo the evolution of groups, so it may threaten other emergent biological entities that depend on cooperation, like Gaia. Furthermore, it's all very well to say that Dawkins' criticisms of Gaia assume that they are a Darwinian individual, but this is moot unless there is a robust conceptual distinction between organisms and Darwinian individuals.

Thus we are left with several questions. First, what is the distinction between Darwinian individuals and organisms? Second, can a biological entity be an organism without being a Darwinian individual? Third, what are we to make of terms like "function" and "adaptation" that are associated with the Gaia hypothesis and whose meanings are often assumed to be derived from natural selection? And fourth, how do we square Gaia as a biological entity with its Darwinian individual parts? After all, even if Gaia is not a Darwinian individual, they are surely the result of evolutionary processes, including natural selection.

5. Organismality and the case of the holobiont

In order to get any traction on these questions we must first get some clarity on organismality. Happily, Peter Godfrey-Smith (2013) and Subrena Smith (2017) have done the necessary work for us, so we depend on them. We recognize that this is something of a shortcut. There is a large and growing literature on organismality and its relationship to biological individuality (e.g., Dupré & O'Malley 2009; Booth 2014; Clarke, 2013; see also Prieto 2023 for an overview). Ultimately, if the project of this paper is successful, so that the Gaia hypothesis redirects current research programs in the ways that we propose in the final section, careful engagement with this literature will be imperative.[6] However, the project of this paper is sufficiently circumscribed that only a basic characterization of organismality is necessary. Here we simply seek to show that it is plausible to say that there is a distinction between being an organism and being a Darwinian individual and that the Gaia hypothesis should be understood as stating that the world is an organism as distinct from a Darwinian individual. If the Gaia hypothesis is to be rejected this should be done on the basis of its failure to embody certain defining organismal characteristics rather than its failure to qualify as a Darwinian individual.

Both Smith and Godfrey-Smith emphasize that organisms are not defined by their evolutionary character but by the mutual dependency of parts and whole over time. Godfrey-Smith foregrounds the metabolic integration of organisms. In his words, "organisms are systems comprised of diverse parts which work together to maintain the system's structure, despite turnover of material, by making use of sources of energy and other resources from their

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[6] For instance, while our discussion refers to homeostasis as an important feature of organisms and biological individuals, entities might need a higher level of organization to qualify as an organism. Researchers working within the 'autonomy' paradigm of organismality have argued that organismality requires as constitutive of an entity a set of mutually constraining processes that simultaneously enable their continuous maintenance as a form of organizational closure (Mossio & Moreno 2010, p. 281; Bich & Bechtel 2021, p. 13), as well as the importance of second-order control systems that act as constraints on other control mechanisms (Bich et al. 2016; Bich & Bechtel, 2022a, 2022b; Bechtel & Bich 2024). Gaia may not, at least at first glance, possess this level of integration. However, as Ruiz-Mirazo and Moreno (2012) note, plants and fungi also show relatively weak integration, and that "the decision to consider many of these multicellular systems as full-fledged individual organisms is a matter of degree rather than of clear conceptual differences" (2012, p. 20). The same suggestion is made for superorganisms, given the possibility that "some new mechanism(s) of integration is(are) found and realised in nature" (Ruiz-Mirazo et al., 2000). Presumably, then, Gaia's more diffuse organization need not disqualify them from organismal status. Nor does Gaia's lack of reproduction in the standard sense understood by Darwinian selection pose as a barrier to their organismality; Gaia, as the biosphere, can still grow—a 'statistical' kind of reproduction, as Ruiz-Mirazo et al. describe growth (and division) (2004, p. 334)—and as we discuss below, their parts can undergo selection, even if Gaia as a whole does not.

environment" (Godfrey-Smith, 2013, p. 25). As both he and Smith observe, these systems have high levels of cooperation and low levels of conflict and, unlike Darwininian individuals that are characteristically reproducers, organisms are persisters.

Another point of agreement is that organismality admits of degrees, so there may not be any clear, acontextual, final answer as to whether a system is an organism or not. However, for any given set of nested systems, Godfrey-Smith maintains that there is some level that is more organismal than the others (2013, pp. 26–27). Smith does not follow him on this, presumably because of the centrality of the holobiont concept to her discussion. When some organisms are composed of other organisms, such questions become fraught. While she mentions the immunological capabilities of organisms that reveal a capacity to determine self from other (see Pradeau 2013 for a fulsome discussion), Smith emphasizes the continuity of the organism with its environment. As she notes, "organisms are not sharply distinguished from the worlds they inhabit--…they are *constitutively embedded* in their worlds" (2017, p. 2).

This is where the holobiont serves as a case in point. Holobionts are symbiotic composites of various species typically understood as being comprised of a host and their microbiome—thus the holobiont is a multicellular organism *and* all the microorganisms that live in and on it in a mutualistic fashion. For Smith, holobionts serve as a prime example of biological entities that are organisms but not Darwinian individuals. Importantly, Smith notes, "[t]he symbiont populations do not just come along for the ride. They are vital for the persistence of the system, and are increasingly shown to have significant effects on the macrobial phenotype" (2017, p. 11). A paradigm case is humans and our much lauded—and increasingly medicated and cultivated—gut biome (Douglas 2022, esp. pp. 106-20; Dryden, 2023). Though humans *might* be able to survive without the ecology within us (with some technological help), we would hardly count as healthy without them (J. A. Gilbert & Neufeld, 2014). Moreover, there are stable predictable functions that are served by the organisms in our guts across the human population (with some variation, depending on our diet and other factors), even as the taxa that fulfill a given function may vary considerably (Huttenhower et al., 2012)). Whether we define the human *organism* as only those cells that are part of the functionally integrated whole and have human DNA, or as all the cells of the functionally integrated whole that constitutes a healthy human being—microbiome and all—may depend on our explanatory (or medical) goals (Inkpen, 2019).

Clearly, we humans (and other holobiont hosts) evolved and were naturally selected to be symbiotically dependent upon—arguably, functionally integrated with—many of the microorganisms that populate our guts (and other regions). However, holobionts are not Darwinian individuals, at least, not as defined by Lewontin's recipe (Inkpen & Doolittle 2022, pp. 67–75).[7] This is because the organisms that inhabit us are not necessarily the descendants of those that inhabited our parents. In fact, we pick them up from all kinds of places. So, while there is a complex, reticulated well-defined ancestral chain reaching back, parent to offspring, for our human DNA, the ancestry of our microbial symbionts (and parasites!) will typically have taken a wide variety of very different paths, many of which have little to do with the lineage of our own strictly (genetically) human cells (Booth 2014). Thus, with the holobiont as our exemplar of organismality, we are able to deftly dispatch the first two questions addressing the conceptual and ontological distinctions between organisms and Darwinian individuals. Darwinian

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[7] Roughgarden et al. (2018) argue that holobionts are, in fact, reproducers. However, they do so by emphasizing the organismal character of the holobiont—the integration of the parts that comprise the whole and the importance of this for reproduction—and at the expense of a robust notion of lineage and a clear notion of inheritance (as vertical and horizontal transmission are both included). Inkpen and Doolittle (2022) suggest that regeneration, not reproduction, is a better way of thinking about the re-production of functionally equivalent populations of microorganisms across generations of hosts.

individuals are members of populations that replicate/reproduce offspring that inherit their traits from their parent(s) and form distinct lineages. Organisms are wholes with distinct but integrated parts that develop and persist over time and that "are constitutively embedded in their worlds" to a degree that blurs the distinction between organism and environment (Smith, 2017, p. 2). Membership in a population and lineage are not integral to organismality. The very features of Darwinian individuals necessary for Dawkins' dismissal of the Gaia hypothesis—populations and reproduction—are not central to organismality. Thus there are good reasons to think that these arguments are simply irrelevant to the question of whether the Earth and/or its biosphere is an organism.

This still leaves us with the last two questions posed above. How do we relate Gaia to the Darwinian character of their parts? And what are we to make of the functional and adaptive language associated with the Gaia hypothesis? Here, again, the analogy with the holobiont, which faces similar puzzles, is instructive. If holobionts are not Darwinian individuals, how can we understand them as entities that are the products of natural selection?

Joan Roughgarden and colleagues (2018) identify multiple ways in which the holobiont is a unit of selection. Although, for the reasons articulated above, we disagree with their overall project, which argues for treating holobionts as Darwinian individuals, much can be learned from their analysis. Though their case for treating holobionts as reproducers/replicators is controversial, they—following Lloyd (2024)—explore three other possible roles associated with "units of selection." For our purposes, these roles—interactor, manifestor of adaptation, and beneficiary—when seen through the lens of the holobiont, speak to how organisms relate to Darwinian individuals and can be produced and involved with evolutionary processes like natural selection (even when they themselves are not Darwinian individuals). We will argue they may also apply to Gaia.

First is the interactor role. The interactor is the phenotype that interacts with its environment to survive and reproduce. As such, interactors are the actual biological entities that are selected by natural selection. Importantly, though the interactor may be identical with the replicator, it need not be so, nor need it be in a neat one-to-one relation with the replicator. Dawkins' own gene-centric view of natural selection exemplifies this, with the gene as the replicator and the whole organism—including its extended phenotype, which typically comprises other organisms—as the interactor or, in his terms "vehicle" (Dawkins 1982/2016, pp. 173-8). The extended phenotype seamlessly extends to the holobiont; even if holobionts as integrated wholes don't qualify as Darwinian individuals, they are intimately related to evolution on this model as the interactors that provide the vehicle for Dawkins' selfish genes.

The extension of the interactor role to Gaia depends, in part, on the extent to which Gaia functions as an integrated whole. This is, in effect, a question about the degree to which Gaia exhibits organismality. As this is precisely the kind of research question the Gaia hypothesis was articulated to pursue, it should come as no surprise that there is, as yet, no final view on this matter. However, even if Gaia is reasonably thought of as an interactor *qua* the mutual dependency of their parts, some challenges remain. After all, the interactor is in some sense distinct from the environment that selects it, as it differentially survives in a population of competitors. Furthermore, one might reasonably complain that the interactor as a unit must be part of a lineage and so the holobiont fails in this respect as it is the offspring of multiple (contingent) lineages, as we describe above (Booth 2014) (though we note this is no more a problem for the holobiont than it is for Dawkins' extended phenotype, which likewise suffers from innumerable parents).

If we extend the holobiont to Gaia, this lands us with the population of planets that Dawkins derides. In response to such concerns about his own version of the Gaia hypothesis, Ford Doolittle (2017, p. 17; 2024, chapters 8 and 9) has suggested clade selection as a possible solution, albeit with some modification to Lewontin's recipe. He notes that Gaia can be understood as a clade rooted in the last universal common ancestor (LUCA). Other organisms beyond those comprising LUCA can also be assumed to have existed for at least part of LUCA's history but have since become extinct. Thus Gaia, the descendent of LUCA, is the sole survivor of this selective regime.

Regardless of what one makes of Doolittle's suggestion, it must be noted that the population of planets complaint is a problem for the idea that Gaia is an *interactor*, not the idea that Gaia is an organism. Moreover, even if it is a stretch to think of Gaia as a member of a population of clades (following Doolittle) or a population of planets (following Dawkins), the idea that Gaia is an organism persisting in an environment—i.e., our solar system, including the rocky planet at Gaia's core—that has shaped how Gaia has changed over time is not much of a stretch. After all, part of the explanatory project of the Gaia hypothesis has always been to investigate how life could be sustained on Earth even in the face of a possibly changeable astronomical environment (Lovelock and Margulis 1974). The extent to which solar radiation, for instance, initially shaped and continues to shape the biogeochemical cycles that have been called 'ocean metabolism' (Saito et al. 2024)[8] is a question raised by thinking of Gaia as an organism that is adapted to their

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[8] We thank Elis Jones and Erin Bertrand for drawing our attention to this.

environment, whether or not they have outcompeted anything else. Similar questions are raised by other aspects of Gaia's environment, such as the role of the Moon's gravitational pull, plate tectonics, or the Earth's magnetic core in shaping the integrated biogeochemical systems that comprise Gaia.

Insofar as Gaia was shaped by this environment to survive and persist, the traits they bear are adaptations in the evolutionary sense of the term. In this light, Gaia can be seen as a manifestor of *adaptations*. As Roughgarden and colleagues note, the interactor and manifestor roles are often conflated (2018, p. 55; see also Lloyd, 2024, §2.3), which has led to considerable confusion. This is most obvious with certain types of multilevel selection, where although interactor-replicator dynamics can explain the process of natural selection at the level of individuals, the adaptation—meaning the "engineering" of traits so that they increase fitness—emerges at the level of the group (see e.g., Jones et al., 2023). Importantly, the lesson is general. As Elisabeth Lloyd explains, the manifestor points to the "traits that provide a 'better fit' with the environment through accumulated build-up of modifications in phenotype that intuitively satisfy some notion of 'good design' or 'improved engineering' that goes beyond the original range of variation in the population" (Lloyd, 2024, §2.3). In the case of the human holobiont, the many species that comprise it follow various evolutionary trajectories, but the manifestor of the adaptation of digesting food well emerges at the level of the holobiont as a whole.

With this in mind, Doolittle's (2017) ITSNTS approach to Gaia can perhaps best be understood as an account of the global level of manifestation of adaptations in a single individual. ITSNTS—It's The Song, Not The Singers—offers a novel account of a planetary-level evolutionary process that takes the lessons of holobiont functions, like the gut microbiome, and extends them to planetary systems. There is significant diversity in the taxa comprising the microbiome from human to human; however, there is remarkable consistency in the functions they perform (Huttenhower et al., 2012). Doolittle's hypothesis is that the evolutionary process explaining this adaptation is driven by the functions performed—the song—rather than the individual organisms or species—the singers—which are fungible.

The point is that integrated functions of the gut microbiome have an analogue in Earth biogeochemical systems like the nitrogen cycle. Moreover, there is not only one system—one tune being sung—but a whole harmonious chorus—comprising the carbon, hydrogen, sulfur, oxygen, nitrogen, and iron cycles (Doolittle, 2017, pp. 14–16; Falkowski et al., 2008), presumably, among others. Any instance of one of the various steps within these interlocking cycles can typically be explained by interactor-replicator dynamics at the level of specific taxa (the singers) but the persistence of any given cycle as a whole is explained by the song maintaining itself. Insofar as the song perpetuates itself, these cycles are adaptations manifested at the level of Gaia, even if there is no one replicator-interactor story to be told about any one of them. We began the discussion with Margulis identifying Earth Systems Science as Gaia by another name. Insofar as the Earth systems investigated under this moniker are complex, integrated, homeostatic systems, they display organismality.

Because Doolittle is particularly concerned to emphasize Gaia's role as an evolutionary entity despite being alone and non-reproducing, he follows Bouchard (2008) in amending Lewontin's recipe to extend reproduction to include persistence. However, by treating Gaia as an organism whose parts evolve, manifesting adaptations for the whole, we can avoid this possibly dubious move. Indeed, as Smith (2017, p. 2) and Godfrey-Smith (2013, p. 25) both point out, organisms are essentially persisters.

We now have an account of how Gaia can be a manifestor of evolutionary adaptations, and thus a clear sense of what Lovelock and Margulis might be taken to mean when they assert that Gaia is “an active adaptive control system able to maintain the Earth in homeostasis” (1974, p. 3). It is, nonetheless, worth noting that there is another sense of “adaptation” that might be instructive. If Gaia is an organism, then the history of the planet is a *developmental* history, presumably in service of the functional integration of their parts, which maintains their persistence. ‘Adaptation,’ in this developmental sense, identifies the physiological adjustments of phenotypically plastic individuals that result from interactions with their environment or their behaviour (West-Eberhard, 1992, p. 13). Through the organismal lens, the natural history of Gaia and its parts is seen as a maturation process. This makes better sense of the cumulative and seemingly directional character of Gaia’s history than evolutionary theory does, which, as we are often reminded, is not progressive (see e.g., Gould, 1990).

The manifestor role and its focus on *engineering* also directs us to the appropriate interpretation of “function” when used to describe Gaia’s traits. The “functional” integration referred to by Smith is best thought of as causal role function, not selected effect function. Thus the self-regulating systems of Gaia, like the nitrogen cycle or carbon cycle—the balance of nature that so annoys Dawkins—are functional in this causal role sense even if they were not straightforwardly selected for through replicator-interactor dynamics and thus lack a selected effect function. The point is that there is a perfectly good sense of function that is the appropriate one to use when we are talking about organisms that implies nothing about their evolution (Amundson & Lauder, 1994).

The final role for units of selection identified by Roughgarden and colleagues is that of *beneficiary*. The idea of the beneficiary picks out the potentially immortal character of genes.

Organisms in a population are constantly turning over and species, genera, families, etc. come and go. The gene, or at least some genes, remain throughout these changes and are thus the ultimate beneficiaries of selection. As Dawkins announces, “[t]he basic beneficiary of any adaptation is the active germ-line replicator” (1982/2016, p. 130). However, if it is longevity that counts—persistence through time—Gaia is clearly the most basic beneficiary of evolution. If indeed they are a real biological entity—an integrated whole, whose life spans the history of life on Earth—then Gaia is the ultimate beneficiary of all evolutionary processes on this planet.

We now have answers to the questions with which we started this section. Darwinian individuals are defined by following Lewontin’s recipe (broadly and flexibly construed), while organisms are persisters with well-differentiated and integrated parts. The holobiont exemplifies how biological entities can be organisms without being Darwinian individuals. There are two ways we might treat the idea of function as applied to Gaia. First, the causal integration of parts into larger systems exemplifies causal role function. Perhaps more interesting is the possibility of functions understood as correlates of being a manifestor of adaptations. This can be gleaned from addressing the different senses of the term “unit of selection” and recognizing that, even if a biological entity is not a replicator and only dubiously an interactor, it may, nonetheless, be a manifestor of adaptations and the beneficiary of selection. In this light, the biogeochemical cycles at the heart of ITSNTS can be seen as engineering adaptations for the persistence of the living planet as a whole. This persistence is importantly forward looking. Unlike the Darwinian individual that is defined by past and present selective (and other) processes, persistence is about the characteristics of an object that take it from the past, through the present and into the future. This appears to be precisely what Lovelock and Margulis sought to understand when they first proffered the Gaia hypothesis. Insofar as the ultimate beneficiary of selection is that which persists through all the contingencies of evolution, no biological entity on this planet has a more legitimate claim to this than Gaia.

Conclusion

We have given what we hope are compelling reasons for reconsidering the Gaia hypothesis. They rest primarily on the observation that arguments used against it, exemplified by those of prominent critic Richard Dawkins, treat the Gaia hypothesis as the claim that the living planet is a Darwinian individual and then argue for the incoherency of this claim. By clearly distinguishing Darwinian individuals from organisms and identifying the distinctive features of organismality, we have shown that the claim that Gaia is an *organism* does not fall prey to these criticisms. In effect, Dawkins' arguments and those in a similar vein attack a straw figure. Drawing from theoretical work on holobionts we have clarified how, despite not being a Darwinian individual, Gaia has features that have been shaped by natural selection. They are a persisting entity with differentiated and integrated parts constitutively embedded in their world that have adapted over time to their environment. However, whether this clarification of the Gaia hypothesis is merely semantic or has significant scientific implications is yet to be seen. It has been said that "the philosophy of science is about as useful to scientists as ornithology is to birds" (Weinberg, 1987, p. 433) and one might reasonably wonder if our specification of Gaia as an organism as distinct from a Darwinian individual exemplifies this quip.

In response, we begin by noting that even if ornithology isn't of much use to the birds being studied, it can be very helpful to those who live with them. Scholars in Science and Technology Studies (Hird, 2010; Latour, 2017; Lenton & Latour, 2018; Stengers, 2015) have already fruitfully discussed the revival of the Gaia hypothesis in service of addressing anthropogenic problems and deployed both symbiosis and holobiosis to think through various initiatives and ventures into addressing ecological and planetary problems. Lorimer (2020), for instance, alludes to the supplementation of human gut microbiome function through foods such as yogurt when analyzing the reintroduction of keystone species in order to restore or stabilize ecosystems; such initiatives by scientists and policymakers constitute a ‘probiotic’ approach, in which the flourishing and functioning of animal communities is supported to promote ecosystem or planetary health. Still closer to Gaia, Folkers and Opitz (2022) trace the scientific and economic connections between industrial agriculture and methane production and attempts to regulate and manage life through life. Focusing on the addition of methane into the atmosphere through belching by cows, Folkers and Opitz detail interventions into the processes of ruminant metabolism and the gut microbiomes responsible for the production of methane in order to reduce this production at the molecular level. In effect, we have here an intervention into the structure and function of holobionts in order to alter planetary conditions and stabilize biogeochemical cycles, linking bioengineering to geoengineering.

Treating Gaia as an organism with differentiated and integrated systems demands that we consider such biogeochemical engineering in terms of the planet as a whole. These considerations draw attention to the fact that these putatively “clean” cows still contribute to other devastating effects of industrial animal agriculture, such as deforestation, which have their own roles in the various cycles that collectively comprise Gaia. Thinking about the Earth as an organism exposes the weaknesses of quick solutions to environmental problems that are insufficient or can be reasonably predicted to disrupt other planetary systems. As ever more interest is directed toward geoengineering as a response to the catastrophic effects of modern human lifestyles, a Gaian perspective may help guard against attempted remedies that are worse than the disease.

An organismal perspective may change how we think about global processes generally. There are obvious continuities between accounts of organismality that focus on, say, mechanisms that constrain "the flow of free energy" (Bechtel & Bich, 2024) and the role of constrained free energy in the ontology of Gaia (Lovelock & Margulis 1974; Lovelock 2000, chapter 3). References to things like ocean metabolism and ecosystem health may be more than mere metaphors. Interestingly, in light of the rich literature on organismality (Díaz-Muñoz et al., 2016; Godfrey-Smith, 2013; Pradeu, 2010; Prieto, 2023; Torres & Trainor, 2008), Gaia may be more organismic than other more readily accepted organisms, depending on the account considered. Investigating Gaia as an organism may offer a new paradigm with its concomitant set of problem-solving approaches, models, and values.

The growing scientific literature reconceptualizing human health in terms of our dependency on the microorganisms inhabiting us (Douglas, 2018, 2022; Inkpen, 2019) offers something of a model for how Gaian thinking might help us investigate their parts in different ways. If Angela Douglas is right to expect "the extensive rewriting of the next edition of every physiology textbook and undergraduate lecture course to accommodate the pervasive role of the microbiome in animal biology" (2018, p. 194), perhaps large swaths of the life sciences, particularly ecology and evolutionary biology, might also need revision in recognition of the organismal character of our planet. Here Smith's approach is instructive, dissolving possibly endless debates about whether Gaia is *really* an organism, by recognizing organismality as a matter of degree and not kind, with organisms dependent on and embedded in their environments. The Gaian perspective mandates a shift of focus to understanding the (engineering) adaptations of Gaia, their developmental history and trajectory—how various homeostatic systems came to be and maintain themselves and interact with others both globally and locally—and their concomitant vulnerabilities.

Such reframings are not without their perils. There are social and political risks. The challenges associated with the Anthropocene, including climate change, very easily lend themselves to vilifying certain groups of people. Beyond mere misanthropy, the urgency of these challenges leads some to embrace isolationism, xenophobia, and ecofascism (Aufrecht, 2012; Hartmann, 2010; Meierotto, 2012, 2014; Zimmerman, 1995). Lest this seem alarmist, this kind of discourse has been seen before; antisemitism and worries about the health of the political body in the past led some biologists, like Jakob von Uexkull, to label Jews and other races as parasites or pathogens within a society in need of a cure (Feiten, 2020, p. 8; S. F. Gilbert & Sarkar, 2000, pp. 4–5; Harrington, 1996). Lovelock, in response to Doolittle on Gaia, engages in this kind of rhetoric when he claims that “there is only one pollution, namely people,” and while he decries that "[a]pparently it is OK for Indians to suffer rickets from lack of UV but it would be terrible if a few whites suffered cosmetic damage from curable skin cancer," (Lovelock, 1981, p. 63) this can also serve as a discursive space for labeling marginalized human subgroups as the pollutants harming Gaia. As Taylor and Wald observe, “governing in the name of life necessarily entails privileging some forms of living over others” (2019, p. 901). If major social transitions are required for the continued flourishing of Gaia, at least so far as they are able to support human life on the planet, then they must be just.

Recognizing these dangers, however, does not relieve us of acknowledging the reality of Gaia, whether we claim that they are a paradigmatic organism or only possess “qualified organismic status” (Smith, 2017, p. 1). Certainly, more work, both conceptual and empirical, needs to be done not only to properly verify or amend the Gaia hypothesis, but better understand the possibilities and vulnerabilities of the collective web of relations that comprise life on Earth.

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