



## Darwinizing Gaia

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### ABSTRACT

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

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### 1. Introduction: Gaia and why Darwinists scorned her

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

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

In this section, I introduce the Gaia hypothesis of Lovelock and Margulis (1974); see also Margulis and Lovelock (1974); Lovelock, (1972, 1979) and explain why Darwinists found it so difficult to accept. In Section 2, I discuss the (in my opinion) unsatisfactory attempts of Gaia’s defenders to “Darwinize” the notion by assuming that it is organismal lineages or communities that natural selection must address. In Section 3, I develop a novel Darwinizing tactic, holding that for biogeochemical cycles or other Gaian homeostatic systems, it is the cycles or systems themselves – not the organismal lineages or communities that implement them – that are best viewed as *units of selection*. I take that term to mean membership in something like a “Darwinian population”, as conceived by Godfrey-Smith (2009) but necessarily expanded to accommodate the fact that differential persistence as well as differential re-

production can define *fitness*. In the fourth section, I argue that Lewontin’s three-part formulation for evolution by natural selection (ENS) could fruitfully be relaxed or expanded to accommodate both persistence and reproduction. In the penultimate, fifth section, I discuss some attempts to cast entire planetary biospheres – assemblages of homeostatic systems – as units of selection. In the final paragraph I remind the reader of my purpose.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## 2. Defending Gaia

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

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

Daisyworld. The second and overriding problem is that there is not a credible origin and maintenance scenario, based on natural selection as commonly understood, that makes the collection of global homeostases comprising Gaia anything like a *probable* outcome. Simple *possibility* was not good enough for us Darwinists: we wanted a selection-driven explanation with some causal force and a predictable stability-enhancing outcome. Ruse, (2013,164) quotes Hamilton articulating this position in a 1997 letter to Lovelock,....

You are right in saying you have n.s in your model, but it is if a very simplistic type so far and to my mind is very far from showing how natural selection promotes planetary stability.

Lenton and Andrew Watson (the original co-developer with Lovelock of Daisyworld models), in their recent book *Revolutions that Made the Earth* (2011) recognize this, and suggest that Gaia-supporters need to establish a *probable* Gaia, not just a *possible* one....

According to Lucky Gaia, it is just good luck that the Earth happens to possess predominantly regulatory feedbacks that have helped maintain a habitable state. The coupling between life and its planetary environment could equally have sent the planet into an uninhabitable state, or had a neutral effect on habitability. In contrast, Probable Gaia postulates that there are some basic principles at work that lead one to expect regulatory feedbacks to predominate on planets with abundant life, at least statistically, if not in every case. In our view, the present debate about Gaia boils down to whether Lucky Gaia or Probable Gaia is closer to the truth (Lenton and Watson, 2011, 106).

They root for the latter, of course, and offer several arguments for Probable Gaia. Of particular importance is the origin and maintenance of the biogeochemical cycles that ensure that elements essential for life do not wind up in biologically unusable states. One can easily imagine that accumulation of an element in some particular usable form (say nitrogen in nitrites, as part of the nitrogen cycle) creates a niche for the adaptive radiation of microbes converting it to the next intermediate in the cycle (nitrate). Indeed every step in the complete cycle will come to be serviced by a guild of functionally, though not necessarily taxonomically, related species. Each makes a living at performing its role, and organism-level natural selection is surely the driver. But no organismal lineage is selected *just because it completes the cycle*: that payoff is just too remote.

Indeed, the earth systems scientist Tyrell (2004) describes situations he calls “biotic plunder”, in which “the tendency of all biological populations to proliferate when conditions are favorable frequently exerts a pressure on resources.” Then, he argues, “resources become exhausted and stay that way”.

More recently, and at book length, Tyrrell expresses doubt about any Probable Gaia ....

... it is not inconceivable that Gaia could be produced by evolution. It could be some sort of emergent property that arises in some as-yet-unappreciated way out of the extraordinarily complex web of ecosystem and evolutionary interactions. That said, it has not so far been possible to identify, even in outline, any plausible reason why such an emergent property would be likely to arise (Tyrell, 2013, 201).

There are to be sure many other attempts, some involving very sophisticated simulations, to make Gaia a probable outcome of lower-level processes, not always selective (see Dyke and Weaver, 2013 and references therein). Other than alluding as above to an accumulating intermediate mechanism for the origin of cycles, I remain agnostic on these, while insisting that proper Darwinization requires that we interpret global homeostases as resulting

from natural selection operating directly to favor global stability, at some level and on some entitie(s). That is, we need *selection for* homeostasis, not accidental *selection of* homeostasis as a fortuitous byproduct of lower-level processes.

In any case, efforts to show probable emergence by other mechanisms are almost irrelevant (Doolittle, 2014). Even if it is wildly improbable that life on this planet has lasted long enough for intelligence – perhaps even the computer in which I type this – to evolve, both did indeed happen (King, 2004). Figuring out the *most probable* route to this end is our job as scientists, in fact it is what I partly take on here in developing an argument that, although “biotic plunder” might be a default outcome, there can be selection against it. But all steps could have been extraordinarily *unlikely* – lucky accidents. Still, here we are, and only strong versions of the anthropic principle would see that alone as *causal*. And even if there are other (nonDarwinian) “emergent properties” biasing the outcome, as Darwinists we are left with Godfrey-Smith’s invocation of “fortuitous byproducts”.

Unintimidated by conventional thinking as always, Margulis took a different tack than Lovelock and his students and defenders like Lenton and Watson, imagining a deeper and fundamentally nonDarwinian symbiogenic force in operation in all of evolution. She often described Gaia as a continuous ecosystem, not an organism (Ruse, 2013). Embracing “autopoiesis” (Maturana and Varela, 1980) she and Sagan wrote ...

Life today is an autopoietic, photosynthetic phenomenon, planetary in scale. A chemical transmutation of sunlight, it exuberantly tries to spread, to outgrow itself. Yet by reproducing, it maintains itself and its past even as it grows. Life transforms to meet the contingencies of its changing environment and in doing so changes that environment. By degrees the environment becomes absorbed into the processes of life, becomes less a static, inanimate backdrop and more and more like a house, nest, or shell—that is, an involved, constructed part of an organic being. (Margulis and Sagan, 2010, 350)

If we hope to Darwinize such a poetic Aquarian vision, the important move is to abandon attempts to see Gaia, or the consortium of species that maintain her, as a “major evolutionary transition” in individuality in the usual sense. Such transitions are usually understood in terms of selection on entities at some level in a biological hierarchy – genes, cells, organisms, species (Okasha, 2005) – that in the end comprises material things or assemblages thereof. In this context, what Darwinists cannot accommodate is the notion that participating organisms or species sacrifice their own evolutionary interests to a larger collective made up of the whole biosphere. The model sketched out below entails no such sacrifices, and the selection that is imagined is in a sense in a parallel (perhaps “immaterial”) dimension, not at another hierarchical level of biological organization.

### 3. Reformulating Gaia

Start with a very recent observation. Louca et al. (2016) clustered more than 30,000 marine microorganisms on the basis of (1) taxonomic relatedness and (2) functional potential as assessed from annotations in the literature. Then they correlated both with the inferred ecology of the site in which the organisms were found. They concluded that ....

... we were able to disentangle functional from taxonomic community variation. We find that environmental conditions strongly influence the distribution of functional groups in marine microbial communities by shaping metabolic niches, but only weakly influence taxonomic composition within individual functional groups (Louca et al., 2016, 1272).

In a way this is unsurprising, just a confirmation of a traditional microbiological belief, that “everything is everywhere, but the environment selects” attributed to Baas Becking (O’Malley, 2007). Although microbial species are cosmopolitan, local conditions favor the differential growth of lineages that are adapted to such conditions, whatever their taxonomic affinities. Indeed, this is also the take-home message of much of the research in the burgeoning field of microbiomics, the focus of which is the microbial communities in or on some particular macrobe, for instance us. A summary report of the Human Microbiome Project Consortium concludes that “metagenomic carriage of metabolic pathways was stable among individuals despite variation in community structure” (that is, taxonomic composition), and that “the relative abundances of pathways in community metagenomes ... were much more constant and evenly diverse than were organismal abundances, confirming this as an ecological property of the entire human microbiome.” (Human Microbiome Consortium, 2012, 207). So, many taxa, sometimes quite unrelated phylogenetically, can perform the functions appropriate to a given niche or ecological situation, at whatever spatial scale. I like to summarize such observations in the phrase “It’s the song, not the singer” (Doolittle, 2013; Doolittle and Booth, 2016) – inspired by *It’s the Singer, Not the Song*, a 1961 movie starring Dirk Bogarde, and a similarly titled Rolling Stones’ track a little later.

Why such observations matter is that they focus attention on metabolic and biogeochemical functions and interactions, rather than organisms. This frees us to consider global cycles, systems and interaction patterns at many scales as the *cause* of the existence, composition and character of organismal lineages and communities, not just the *result* of their activities. Systems and patterns could then – themselves – become the relevant units of selection, understood to exist in some abstract dimension distinct from that of organisms, species or collectives thereof, which are all spatiotemporally definable physical objects. In many ways, systems and patterns are like the immaterial memes in early theories of cultural evolution (Dawkins, 1976).

Elements of this way of thinking still need to be worked out, and may always be controversial, as in memetics. What I sketch below are what I suggest are the right initial steps towards a the-

ory, inverting the usual evolutionary logic. They are presented as a theory of *maintenance* and *selective improvement* rather than origin, though the latter can be imagined. I start with the relatively unarguable claim that, once biogeochemical cycles are in place, they drive the evolution of microbes that are able to perpetuate them.

1. *Because there’s a song, there are singers.* Take as a given the existence of global feedback in biogeochemical cycles such as that for nitrogen, or even an interconnected network of several such cycles (Fig. 1). Multiple microbial taxa are able to make a living (grow and reproduce) by performing one or another of a cycles’ steps. Natural selection at the organism level will act to amplify and diversify such taxa and improve their biochemical capabilities, which can have arisen independently at different times in different lineages, or have spread between unrelated lineages by lateral gene transfer. Indeed, this later process has been crucially important in distributing among taxa those biochemical capacities that seem to have arisen only once (nitrogen fixation for instance; Raymond et al., 2004), allowing for broader and more varied environmental implementation of biogeochemical cycles. I hold that existing cycles (or other interaction patterns) thus play a *causal role* in the evolution of microbial guilds. An alternative view, suggested to me by Godfrey-Smith (personal communication) is this:

The situation is coevolutionary. Each participant in the chemical cycle evolves in a way affected by the others. It’s not that the chemical cycle (song) is making the participants evolve the way they are; it’s the local presence and interactions of particular organisms and their products. Because there is oxygen around, made by some organisms, consumers of oxygen are more likely to evolve. They evolve and they produce other chemicals, which provide opportunities for yet other organisms. In some cases, the ‘song’ persists as a byproduct of all this. In other cases, the song fails to persist. But the song is not playing any role other than *being a persisting object*.

I do not think that such objections are fatal to the theory advanced here. Consider a lower-level coevolutionary analogy.

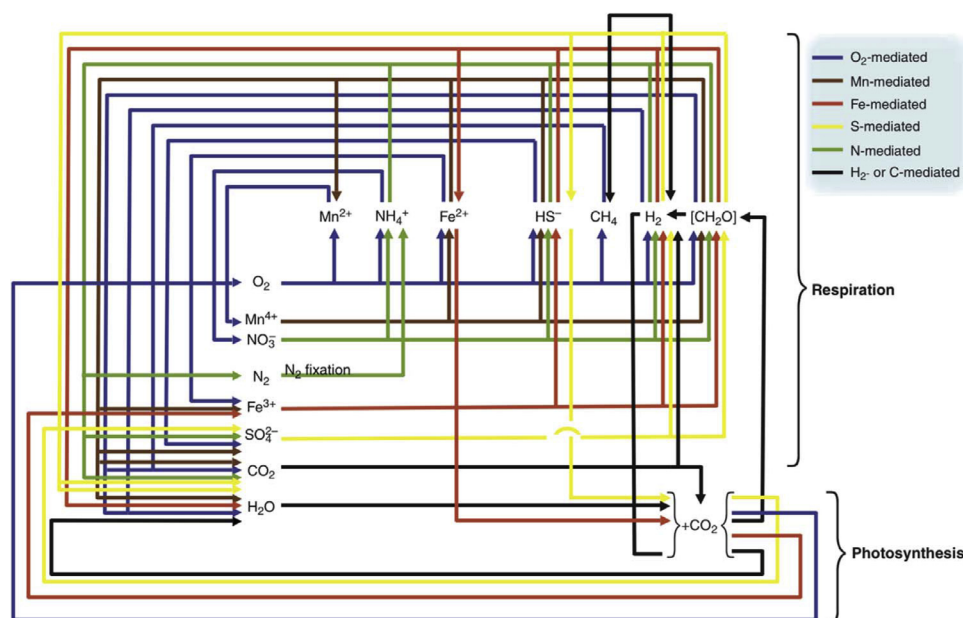


Fig. 1. Earth’s interconnected biogeochemical cycles. Linkages between cycles are often effected by microbial taxa that are involved in two or more processes. More details in Falkowski et al. (2008).

Source: Reproduced with permission from AAAS Falkowski et al. (2008).

In the debate about whether holobionts should be considered units of selection, it seems that most skeptics (including me) require it to be the case that the parent macrobe harbors the parents of the microbes that will partner with its own microbial offspring. In this way there will be *collective reproduction* (Godfrey-Smith, 2015b) and strictly coupled parent-offspring lineages for both macrobe and microbes. When instead new microbes are recruited each generation – even if always from the same species or strain (as with the Hawaiian bobtail squid; Nyholm and McFall-Ngai, 2004)– we are talking mere *co-evolution* between the two *species*, host and symbiont. Genes will have been fixed in populations of the former because individuals within them benefited from association with microbes, and *vice versa*, but such fixations occurred separately and likely not simultaneously in the two species. Each is the other's environment, and their collective behavior can be viewed as the fortuitous byproduct of “selfish” individual selection within each of the two species.

But at the same time, if no individual from one species can now live without an individual from the other, the species' evolutionary trajectories are obliged to be identical: the two interdependent lineages speciate or go extinct together. They are effectively a single unit of selection at the next higher level – that of species. If the obligatory species partnership enhances rates of speciation or decreases rates of extinction (increases species diversification), the higher-level unit is an entity that natural selection can address.

The Gaia hypothesis, then, might be taken as a claim that all or most of the Earth's biota are, in the very long term, at least indirectly interdependent, and comprise a similar unit of a rank much higher still than species. In this sense, all species, because they have adaptations to the biotic (as well as the abiotic) environment around them, are to various extents co-evolved with all others. Indeed, that is one way Gaia's supporters speak of her, generally failing to present the notion in terms of levels of selection. But it seems simpler to see the biota as evolving directly in response to environmental conditions, while acknowledging in the background that these conditions are the consequences of both biospheric *and* geospheric evolution over thousands and millions of years. To differentiate environmental drivers (causes) of evolutionary change on the basis of whether or not they are ultimately of biotic origin seems arbitrary.

Moreover, so rapid is the turnover of microbial genomes compared to several biogeochemical cycles that it could easily be that the particular environmental molecules that contemporary species are now evolving to metabolize are the products of microbial species that have been extinct for some time. Perhaps species-on-species co-evolutionary models as suggested by Godfrey-Smith are most appropriate when interactions are direct, local and close in time, while thinking of taxa as “recruited by cycles” is a good framework for more distant and long-term interactions, preferable anyway to invoking biosphere-wide co-evolution. In wrapping up his comments, Godfrey-Smith writes ...

... well, perhaps what I just said goes too far. This object – the persisting chemical cycle – is like a big set of niches in which organisms can make a living. As they do so, they create or maintain the other niches. They all coevolve, and we can think of that, at least in a coarse-grained way, by thinking of the cycle (song) as a big set of mutually maintained niches that provide opportunities for organisms. And cycles that are bad at providing such niches do not stay around.

Niche construction (Laland et al., 2016) – construed as the molding of selective pressures on subsequent generations by the extended phenotypes of earlier generations – indeed might

offer another well-elaborated body of theory in which to embed the argument that there is a causal connection between a song and its singers. Relevantly, Laland and Sterelny (2006) argue against the concern that “niche-constructing effects have no independent causal significance.” First, causal factors other than the genes of parents are involved – an argument directed at gene-culture coevolution but surely also applicable when abiotic factors are causal. Second, there is legitimate “circular” or “reciprocal” causation, in which cause and effect are interchangeable.

Provided niche-constructing by-products are consistently generated, modify selection pressures, and precipitate a genetic response, niche changing will be correlated with, and prior to, genetic change. (Laland and Sterelny, 2006, 1757)

2. *Because there are singers, there's a song.* Call collections of functionally similar (but often not taxonomically related) microbial species, *guilds* (Burke et al., 2011). Given pangenomic diversity within most designated species, many guilds might boast thousands or millions of taxonomically distinguishable members (Vernikos et al., 2015). As long as there are representatives of the appropriate guilds present at a physically suitable site, the cycle will be implemented: it need not be continuously in operation. Indeed, photosynthesis-dependent processes have been temporarily interrupted and quite reliably resumed daily at billions of individual sites for billions of years. Since such instantiations (henceforth, implementations) of a cycle result from *de novo* recruitment of microbes that individually perform only a part of their steps, our metaphor might need to be further refined. Songs are not just simple one-line melodies but multi-part choral compositions – soprano, alto, tenor, bass. Singers know only their own parts, but when multi-lineage microbial communities are assembled (recruited by environmental circumstances) the whole piece will be sung again.
3. *Re-production without reproduction.* Although some particular microbial species or strains might be frequently recruited for independent implementations of an interrupted cycle over time (or often involved in cycles in continuous operation) there is no guaranteed lineage continuity. Lineages from requisite guilds are continually changing over and re-associating. This is also true of many “holobionts” (Doolittle and Booth, 2016). Thus no particular implementation of a cycle (or particular performance of a song) can be said to be the offspring of any particular earlier implementation. There are no definable parent-offspring lineages at this level: a particular implementation can have as many “parents” as it has participating organisms. And to think of a cycle itself as parent to any particular implementation of it (let alone all such implementations) is a category error, just as it would be to conflate songs (abstract and potentially “immortal” information) with specific performances of them (spatiotemporally restricted and concrete events). Clearly there is some sort of causal relationship, but it is not that of parent to child.

At the “higher” (or possibly orthogonal) level of cycles or songs there is also no close analogy to organismal reproduction, especially if this requires “material overlap”, as some would argue (Griesemer, 2000). But there is relative continuity of identity. The nitrogen cycle now is no doubt nearly “the same cycle” that was in operation a million years ago. Even cycles that are regularly (daily or seasonally) discontinued change only slowly over time. Some cycles will have many more implementations than others (some songs will be much more often sung), but we must avoid the temptation to see this as differential reproduction or taking it as equivalent to being selected for. Multiple implementation might indeed increase the propensity to persist (see below) but is not equivalent to it.

4. *Persistence is what is selected for.* What cycles do instead of reproduce is *persist*, through implementations recurring over time. (Persistence in this sense requires continual but not necessarily continuous implementation, so *perseverance* or *reliable recurrence* might be more appropriate terms). The propensity to recur will differ between cycles, and depends on ...

- (a) physical and chemical features of their environment and the patchiness of such features' distributions,
- (b) the ease of establishing microbial guilds of adequate size and diversity to carry out the cycle's steps under physically appropriate conditions (including the frequency of intra- and interspecific lateral gene transfer of relevant traits), and
- (c) interaction of the cycle with – and the possible overlapping role of participating microbes in – other biogeochemical feedback loops (Fig. 1).

Different variants of a cycle are possible. A simple variation might substitute one metabolic step performed by members of a single guild by two steps performed by two, or replace one reaction mechanism or temperature or pH optimum with another, or establish or break connections with other cycles, all effected by selection for differential reproduction of the microbial taxa involved, but then further selected among cycles by their consequences for cycle persistence. That is, variant cycles could be said to be in competition with each other and differentially persist (be differently “fit”) by natural selection defined broadly, as later in this essay. Of course “rogue guilds” whose members for their own short-term benefit siphon off an intermediate and produce some unmetabolizable endproduct, or otherwise disrupt a cycle, might arise. So we would expect surviving cycles to exhibit chemistries that are less vulnerable to such subversion. Among the rationalizations for the overall similarity among living things in chemical composition we might add the ease of establishing (and difficulty of disrupting) the biogeochemical cycles that keep them in circulation (Exley, 2009).

5. *Songs together form a choral concert.* Fig. 1 is reproduced from a review by Paul Falkowski and others (Falkowski et al., 2008) and is meant to show linkages between major biogeochemical cycles. Of such linkages, these authors write ...

Although single cycles are often described in separate models, microorganisms have evolved to couple specific cycles of CHNOS within their energy transduction schemes. For example, the oxidation of reduced sulfur species (e.g., sulfide, thiosulfate, elemental sulfur) is often coupled with the respiration (reduction) of oxygen or nitrate. The resulting energy obtained from these reactions is used to fix carbon dioxide within the same organism. The coupling of different CHNOS half-cells within an organism effectively interconnects the major biogeochemical cycles across time and space. This intimate connection between separate cycles can also be seen at the ecosystem level, with processes like denitrification able to limit the carbon cycle on large scales. The individual species responsible for these reactions are largely irrelevant—as long as the metabolic processes are transferred across geologic time. (Jelen et al., 2016, 51)

Thus cycles are interconnected, as different choral compositions might be in a concert sung by variable members of a larger choral group, some singing several times, others once. The ability to form such connections might increase the persistence propensity of a single cycle. How selection on such an assemblage of cycles might be conceived is discussed in Section 5.

Individuation of cycles (deciding which variants of one cycle are in potential competition by differential persistence and which are potentially cooperative as in Fig. 1) will not be easy. This does not mean that natural selection is not somehow involved: the problems parallel those of memes in cultural evolutionary theory. In-

deed, allowing differential persistence rather than differential reproduction to be a measure of fitness would also benefit the latter discipline. As Bourrat (2014) put it ...

... if a replicator is not necessary for ENS in the biological realm, then efforts to find a cultural analog may be unnecessary. This conclusion should be welcomed by cultural evolutionists, since forms of “memetics” relying strongly on the notion of replicator have failed to produce many significant results and their theoretical foundations have been heavily criticized. (Bourrat, 2014, 536)

#### 4. Reconciliation

Many philosophers and biologists would agree that Richard Lewontin nicely captured the theory of ENS in three principles, here in his 1970 version. I take this as the Darwinian consensus with which I am trying to reconcile Gaia (for instance Godfrey-Smith, 2009).

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).

These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change. (Lewontin, 1970, 1).

At least implicit in such a formulation is that entities engaging in ENS comprise populations of *reproducing* individuals – otherwise what meaning can there be in ‘parents’, ‘offspring’ or ‘heritable’? (Bourrat, 2015). And population genetic modeling, a foundation of the New Synthesis, generally assumes such populations, often constrained in size by limited resources. Many verbal encapsulations of ENS (the above included) invoke “survival and reproduction”, but the former really serves only to support the later: it is in terms of differential reproduction and numbers of offspring that “fitness” is to be realized.

Lewontin’s formula applies equally well to genes, cells, individual organisms and species, insofar as these exhibit level-specific heritable traits affecting fitness. Generally, some analog of differential reproduction (gene replication, cell division, speciation) is invoked (Gould and Lloyd, 1999).

However, the philosopher Frédéric Bouchard has, since the early part of this century, been arguing that ...

... for many species, Persistence Through Time (hereafter PTT) is the property maximized by evolution by natural selection: maximization of relative reproductive success is only one strategy for persistence of a lineage, but for many asexual species (but not all) reproductive success is actually minimized if not eliminated (Bouchard, 2008, 562).

Bouchard takes his cue from clonal organisms like the quaking aspen, in particular the individual named Pando, comprising 47,000 runner-propagated trees of a single genotype, founded by a single seed germinating in Utah some 80,000 years ago. He notes that such a clonal organism will adapt to environmental change (and thus become more persistent) as a consequence of natural selection on its ramets (individual trees propagated by runners). Most recently, Dussault and Bouchard, 1) (2016) have extended such a view to more complex communities, reasoning “that ecosystems, by forming more or less resilient assemblages, can evolve even while they do not reproduce and form lineages”.

Similarly, Pierrick Bourrat (2014, 2015) and I (Doolittle, 2014, 2017) have made general claims for differential persistence. We recognize that a difficulty is in going from what Bourrat calls *weak ENS* – one-off selection or sorting, which does not lead to complex adaptation – to *paradigmatic ENS*, which does. This later is a reiterated “creative” process – most typically enabled through the differential reproduction of successively selected individuals in successive generations of a constant or expanding population. Arguably, prolonged survival, by increasing the time available for further survival-prolonging “mutations” to happen, similarly increases their probability (Doolittle, 2014). But differential reproduction of parts of the persistent entity (as in selection on individual aspen trees) might be a more credible way around this, one on which Bouchard, Bourrat and I would probably agree. Selection on the parts does not in principle require that there be populations of competitors at the highest level (Doolittle, 2014).

Bourrat (2015) shows that such approaches are not only compatible with a Price equation approach to ENS, but can be vindicated by it, grounding a persistence view of ENS in standard theoretical biology work. Starting with a form of the Price equation developed by Okasha (2006) and formulated in the terms proposed by Lewontin, he notes that the Price equation analysis can be applied to a population over any time interval – even those shorter than a generation or with entities that never or rarely reproduce – and at levels higher than that of organisms. If the Price equation is true by definition, this necessarily means that heritability cannot be solely defined in terms of parent and offspring resemblance. Rather parent-offspring resemblance is one way heritability can manifest in a population. Another is merely through the similarity at the population level of the same persisting entities at two different points in time.

From a somewhat different perspective, I applied strictly verbal reasoning to clade selection (Doolittle, 2017). By definition, clades cannot reproduce, but they will differ in their propensities to survive or persist. Clade-level properties, not reducible to those of constituent species, are the number, geographic dispersal and ecological diversity of such species, and possibly the frequency and range of intra-clade gene transfer. Those properties can and sometimes will be enhanced by selection at the species and lower levels, so that clade selection might be seen as a superimposed additional creative force, in spite of lacking reiteration at the target level (clades). Gaia is, of course, the largest and only surviving terrestrial clade.

Thus a more general and relaxed formulation of ENS, merging Lewontin’s formula with persistence selection as described here, and allowing some kind of Darwinization of Gaia, might look something like this:

1. Evolution by natural selection (ENS) results in greater relative representation at some time  $t_n$  later than  $t_1$  of certain types of entities by virtue of those types’ possession of certain traits, these traits for that reason being *adaptations*, and those entities being *selected*.
2. Greater relative representation at time  $t_n$  than time  $t_1$  is equivalent to an increase in the numerator or a decrease in the denominator of the ratio  $[\text{selected entities}]/[\text{total entities}]$ . *Reproductive selection* generally is taken to result from an increase in the numerator with the denominator held constant, and is what is usually understood as ENS. *Persistence selection* can be achieved through denominator decrease alone. In the reconciliation proposed here, both types of selection require only some causal relationship, loosely defined and not necessarily resulting in parent-offspring lineages, between entities at  $t_n$  and  $t_1$ .
3. For “creative” ENS – that which produces complex adaptations – reproductive selection requires only reiterated rounds of selection, with reproductive or multiplicative replenishment of

selected variants at each round. Persistence selection can also be creative, in that the *means by which persistence is underwritten* become more complex over time. In most cases this complexification relies on reproductive selection or drift among parts of a complex persister. In the case of cycles, it is easy to elaborate on this: reproductive competition among singers will ultimately alter songs, and sometimes link them together in complex ways.

Such a reconciliation requires much more conceptual work than so far done, here or elsewhere, and acceptance will always be a matter of choice. What we call ENS is, after all, up to us. My claim is only that this is a direction that “Darwinization” of Gaia could take.

## 5. Final steps toward Gaia

The argument so far has looked primarily at idealized biogeochemical cycles constituting some of the homeostatic mechanisms Margulis and Lovelock considered adaptations for Gaia. For Gaia to be cast as a suitably Darwinized entity capable of possessing adaptations – even in terms of the relaxed reconciliation above – we must imagine that collectively such cycles make up a still more inclusive single unit. Dawkins’ objections (quoted above) were that such a unit could not reproduce *and* was most probably not one of a population of similar units, upon which natural selection could be said to impinge. Indeed, even granting that persistence might be substituted for reproduction seems to leave us with the Gaian “population problem”.

Three responses are possible. The first is “So what?” Bouchard’s understanding of Pando does not require that there be other quaking aspen groves, and evolutionary models of learning do not require multiple minds in which it occurs (Fernando et al., 2012). Persistence may actually relieve us of a requirement for populations (Doolittle, 2014).

The second and third responses allow that there are, or at least once were, relevant populations. Dawkins, after all, had no real basis in fact for his claim that a universe full of dead planets is an “improbable scenario”. Chopra and Lineweaver (2016), in very recent article in *Astrobiology*, suppose that our failure so far to encounter or be invaded by aliens, even though there seems to be a plethora of planets suitable for them to come from, is not because origins of life are very difficult and rare. Rather, the problem is that

....

... if life emerges on a planet, it only rarely evolves quickly enough to regulate greenhouse gases and albedo, thereby maintaining surface temperatures compatible with liquid water and habitability. Such a Gaian bottleneck suggests that (i) extinction is the cosmic default for most life that has ever emerged on the surfaces of wet rocky planets in the Universe and (ii) rocky planets need to be inhabited to remain habitable. (Chopra and Lineweaver, 2016, 7)

Alternatively, we can recognize that Gaia (or at least its biotic component) is a monophyletic clade comprising the descendants of a last universal common ancestor (LUCA), an individual of uncertain definition but which surely must have had contemporaries who for one reason or another did not leave present-day descendants (Hermida, 2016). Jankovic and Cirkovic (2016) have recently claimed that members of the LUCAn clade share an especially advantageous set of information-transmission machineries. 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, through alterations of planetary conditions, including at least five catastrophic events linked to major mass extinctions (Jankovic and Cirkovic, 2016, 67).

Current models of Life's origins imply that this is, to some unknowable extent, true (Booth et al., 2016). One might also imagine (actually, one can predict) that in some distant future all living things will descend from a common ancestor more recent than LUCA, all contemporaneous lineages having gone extinct. Chance will play a role, but so will selection. Differential persistence does not preclude, indeed it entails, continual turnover and redefinition of persistors (Doolittle, 2017).

## 6. Coda and caveats

My claim is that if one wants a Darwinized Gaia, what I sketch out is one possible way to achieve it. Attempts to see Gaia as something like the “mother of all evolutionary transitions”, with Gaia-level adaptations produced by selection on organisms or species for the maintenance of global homeostasis ignore the tempo and mode of selection on organisms and species. It's a question of *selection for vs selection of* (Sober, 1984) and levels or entities on which the former might be targeted. From the evolutionary perspective of organisms and species, Godfrey-Smith is right that global homeostases are merely “fortuitous byproducts”. Only insofar as Life as the assemblage of all living things is taken as a single evolving entity – with its own “evolutionary perspective” – might its persistence be seen as something that can be selected for, and then Dawkin's dead planet problem must be faced. It is faceable, but many may not want to accept the seemingly science-fictional “Gaian bottleneck” scenario of Chopra and Lineweaver, or Jankovic and Cirkovic's “coding concept”.

The “It's the song not the singer” perspective recognizes that biogeochemical cycles and other organismal interaction patterns (such as in holobionts: Doolittle and Booth, 2016) are in fact much better persistors than the organisms that implement them, and are reliably re-produced, if not reproducing. They offer a way to break the entire “autopoietic” global system into parts that a Darwinist might get his or her mind around. They are the most easily identified *units of selection* and a good starting point if our goal is to Darwinize Gaia. Or so I have argued. The collectivity of such cycles and interactions, that is Gaia, might next be taken as merely the “fortuitous byproduct” of selection on them, but notions of larger populations of Gaia-like entities (processes, not organisms or species) are not beyond the pale of rationality, nor are learning-like formulations that might not require populations. Selection at higher or other levels is one way to convert “fortuitousness” into necessity.

Interestingly, chemical origins of life and metabolism scenarios often also invoke cycles and the differential persistence or sustainability of prebiotic replicators (Schuster and Eigen, 1979; Hordijk et al., 2012). Pross (2013) notes, for instance, that “dynamic kinetic stability” selects for more stable replicators even when these are abiotic molecules, and thus that “function” predates biology. Coevolution of abiotic and biotic processes (so that any separation seems arbitrary) might also be inferred (for example, Grosch and Hazen, 2015). The extent to which geosphere and biosphere “co-evolve” (to severely stretch Janzen's definition) and might bias towards a Probable Gaia has not been my concern here: even the relaxed ENS formulation above does not embrace all processes that might have helped life on this planet survive (Jelen et al., 2016). It is also a reasonable complaint that contingent events, both biotic and abiotic have been under-emphasized as drivers of evolu-

tion (O'Malley and Powell, 2016). Again, my concern has been only to formally identify possible units of selection, to Darwinize Gaia.

A final point: the Gaia hypothesis can be used to support either environmental caution (“Who says the system is unbreakable?”) or recklessness (Gaia is in charge and our perturbations are of small effect.) Supporters and critics can support or criticize the notion from such ethical standpoints, but there's no deciding either way. Darwinizing Gaia or refusing to do so are not normative moves. And as we enter the Anthropocene, even those who see Gaia as an organism must admit that she can be killed.

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