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Opinion

Making Evolutionary Sense of Gaia

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The Gaia hypothesis in a strong and frequently criticized form assumes that global homeostatic mechanisms have evolved by natural selection favoring the maintenance of conditions suitable for life. Traditional neoDarwinists hold this to be impossible in theory. But the hypothesis does make sense if one treats the clade that comprises the biological component of Gaia as an individual and allows differential persistence – as well as differential reproduction – to be an outcome of evolution by natural selection. Recent developments in theoretical and experimental evolutionary biology may justify both maneuvers.

Why Gaia Seems Impossible in Theory

Given that we are here to wonder about it, life on this planet must not have all gone extinct since it last started, nearly 4 billion years ago. Is this just anthropic (observer) bias [1], or do underlying abiotic and biotic forces [2] make such an outcome probable? Iif biology is in any part the cause, is it simply that lower-level processes on balance tend towards global stability [3], or is there selection on the whole? In other words, do all or most living things together comprise a single unit of selection, and is this unit under selection for stability? Only then could we claim that biogeochemical cycles and other global feedbacks have evolved functions, adaptations whose purpose is to maintain conditions suitable for life in the same sense that the circulatory system has the purpose of oxygenating tissues.

Traditional neoDarwinians doubt this last explanation, which is James Lovelock's Gaia hypothesis in an early popular form [4–7]. Their objection is that any life-stabilizing global homeostases – though not impossible – could not be anything more than fortuitous byproducts of lower-level abiotic and biotic processes. If we wanted to see them as selectable properties at the biosphere level – originating accidentally but then selectable in the same way that mutations arise without direction but then are selectable at the organismal level – we would have to imagine a population of biospheres, each reproductively competing with the others for space in the universe. Such strictures were embodied in an attack on Gaia mounted by the arch-neoDarwinist Richard Dawkins in 1982 [6].

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

Here, I argue that Dawkins (and I, who held a similar position in the 1980s [5]) were wrong on both counts. First, there in fact was, is, and always will be a relevant population of interacting (often competing) individuals, and second, evolution by natural selection can proceed by the differential persistence of these individuals as well as by their differential reproduction. If we accept both, then global homeostatic mechanisms can be selected for.

Pushing Back (First Step): Gaia as the Surviving Clade

Dawkins' first point – that evolution by natural selection (ENS) needs a population and there is but a single Gaia – is not so hard to counter, even without involving other planets. A population of potential competitors is plausible; in fact, it may be required by current understandings of early evolution.

Highlights

The Gaia hypothesis – the notion that this earth has homeostatic feedbacks evolved as adaptations through natural selection – is not easily squared with traditional Darwinian thinking.

Alternative formulations consider that differential persistence (as well as differential reproduction) is a legitimately Darwinian mechanism or outcome of evolution by natural selection.

Thinking this way points to new directions in philosophical and empirical research.

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According to the majority of evolutionary biologists, all contemporary life derives from a single common ancestral individual (or species) usually called LUCA (the last universal common ancestor), living ≥3.5 billion years ago, perhaps in some 'warm little pond' [8]. However, most evolutionary biologists do not believe that LUCA was the only individual (or species) in that pond, or that this pond was the only one on Earth at that time. Rather, LUCA was just the only one of these individual organisms or species to leave contemporary descendants (Figure 1).

Even those who hold that LUCA was a multilineage population spread over time probably think that there must have been other populations evolved either earlier or later that did not for some reason or reasons leave modern descendants. These reasons could be the possession of less stable information carriers (DNA and RNA), failure to transition from the 'RNA world', having a less optimal genetic code, use of D-amino acids, or greater resistance to lateral gene transfer (LGT), for instance [9]. There must have been some facts of the matter, even if we cannot know them now.

So, at the time of LUCA there was a population of individuals, any one of which could have in principle established Earth's biota, and many of which did found clades that only later went extinct. The initial competition of these population members might best be understood as the differential reproduction of organisms or species (the latter by speciation). However, after some of these population members successfully reproduced or speciated to gave rise to clades, we might better think of competition between them as over differential persistence, as discussed in the next sections.

The present biota (the biotic component of Gaia) is then the unique clade descended from LUCA, which we have elsewhere called Life [10]. The capital L designates Life as an individual, in the same spatiotemporal sense that many biologists now consider species like *Homo sapiens* or
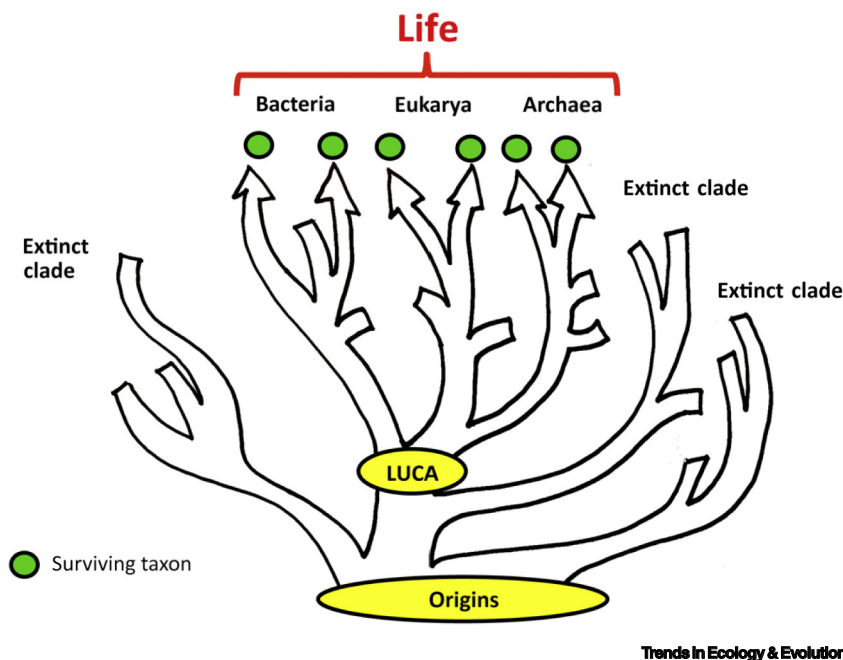
Figure 1. Common Understanding of the History of Life. All extant organisms descend from a single common ancestral organism or species, LUCA (the last universal common ancestor). LUCA was however not the only organism or species then inhabiting the planet, and some of the others must have given rise to clades that went extinct after the time of LUCA.

Escherichia coli to be [10,11]. It is not inconceivable that there will come some time in the far future when all earthly life descends from a single descendant of LUCA yet to be born (as in the folk belief that when *H. sapiens* is gone, descendants of some species of cockroach will take over the Earth). All the competitors of this new LUCA will be its population, at the future time at which it lives. We do not need to go to other planets to define a population, as Dawkins claimed. Clades continually make their own populations, here on Earth. It is always contemporaneous subclades that can be said to differentially persist within populations, but insofar as all are part of a more inclusive clade, this larger entity can become more persistent over time.

Pushing Back (Second Step): Clade Selection

Dawkins' second objection was that any evolving Gaian population must be made up of reproducing Gaia-like entities. However, LUCA and its descendants are, as a clade, unable to reproduce – by definition. A clade includes all the descendants of a single ancestor (or ancestral species), so it cannot have descendants (as individuals or species) that are not just more parts of it [12]. Dawkins was right on this and it is not just some sleight of logic: there is in fact no conceivable collective mechanism for clades above species (let alone biospheres) to multiply or reproduce. As Ghiselin is supposed to have put it, 'Species speciate but genera don't generate' [13]. Clades can only persist or go extinct, and any competition between them must be for persistence. The competitors of Life that went extinct in the past or will in the future are also clades. So, at issue is whether we can tweak the theory of ENS to accommodate clades competing for survival, differentially persisting rather than differentially reproducing.

Justification of such a claim might begin by drawing an analogy to species selection, a now not especially contentious element of multilevel selection theory, in which speciation and extinction substitute for birth and death in something akin to the standard model, with differential diversification (speciation rate – extinction rate) standing in for differential reproduction [14]. Although no species has properties that are not at bottom caused by those of the organisms making it up, all do have properties that organisms cannot be said to possess, or be under selection for. Number of organisms, their variability and geographic dispersal are such emergent properties, and species-level natural selection can be said to act on them. For instance, many rationalizations [15] for the prevalence of sexual reproduction are based on the advantages conferred by such properties on species – in particular the avoidance of extinction – outweighing the 'twofold cost' of sex for the individual organisms whose genes must underwrite sexual behavior.

Although clades cannot 'cladate' and thus can only go extinct, they are similarly less likely to do so the more numerous, ecologically diverse (variable), and geographically dispersed are the species that make them up. As discussed in the next section, we might add intraclade, between-species cooperation to this list. There will be underlying species-level traits that cause any clade-level properties, just as there are underlying organism-level properties causing the traits on which species selection acts. However, the number, diversity, or dispersal of other species in its clade – or indeed interspecies cooperation – are not properties of any single species, and species selection cannot act on them. Clade selection can, even though differential extinction is its only tool. Studying such phenomena is a large part of what paleontologists do, gathering data on the geographic distribution of fossil clade members for instance [14]. Had Mendel not been rediscovered, population genetics would not be seen as central to evolutionary biology.

It is not new to claim that differential persistence is an alternative to differential reproduction in underwriting ENS. Frédéric Bouchard has, for more than a decade, been mounting parallel arguments [16–18] in favor of differential persistence, starting from the concept of fitness to the environment (ecological fitness) and the observation that clonal organisms (nonmicrobial individuals like the >100 acre, >13 million-pound quaking aspen grove in Utah called Pando) have been

surviving (and adapting by both genetic and nongenetic means) for tens of thousands of years, and must be 'doing something right without reproduction'. He writes [17]

> for clonal systems and many others, adaptive change is obtained through slow accumulation of changes among the parts of the system not through intra-generational change within populations. This will have to be so since the systems examined here do not have offspring *per se*.

Among clonal organisms, those in which seemingly independent progeny (such as the individual trees in Pando) are actually integrated (physically and physiologically) with their parents (by underground runners in this case) are the most interesting and problematic. Bouchard [16] considers that when such physical ties are severed 'the received view, in terms of reproductive success might be adequate'. This may be so, but the clade perspective introduces a new higher-level sort of entity to which something like Bouchard's analysis also applies. Changes among the parts (species in this case) that lead (however fortuitously) to clade-level species richness, diversity, or dispersal will be selected for at that higher level, for persistence. As well, as argued below, intraclade cooperation via material and informational exchange and the promotion of global stability might confer selectable organism-like integrative properties on clades.

Pushing Back (Third Step): Differential Persistence

In 2014, I suggested a simple and general model of differential persistence in which a certain number of nonreproducing starting entities is subject to extinction occurring randomly with respect to time [19]. If extinction cannot be avoided, then the properties of entities remaining after most have gone extinct will not differ from those of entities present at the beginning. They will have simply 'been lucky'. However, if there are any means (analogous to mutations) by which extinction might be forgone or delayed (persistence enhanced), entities left when there are but a few have an increased likelihood of having acquired them. Moreover, if such persistence-enhancing mutations occur randomly with respect to time, the acquisition of a first one increases the time available for a second to occur, and so forth, in the same way that differential reproduction of selected mutants increases the population available for further mutation in standard accounts for the evolution of complex adaptations. A similar dynamic is what Lenton *et al*. [3] call sequential selection.

I also argued that such differential persistence underwrites a form of ENS, generalized to include any reiterated process by which selected entities increase as a fraction of total entities [19]. The current claim is that clades are, in the Gaian context, such entities, that LUCA and its descendants are the winners, and that there were reasons for this: chance alone is not an adequate explanation. Jankovic and Cirkovic [9] may have identified some of the reasons. They write

> This biosphere, be it alone or one of many, is, accordingly, itself a product of natural selection, since the overall evolvability conferred by its coding concept (nucleic acids as information carriers with the "rulebook of meanings" provided by codons, as well as all the subsystems that regulate various conditional information-reading modes) certainly played a key role in enabling this biosphere to survive up to the present.

As noted earlier, species richness, diversity, and dispersal might be supplemented by a fourth clade-level property, also alluded to by Jankovic and Cirkovic [9], and by Hermida [11] in her arguments, similar to ours [10], for the individuality of Life. That property is intraclade cooperation, as manifested in the exchangeabilty of metabolites and even genes between lineages as well as alterations to the planet (Gaia's) abiotic parts – niche construction on a global scale [20]. Although explicable through common ancestry and the operation of selfish forces, and permitting exploitation as well as mutual benefit, long-term intraclade beneficial interactions, such as the recycling of essential nutrients such as oxygen, carbon, and nitrogen, should also be selected for at the clade level – the Gaia hypothesis in a strong form. That is to say, clades whose species richness, diversity, and dispersal are enhanced by interactions between those species are that much more likely to

persist. What might look like altruism for species is in fact self-interest at the clade level, where selection actually acts. Indeed, self-interested interaction patterns such as biogeochemical cycles might be seen, individually or collectively, as units of selection perpetuating themselves by evolutionary recruitment of taxa performing their steps [21]. Again, no problematic altruism or group selection needs to be postulated. It is in this context that regulating/stabilizing feedbacks and nutrient recycling mechanisms can be seen as Gaian adaptations, at the heart of Lovelock's claim [4]. Demonstrations that lower-level processes can indeed underwrite them are highly relevant [3].

Concluding Remarks

If (i) the history of Life on this planet is understood as entailing the differential success (through persistence) of clades in an ever-regenerating population of potentially surviving clades; (ii) clade-level properties, including intraclade cooperation, on which such differential success rests are accepted as properties evolving by natural selection; and (iii) Life itself is taken to be a successful clade, then it does make sense to speak of global homeostatic mechanisms as adaptations, having functions. Their purpose is to maintain conditions suitable for life in the same sense that the purpose of the circulatory system is to oxygenate the tissues. That some species do not participate or are (like our species) destructive to the whole is no more a threat to such a view than is the observation that not all of the properties of an organism contribute to its fitness, or that we are vulnerable to cancer.

Darwin's theory of evolution by natural selection embodies an *a priori* truth: entities showing heritable variation in fitness will evolve by natural selection. The pushback here is meant to similarly establish the logical legitimacy of claims that global homeostasis can arise through selection on global entities. What remains at issue (see Outstanding Questions) is how often this view helps us understand global interspecies biology and stability, and the obviously crucial reciprocal interaction of Life with the abiotic components of Gaia. We do not actually require that globally beneficial happy accidents are more likely to occur than globally destructive ones, although efforts – philosophical, computational, and empirical – to show if and how happy accidents are likely are of course relevant [2,3]. However, their success is neither necessary nor sufficient to legitimize the popular form of the Gaia hypothesis presented earlier: Gaia, in the view defended here, is not impossible in theory.

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