

Evidence for the existence and early origin of genes making possible the Darwinian evolution of biogeochemical homeostasis at planetary scale

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Abstract

This paper uses empirical evidence to address the subject of when and how the processes for the homeostatic influence of the biota on planetary-scale biogeochemical processes first arose. From Lovelock (1972) this planetary-scale homeostatic influence has been referred to as Gaia and we also do so in this paper. To set the scene for the study, the paper first proposes three core necessary attributes for Gaia: (1) individual organisms possessing control systems using feedback loops to regulate their external environment (the *environmental regulation* core attribute); (2) joint action of groups of such organisms leading to the achievement of larger scale environmental regulation (the *joint action* core attribute); and (3) such action occurring at a planetary scale. The paper next identifies representative examples in contemporary organisms of each of the two non-planetary core attributes of Gaia in operation. For each of these examples, genes making up part of the genetic specification of the example were identified. We then sought these same genes in the earliest examples of life that have been genetically characterised in empirical terms - the Last Universal Common Ancestor (LUCA) and the Last Bacterial Common Ancestor (LBCA). These arose respectively between 4 and 3.5 billion years ago. Examining both the pools of known modern genes and demonstrated LUCA and/or LBCA genes, a number of modern genes related to functionality analogous to that of Gaia core attributes were also found likely to be in LBCA and/or LUCA. In other words, the potentiality for the eventual evolution of Gaia arose between 3.5 to 4 billion years ago. The paper also provides case studies showing similar results at increasing scales of organismal aggregation over the intervening period to the present. Doolittle (1981) and Dawkins (1982) stated, in essence, that it was impossible for them to imagine any evolutionary way by which Gaia could have arisen. Dawkins (1982) defined Gaia as was at the time predominantly done in terms of its planetary attribute. This posits that there is *one* Gaia on Earth. Dawkins pointed out that neo-Darwinian natural selection requires competition between *multiple* units of selection. Given the absence of such multiple units of selection, Dawkins proposed that Gaia could not come into being by neo-Darwinian natural selection. The Doolittle and Dawkins positions were influential and interpreted by some as evidence that Gaia could not exist at all. The evidence of the present study is that genes for processes analogous to the non-planetary core attributes of Gaia have been available from near the start of life. With such genes being units of selection, planetary Gaia could come about by a series of developments commencing near the start of life, each involving standard gene-based Darwinian natural selection. We consider these results to resolve the issue raised by Doolittle (1981) and Dawkins (1982).

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Significance

This paper identifies genes in modern organisms that relate to functionality that is analogous to that of each of two of the core attributes of modern Gaia. A number of these modern genes are also found from phylogenetics to be statistically significantly likely to be present in the Last Universal Common Ancestor or the Last Bacterial Common Ancestor 3.5 to 4 billion years ago. These results provide statistically significant evidence that functionality analogous to core attributes of Gaia was present in LBCA and/or LUCA. In other words, the potentiality for Gaia arose between 3.5 to 4 billion years ago.

1. Introduction

Doolittle (1981) and Dawkins (1982) stated, in essence, that it was impossible for them to imagine any evolutionary way by which Gaia could have arisen.

Specifically, Doolittle (1981) wrote:

The Gaia Hypothesis says that Earth's biosphere is in effect one organism. How does a species of one evolve? There's nothing for natural selection to select among.

Dawkins (1982) stated:

(Lovelock) might ... 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...

This paper considers these positions. It does so by asking two questions.

Firstly, is there now sufficient empirical evidence to conclude that Gaia exists? With respect to this, evidence has been provided that there is a planet-level atmospheric temperature control system (Leggett and Ball, 2021). This displays processes with highly specific attributes. In the same paper it is argued that this control system is an aspect of Gaia in action at the present time. Hence, the position of Doolittle (1981) and Dawkins (1982) cannot be supported: because Gaia exists, it must have evolved somehow.

Secondly, we ask what might be the evolutionary building blocks from which Gaia could have been assembled. The answer to this second question is sought via three lines of enquiry.

The first line of enquiry arises from the above-mentioned empirical evidence that there is a planet-level atmospheric temperature control system in existence displaying processes with highly specific attributes, attributes like those expected from Gaia. For the purposes of the present paper we therefore term these highly specific atmospheric temperature control system processes ‘Gaia processes’. The existence of these Gaia processes means that Gaia-process-related genes and other Gaia-process-related building blocks such as proteins must exist. Hence in this paper we look for Gaia-process-related genes. These would be genes which natural selection leading to Gaia could select from.

If found, those genes can be considered to be components from which a planetary Gaia could be made. In answer to Doolittle (1981) and Dawkins (1982) who said this was impossible for them to imagine, these would be building blocks from which a Gaia could, over time, have arisen.

The second line of enquiry is to seek to find if certain of these genes are ancient. If so, there will have been much time over which Gaia could evolve, making such evolution more likely.

Thirdly, if we find groups of organisms operating in a manner that planetary Gaia is postulated to and/or observed to, at a range of sub-planetary scales even to near planetary (the Gaian) scale, this further increases the chance that a planetary Gaia could evolve.

If all three of these pieces of evidence are able to be demonstrated, this would further answer Doolittle (1981) and Dawkins (1982) by constituting evidence of components and pathways by which Gaia *could* have arisen through gene-based natural selection.

1.1 Background

A considerable number of studies provide evidence consistent with the idea that homeostatic regulatory influences operate within biogeochemical processes at a planetary scale. These studies span a period of time from Lovelock (1972) to the present (for example, Leggett and Ball, 2021). Since Lovelock (1972), studies involving this concept have often referred to the object of the research as Gaia, a term we will therefore also use in this paper.

In the early 1980s, two texts (that subsequently became influential) suggested that there was a problem with the notion of Gaia, in that Gaia could not evolve by gene-based natural selection. The two texts were, as mentioned above, Doolittle (1981) and a section of a book by Dawkins (1982). The essence of their critiques is outlined as follows.

From Doolittle (1981):

But it is not the difficulty of unravelling Gaian feedback loops that makes me doubt her existence. It is the impossibility of imagining any evolutionary mechanisms by which these loops could have arisen or now be maintained.

From Dawkins (1982):

The fatal flaw in Lovelock's hypothesis ...: Homeostatic adaptations in individual bodies evolve because individuals with improved homeostatic apparatus 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.

...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. ... In addition we would have to postulate some kind of reproduction, whereby successful planets spawned copies of their life forms on new planets.

I am not, of course, suggesting that Lovelock believes it happened like that. He would surely consider the idea of interplanetary selection as ludicrous as I do.

Obviously he simply did not see his hypothesis as entailing the hidden assumptions that I think it entails.

He 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...

I do not deny that somebody may, one day, produce a workable model of the evolution of Gaia (possibly along the lines of 'Model 2' below), although I personally doubt it.

Boyle and Lenton (2022) interpreted this situation as:

Neither the biosphere as a whole, nor any planetary scale process or feedback, exhibits discrete replication analogous to that of organisms, or occurs in an interacting population of comparable entities. This has led many to the conclusion that any "Gaian" habitability-promoting influence cannot be the product of natural selection and is therefore either non-existent or somehow life-specific without being particularly Darwinian.

According to Dutreuil (2018), these critiques became very well known and were associated with rejection of Gaia not just by evolutionary biologists but by scientists more widely.

This led to an environment that even affected peer review, whereby it seemed work could only be published with acceptance of "...peer review ... censoring any mention of Gaia by name." (Lovelock, 1990).

This inhibiting effect on Gaia studies is still felt to this day. For example, Lenton (2022) states:

...writing now, it feels that not a great deal has changed. I still have the same moments that Jim had of feeling profound isolation from the "mainstream." I still hear the same tired, outdated criticisms of Gaia we heard in the 1980s...

With this background this paper asks if the following can be supported.

- (i) the claims of Doolittle (1981) and Dawkins(1982) that any Gaian habitability-promoting influence cannot be the product of natural selection ; and
- (ii) the claims of others that therefore Gaia cannot exist.

The paper attempts to answer these claims on two levels, asking:

- (i) Is there sufficient evidence that Gaia does exist and therefore has to have evolved somehow?
- (ii) From what empirically observed building blocks might exist from which a Gaia could have evolved?

We address these two questions in turn.

1.2 Is there sufficient evidence that Gaia does exist?

A large body of studies shows (summary in Lenton and Dutreuil 2020) that from very near the origin of life: liquid water has been present at the surface of the Earth; the ozone layer in the atmosphere has protected life from dangerous solar radiation; and the climate has remained within comfortable bounds in spite of the constantly increasing luminosity of the Sun.

The Gaia hypothesis accounted for this stability by positing that:

the ensemble of living organisms which constitute the

biosphere might act as a single entity to regulate chemical composition, surface pH, and possibly also climate (Lovelock, 1979)).

Key further findings consistent with this hypothesis, also summarised in Lenton and (2020) are as follows:

...since the origin of life ... the climate has remained within comfortable bounds in spite of the constantly increasing luminosity of the Sun.

... Over the ages, the parameters necessary for life – free energy, abundance of water, pH, pressure, temperature – have remained within the same broad range.

Noting that six elements - carbon, hydrogen, nitrogen, oxygen, sulfur and phosphorus - account for 97 percent of an organism's body mass and were originally scarce to life Lenton and Dutreuil (2020) summarise studies providing evidence that the elements have all become markedly more available – by multiple orders of magnitude. This has come about through synthesis and then recycling by living organisms.

Therefore the above processes exist that could contribute to the operation of a Gaia. With respect to temporal scales, these processes operate at scales from hundreds of thousands of years, to millennia, and to years to centuries.

This temporal scale range has now been extended to that of months to years, with Gaian attributes shown to be operating in dynamic form in the present (Leggett and Ball 2020, 2021). The two papers provide extensive evidence on processes and mechanisms. We make a case that this evidence can best and possibly only reasonably be interpreted as having been made by a control system in action at global scale – that is, by Gaia.

This evidence is summarised in the following.

The first paper (Leggett & Ball, 2020) showed using empirical data that a better causal fit for global atmospheric CO₂ driving global surface temperature than that produced by the standard linear model, occurs when integral and derivative CO₂ series are also included. This was best mathematically modelled as a control system (see Section 1.5 below for definitions of types of control system.) involving corrective feedback using the derivative and integral components in addition to the commonly-used linear error term.

Of particular note, this made the temperature control system in the atmosphere the same type as the most widely used control system developed by humans, the proportional-integral-derivative (PID) control system. The PID control system uses proportional, integral, and derivative feedback to provide control of an action. PID control systems are based on use of the past (I), present (P) and future (D) control error (Åström and Hägglund, 2000). This control system produced the Gaia-type result of keeping global warming lower than it would otherwise have been.

With this shown, a mechanism to achieve temperature reduction should involve flows of causality through atmospheric processes. The second paper, Leggett and Ball (2021), sought physical processes that might be expected if there were such a control system.

We looked for such physical processes using the major form of non-experimental causality assessment, Granger causality analysis. Using this method, we were able to show statistically significant parallel chains of one-way causality. The causal chains started from a measure of biosphere activity – the Normalized Difference Vegetation Index (NDVI) – leading to effects on elements of the atmosphere. One key causal channel influenced wind, with wind then moving heat out of the atmosphere into the ocean. Another channel led to increased cloud cover, leading in turn to solar heat not reaching the planetary surface because it was being reflected back into space.

These results, then, provide evidence for a global temperature control system involving negative feedback to global atmospheric temperature in response to a (rising temperature) disturbance that has been tending to drive the temperature above a setpoint. This feedback has the result of making the atmospheric temperature lower than it otherwise would have been, hence making it more conducive to life. This process meets the criterion for Gaia-type action.

We consider the above provides clear evidence that Gaia does exist. Even if Gaia only *might* exist, this is still sufficient to dispense with the claim by interpreters of Dawkins (1982) that Gaia *cannot* exist.

1.3 From what building blocks could Gaia have evolved?

We now turn to the second question assessed in this paper: given Gaia might exist or does exist, in what are some of the ways it could have evolved?

One way is that proposed by Doolittle (2014) and Boyle and Lenton (2022). This is that Gaia could evolve not by genes but by persistence, at clade level.

In this paper, as introduced in Section 1.1 above, we seek to determine whether Gaia could evolve on the precise ground stated by Dawkins and Doolittle in their objections – that is, by standard gene-based Darwinian natural selection

In structuring this investigation we commence with the matter of defining Gaia. We do this by seeking what we term the ‘core attributes’ of Gaia. We propose these core attributes of Gaia in detail in Section 3 of this paper, but we summarise them here. Three core attributes are proposed. These are:

1. Individual organisms possessing control systems using feedback loops to regulate their external environment (*environmental regulation* core attribute), and

2. Joint action of groups of such organisms leading to the achievement of larger scale environmental regulation(*Joint action* core attribute), and
3. Such action occurring at a planetary scale.

Such core attributes proposed, the next steps of our investigation are as follows.

Firstly we seek modern individual organisms that both conduct *environmental regulation* and also have active components of the control system pattern observed in Leggett and Ball (2020, 2021). We then seek cases of *joint action* by groups of such modern individuals engaged in environmental regulation.

Having found cases of the above, we seek key genes for the metabolic processes involved in each case. Referring to phylogenomics and phylogenetics data repositories, these genes are traced as far back in time as possible.

If these genes for environmental regulation are ancient, we have a situation where components for the environmental regulation of the planet eventually at planetary scale would have been available for operationalisation from early in life's history. Over time, these could become present in cooperatives of organisms carrying out environmental regulation at a range of scales of biological organisation, even up to planetary scale.

1.4 The Last Universal Ancestor

In terms of the question of ancient life raised above, an important concept is that of the last universal ancestor. For example, the last universal common ancestor (LUCA) is the ancestor of all presently living things (Weiss et al., 2016).

Other such last common ancestors are those of each of the three kingdoms of life – the last bacterial common ancestor (LBCA), the last archaeal common ancestor (LACA) and the last eukaryotic common ancestor (LECA). This study uses genes from gene repositories for LUCA (Weiss et al., 2016) and LBCA (Coleman et al., 2021).

The analyses of Betts et al. (2018) and Betts (2020) provide evidence that LUCA was a very ancient organism that existed close to the time of formation of the planet (> 4.5 billion years ago (Ga)), with a predicted age between ~4 – 4.5 Ga. LBCA is estimated to have emerged from LUCA between no later than 3.5 Ga. (Betts, 2018).

The more widely the same gene is seen across all living things, the earlier in the history of life the gene is deemed to have originated (Weiss et al., 2016). Further, with the use of appropriate phylogenomic techniques, it can be inferred that if a modern gene has a role in a cell function, and that same gene is present in very early life, then that gene performed the same role in early life and that the same cell function existed then (Eisen, 1998; Weiss et al., 2016; Xavier et al, 2021; Coleman et al., 2021).

This, and the fact that many genes seen in modern life are also seen in early life (Weiss et al., 2016; Coleman et al., 2021), enables the inference of (i) the existence of unicellular life up to 4 Ga (Betts et al., 2018), which (ii) in multiple ways is similar to extant unicellular life (Weiss et al., 2016; Coleman et al., 2021).

This pool of genes present in life near its start gives us an opportunity to identify modern cases of environmental regulation in current organisms (at either Gaian or sub-Gaian scale), find genes for the attributes that are associated with Gaia, and then see if those genes were also present in life near its start. It is apparent that it would be futile to seek genes for the core attribute of planetary-scale regulation, but we can seek genes for the other two attributes of environmental regulation and joint action. At a minimum, we consider that adequate evidence for genes for the latter attributes being present in life near its start would be the detection in LUCA or LBCA of a minimum of one modern metabolic pathway and one gene from the full set of genes specifying the modern pathway.

The span of time over which control system and joint action functionality in organisms can be observed, from the present to as far back in time as empirical evidence is available, is sought across several scales of cellular aggregation. These range from unaggregated (single cells: bacteria) to grouped bacteria (biofilms), to multicellularity, and to large-scale multicellularity, including in vascular plants, and particularly trees.

1.5 Types of Control System

Control systems were briefly described in Section 1.2 above. In more detail, control systems (Astrom and Murray, 2008; Svrcek et al., 2014) are systems that carry out control actions to maintain the performance of other systems at a set point or to bring the performance of other systems back to a set point.

The control action is negative feedback resisting the direction of the disturbance that is triggering it. The strength of a control action is termed its ‘gain’, and this can be proportional to the disturbance in various ways. It can be ‘all or nothing’ (on-off control); linearly proportional to the disturbance; proportional to its integral; or proportional to its derivative or its second order derivative. What is more, the overall output of a particular control system can involve combinations of these individual gains. Other than on-off control systems, therefore, there can be Proportional-only, Integral-only, Proportional-Integral, Proportional-Derivative and Proportional-Integral-Derivative, etc. (Derivative-only controls are not used in industry because derivative information only does not lead to useful control (Svrcek et al., 2014).

The most common type of control system used in human industry is the Proportional-Integral-Derivative type. A Proportional-Integral-Derivative-Second-Order-Derivative control system is a further proposed elaboration on this type (Sahib, 2015; Raju et al., 2016).

In referring to control systems in the biological context, Cannon (1926) coined the term ‘homeostasis’. This term describes the regulatory process by which organisms maintain the constancy of their internal state in the face of their own changing needs in a fluctuating environment. Kotas and Medzhitov (2015) have shown how biological homeostasis processes can be expressed in control system terminology.

2. Methods

This paper draws on studies from five areas:

1. Morphology of the anatomical elements undergoing control and/or experiencing joint action;
2. Observational in-vivo stimulus-response experiments, investigating the behaviour of individual anatomical components or organisms potentially experiencing control and/or joint action. Such experiments (Bailey, 2008) involve the investigation of time series of behavioural responses of organisms to applied stimuli (the treatment group) compared to time series of behaviour with no such stimulus applied (the control group);
3. Genetics, looking for the genes specifying the anatomy and behaviour possibly experiencing control, including studies utilising gene mutations;
4. Phylogenetics, seeking evidence of any of the modern genes also being ancient; and
5. Evidence from the physical fossil record that any of the modern morphology is also ancient.

Genes and their corresponding proteins use four-letter symbols for their description., Italics and a lowercase initial letter are used in the symbol for the gene, and non-italics and an uppercase initial letter are used in the symbol are for the protein (Stewart, 1995). For example, in bacteria, *cheY* is a chemotaxis gene and CheY is the corresponding protein synthesised from information in *cheY*.

The methodological process used in this study is hypothesis testing. The empirical information resource used is published literature. While the study does not purport to present individual empirical results that have not previously been reported, and uses pre-existing literature as its research base, it is not a literature review attempting to summarise a field.

What we seek from the pool of previously reported *individual* empirical results is a particular *set* of such empirical results, not having previously been reported as a *set*, to provide evidence relating to a particular hypothesis. We are undertaking original research using pre-existing findings as the information base.

3. Results

3.1 The Core Attributes of Gaia

An entity can have many attributes. Dealing with many attributes in a study can lead to complexity, so here we introduce the concept of ‘core attributes’, the smallest number of attributes that adequately distinguish the entity in question from other entities.

To begin, we identify meaningful definitions of Gaia, and from those, seek to derive the core attributes of Gaia.

Margulis and Lovelock (1981) describe Gaia in terms of two attributes (present authors’ italics):

...*interactions of organisms* of very different species have been continuously important in *environmental regulation*

Turning to how the environmental regulation might be achieved, Lovelock (1989) refers to “an active *control system* regulating atmospheric composition”. From this, a control system is identified as providing the regulation.

In later wording linked to the two attributes derived from Margulis and Lovelock (1981) above, Lenton (1998) and Lenton and Wilkinson (2003) use ‘environmental regulation’ in connection with Gaia. The Gaia effect would be planetary environmental regulation.

Lenton (1998) added the point: “Simple principles suggest that environmental regulation can emerge at levels from the individual to the global.” This can be interpreted then as stating that sub-planetary scale environmental regulation can also occur.

Further, at any level beyond the individual, the other attribute derived from Margulis and Lovelock (1981) comes into play: *interactions of organisms*.

As the *interactions of organisms* produce an observable result, *environmental regulation*, their interactions must be in harmony to the extent that they aggregate to the observable result. In other words, environmental regulation is being carried out by a group or groups of organisms carrying out *joint action*.

The core attributes for the *Gaia-level* environmental regulation system, then, are:

- (i) planetary scale;
- (ii) the presence of control systems involved in environmental regulation in the individuals making up Gaia; and
- (iii) joint action between these individuals to produce the environmental regulation.

In seeking representative cases of the proposed Gaia core attributes, we acknowledge at the outset that control systems must have originated very early in life's history and for most or all of the cell's metabolic processes; otherwise, the cell/protocell would have been unstable and fail to maintain structural integrity (Torday, 2015).

Leggett and Ball (2021) provided empirical evidence that the planet-scale atmospheric temperature control system observed was of the Proportional-Integral-Derivative-Second-Order-Derivative (PID2D) type.

In what follows, evidence is sought of the nature of control systems in the metabolisms of individual biological organisms in terms of the typology outlined above. In this study, well-specified control systems are sought, whether they are internally focused, or external (that is, carrying out environmental regulation).

In finding such well-specified control systems, their genes are identified. These genes are then sought back in time as far as LBCA.

3.2 Genes for environmental regulation core attributes: control systems and joint action

From the extensive literature on genes and their function, many cases of genes can be found that can be considered to be related to aspects of environmental regulation.

From these, what we consider to be representative examples have been chosen. The cases presented in the following are set out starting with planetary Gaia. The remaining cases are of environmental regulation at smaller scales of biological organisation, ordered from those involving single-celled prokaryotic organisms (singly and in groups) to multicellular eukaryotes, also singly and in groups.

3.2.1 Case 1. Environmental regulation core attributes (control systems and joint action) at the level of planetary Gaia

At planetary level, in Leggett and Ball (2021) we provided empirical evidence that the Normalised Difference Vegetation Index (a measure of the global aggregate of the photosynthetic activity of photosynthesising individuals) was the leading element of the control processes observed. These control processes were shown empirically to be subsequently applied to other physical elements of the atmosphere, such as wind and clouds. This is evidence that biological elements of the biosphere are applying a control system pattern to other elements of the atmosphere.

This interpretation is consistent with an interpretation in the IPCC Fourth Assessment Report by Denman et al. (2007), in which the pattern is seen as coming from the influence of the biosphere, particularly the land biosphere. The Report states (*italics denote present author emphasis*):

Interannual and inter-decadal variability in the growth rate of atmospheric CO₂ is dominated by the *response of the land biosphere to climate variations* ... The terrestrial biosphere *interacts strongly with the climate*, providing both positive and negative feedbacks due to biogeochemical and biophysical processes ... Surface climate is determined by the balance of fluxes, which can be changed by radiative (e.g. albedo) or non-radiative (e.g. water-cycle-related processes) terms. Both radiative and non-radiative terms *are controlled by details of vegetation*.

Both Leggett and Ball (2021) and Denman et al. (2007) lead to the interpretation that the signal seen at the global level must originate from individual organisms in the biosphere. For signals from individuals to add in such a way that there is a signal observable at the global level (and not simply noise), this globally aggregated signal must (i) arise out of a sufficient proportion of the individuals of the global biosphere to produce the observed effect; and (ii) be sufficiently preserved to be seen in the globally aggregated output. This is explainable by that proportion of the individuals of the global biosphere contributing to a net beneficial effect, a notion that matches the Gaia core attribute of joint action.

The number of individuals that might be involved in this joint action is striking: the land biosphere, just to take the dominant trees, consists of over three trillion individuals (Crowther, 2015).

3.2.2 Case 2. Environmental regulation: unicellular prokaryote

In the realm of the unicellular prokaryote the largest and most prevalent example of environmental regulation is the biofilm, and within that category, the mineralised biofilms, including the stromatolite (Riding, 2000). This, in primeval times, was present in massive reefs covering extensive sections of coastlines worldwide (Riding, 2000).

Examples of environmental regulation in modern unicellular prokaryotes can be found in the bacterium *Escherichia coli* (*E. coli*). The example used is the control of the behaviour of its flagellum in its role in environmental regulation.

Case 2 Control system core attribute

Control type: Integral control of chemotaxis in *E. coli*.

Role of control type in control of external environment: The flagellum moves each individual bacterium into place to make a biofilm. The existence of the biofilm is essential before commencement of the building of an external matrix of the biofilm.

The prokaryote flagellum provides motility (Bardy et al., 2003). It works like a propeller and is driven by what is essentially a motor – albeit biological and at the micrometre scale. Because, as a moving mechanical part, the flagellum can be observed in action, the modern prokaryote flagellum and flagellar movement have been extensively studied (for review, see Huang, 2019).

There is thus detailed knowledge of the structure of the flagellum, with significant work having also been done on the dynamics of flagellar operation and the nature of its control system (Alon et al., 1998; Yi et al., 2000). The method used by Alon et al. (1998) was a behavioural stimulus/response study of the dynamics of the flagellum during chemotactic motility. Since the initial bacterial chemotaxis study of Adler in the 1960s (Adler, 1966). *E. coli* has been the most prominent model organism used for chemotaxis studies. Over the following three decades, many biochemical and molecular studies have elucidated much about the molecular mechanism of chemotaxis operation in *E. coli* (for review, see Huang, 2019). In *E. coli*, the chemotaxis system consists of five transmembrane chemoreceptor proteins, Tar, Tsr, Tap, Trg, and Aer, and six core component proteins, CheA, CheW, CheY, CheB, CheZ, and CheR.

Of these proteins, CheY (termed the ‘chemotaxis response regulator’), interacts with the flagellum and changes its direction of rotation.

The quantitative relationship between varying levels of CheY and bacterial swimming behaviour was investigated empirically by use of a computerised image analysis system (Alon et al., 1998). This system collected statistics on chemotactic responses by both free-swimming and individual tethered cells.

Alon et al. (1998) showed that despite stepwise increases in the level of external chemical stimulus, the level of CheY always returned to an initial set point.

Yi et al. (2000) showed that these results were consistent with control of the flagellum being of the Integral control system type.

We now use phylogenomics to seek this Integral-type control system in as early life as possible. This requires a return to the nature of the structural and regulatory genes and proteins making up the bacterial flagellum.

In *E. coli*, the apparatus mediating bacterial chemotaxis comprises transmembrane receptors (methyl-accepting proteins) and the products of six *che* genes: *cheA*, *cheB*, *cheR*, *cheW*, *cheY*, and *cheZ*. Instead of *cheZ*, many chemotactic bacteria contain *cheC*, *cheD*, and/or *cheX* (Park, 2004).

Of these nine genes making up the chemotaxis apparatus, all but *cheY* are found in the study of LBCA of Coleman et al. (2021).

In terms of the Bayesian probabilistic method used by Coleman (2021), the eight genes found each displayed moderate to high probabilities of being present ($0.5 < PP < 0.95$) and therefore met the requirement of Coleman to have been a pathway likely to have been present in LBCA.

A separate line of evidence can be brought to bear supporting the early existence of *cheY*. Lai et al. (2020) note that the flagellar motor is currently the best-understood system for bacterial locomotion. There is evidence that the bacterial flagellar motor structure and

amino acid sequence of constituent proteins are present across a diverse range of bacterial species and environments, suggesting an early origin (Lai et al., 2020).

Further, Lai et al. (2020) note that some species of the non-bacterial Archaea also possess flagella with rotary motors that drive swimming. While the structural proteins of the bacterial and archaeal motors differ, both motors use chemotaxis machinery that contains the protein CheY.

This suggests that *cheY* was present before the division of life into bacteria and archaea between ~3.5 – 4.0 Ga (Betts, 2020).

The Coleman (2021) and Lai (2020) results taken together give us evidence of the full set of chemotaxis genes in a modern bacterium also being present in LUCA or LBCA.

Alongside chemotaxis genes, in *E. coli*, about 50 genes have been found to be involved in either flagellar fabrication or non-chemotaxis operation (Lui and Ochman, 2007). Of these 50 genes, some 33 are found in LBCA (Coleman, 2021), adding strong structural gene evidence to the chemotaxis gene evidence mentioned above.

The location of the integrator for the Integral aspect of the control is a complex matter, not yet experimentally resolved (Araujo, 2022). For the purposes of this analysis, it is sufficient to note that the integrator must be either in one of the sets of proteins making up chemotaxis control or in their interaction as suggested by Alon (1998), who describes “...some hitherto undefined molecular interaction within the ... network...”

From the foregoing, there are, therefore, multiple lines of evidence from phylogenetics placing the existence of genes for an Integral control system at the LUCA and/or LBCA stage of life.

Physical fossil evidence has been found for the early existence of the flagellum. Delarue et al. (2021) report the discovery in 3.4 Ga strata – dated by uranium-lead radiometric dating (Gardiner et al., 2019) – of unicellular microfossils exhibiting a tail-like structure. This tail-like appendage shares similar morphological features to locomotory organelles in modern microorganisms such as archaella, flagella, and cilia.

Considering the above genetic and physical fossil evidence overall, we can conclude that this provides empirical evidence for an entity (the flagellum) displaying a control system (of Integral type) in LUCA and LBCA near the start of life.

Case 2 Joint-action core attribute

Joint action type: Communication and coordination between multiple unicellular prokaryotes leading to environmental regulation.

Evidence for joint action between individual cells is drawn from studies of a process between the individuals of a group of bacteria termed ‘quorum-sensing’ (QS).

The quorum-sensing system is an intercellular cell-cell communication mechanism that controls the expression of genes involved in a variety of bacterial cellular processes and that plays critical roles in the adaptation and survival of bacteria in their environment (Wang et al., 2019). For intra- and inter-species communication, bacteria use chemical signals. When an extracellular threshold concentration of the appropriate chemical signal molecules is reached, indicating that the presence of a threshold number of individual bacteria in the group has been reached (analogous to a quorum), these molecules bind to their receptors, thereby activating the expression of the genes for extracellular processes in each individual in the group.

One of the main physiological processes controlled by quorum-sensing is the formation of the structure, the biofilm, that regulates the environment for its constructing bacteria. Bacterial biofilms are surface-attached communities of bacterial cells embedded in an extracellular matrix composed of polymers produced by the microorganisms (Wang et al., 2019). They result from quorum-sensing, followed by coordinated action to form the biofilm. This leads to major net benefits for the bacterial community. For example, the extracellular matrix provides shelter from environmental stress such as UV irradiation and external fluid flux and resistance to the ingress of external deleterious chemicals (Flemming, 2016). Biofilms typically are made up of multiple species, including in the hundreds (Yang, 2011).

Quorum-sensing signalling molecules are termed autoinducers (AI). Four main general types of autoinducers have been described (Combarrous, 2020):

1. AI-1, mainly present in Gram-negative bacteria, are *N*-acylated homoserine-lactones (AHLs) with a core homoserine-lactone ring and a 4- to 18-carbon acyl chain with eventual modifications. The AHLs bind to specific LuxR-type cytoplasmic receptors, which control the transcription of numerous virulence genes, and to LuxN-type membrane receptors.
2. AI-2, present in both Gram-positive and Gram-negative bacteria, is considered to be a universal communication signal because LuxS, the key enzyme in AI-2 biosynthesis, is found to be widespread in both Gram-negative and Gram-positive bacteria (Xavier & Bassler, 2003).
3. AI-3, mainly in Gram-positive systems, typically uses secreted oligopeptides and two-component systems, consisting of membrane-bound sensor kinase receptors and cytoplasmic transcription factors that direct alterations in gene expression.
4. PQS (pseudomonas quinolone signal) makes use of 2-heptyl-3-hydroxy-4(1H)-quinolone, which binds to its specific LysR-type transcriptional regulator receptor to control the synthesis of a rhamnolipid, which has a critical role in the formation of the groupings of prokaryotes called biofilms.

Of the above four main types of autoinducers, the gene for only one is found in LUCA or LBCA. This is the *luxS* gene found in LBCA (Coleman, 2021), which produces AI-2.

That said, there is empirical evidence that AI-2 is an important autoinducer, playing a central role in biofilm formation and control.

In-vivo stimulus-response experiments involving the effect of AI-2 on biofilms (Li et al., 2015) provide empirical evidence of this process.

In the bacterium *Pseudomonas aeruginosa*, the addition of increasing amounts of exogenous AI-2 increased biofilm formation and bacterial viability. Yet higher concentrations of AI-2 reduced biofilm formation and bacterial viability. Gene expression analysis revealed that AI-2 increased the expression of quorum-sensing associated genes at lower concentrations and decreased these genes at higher concentrations. These results are homeostasis-like in that they control the outcomes – biofilm formation and bacterial viability – nearer to their optimal range than they otherwise would have been.

Similar results were found in the bacterium *Streptococcus suis* (Wang et al., 2019). The ability of *S. suis* to form biofilm was significantly increased when a small amount of AI-2 was added during growth. Further, deleting the *luxS* gene led to a decreased ability to form a biofilm.

Noting that the biofilm-inducing gene *luxS* is found in LBCA, physical fossil evidence for the existence of biofilms is sought in the LBCA time period.

In the Strelley Pool Formation in Western Australia (dated to 3.46 Ga), Sugitani (2010) shows fossil evidence of features of microbial mats and stromatolites. Film-like microstructures have been recovered in this material (Delarue, 2020) and elsewhere (Westall et al., 2006; Sugitani et al., 2007, 2010). It has been proposed that the films possibly formed from fossilised extracellular polymeric substances (EPS) (Westall et al., 2006) secreted by prokaryotic microorganisms (Sugitani et al., 2010). EPS is the external structural element of a modern biofilm. Delarue (2020) notes that some film-like microstructures from the Strelley Pool Formation exhibit a striking morphological resemblance to modern EPS.

The film-like microstructures are made up of several morphological types. Taken together, the Sugitani and Delarue results suggest that biofilms made up of multiple species existed at the time of LBCA.

Hence, biofilms of that period would have benefited from a *luxS* process because of their capacity for coordination, including at the interspecies level.

In summary, this case shows:

- communication between modern individual unicellular organisms leading to joint beneficial action in biofilms and the involvement of the *luxS* gene;
- the essential gene for the modern process also being present in LBCA, showing that the same process could have taken place in that time period; and
- corroboration from fossil evidence for the existence of biofilms in the LBCA era.

3.2.3 Case 3. Environmental regulation: multicellular eukaryote

In single individual multicellular organisms, examples are found of both of the environmental-regulation core attributes – control system action and joint action. This study uses an example from within the vascular plants, the woody plants (trees). This case seeks to demonstrate joint action between individual woody plants, with plants such as trees being a prime constituent of modern Gaia.

Case 3 Joint action core attribute

Here, we select a process that has been described for some time, in which an individual plant triggers mutually beneficial joint action in a group of surrounding individual plants (Baldwin and Schultz, 1983). This most commonly occurs when a specific plant in a group is the first to be stressed and/or damaged. The plant generates specific airborne emissions that are received by surrounding plants. If the surrounding plants are later stressed, they experience less damage because defences have been put in place as a result of the earlier receipt of the emissions.

Two main forms of stress on plants are stress on foliage from insect attack (herbivory stress) (Shiojiri, 2006) and metabolic stress from increased soil salinity (Caparrotta, 2018).

The following example involves a vascular woody plant, the conifer *Pinus sylvestris*, undergoing herbivory stress.

Pinus sylvestris occurs in the boreal forest that extends from Western Europe to Eastern Siberia, and the *Pinus* family is often dominant in this forest (Saucier, 2015). This forest comprises one-quarter of the global forest area (Crowther, 2015) and hence can be expected to play a major role in Gaia.

In an in-vivo stimulus-response experiment, *P. sylvestris* seedlings were exposed to either herbivore (weevil)-infested plants or undamaged plants (Yu et al., 2022). The results showed that herbivore-induced plant volatiles emitted by the weevil-infested plants decreased the amount of damage caused to plants that were later infested by weevils.

Environmental regulation can also be demonstrated. In helping the surrounding trees by providing warning, they each defend themselves. However the trees in the group are all part of each other's environment. Because all the trees' defences once activated maximally catch the attacking herbivores, this means fewer herbivores overall: that is, a regulated environment that is better for all. The changed tree group is like the defensive formation of a cattle herd (Geist, 2023), the Roman legion 'shield hedgehog' (Goldsworthy, 2005), or a stromatolite (Riding, 2002).

These results provide empirical evidence for between-plant communication in conifers.

Case 3 Control system core attribute

Control type: On-off control.

The above results also provide empirical evidence for on-off (switching) control of emission of volatile compounds.

Modern genes responsible for this process are now sought. Yu (2022) lists 51 separate volatile compounds as being emitted by the weevil-infested plants in the above experiments. It is not known how many of the 51 separate volatile compounds were responsible for the signalling.

What is known is that of these, a large majority – 47, or 84 per cent – are terpenes. Terpenes, and particularly isoprene, induce stress tolerance in many types of plants (Sharkey et al., 2001; Vickers et al., 2009b; Velikova et al., 2011). The generality of the effects of isoprene in plants that have been studied has led to the suggestion of a general signalling function for isoprene in all plants (Harvey and Sharkey, 2016).

So, it can be concluded that it is very likely that the terpenes emitted in the above experiments have a role in the response observed.

Despite there being so many terpenes involved in the *P. sylvestris* emissions, the specification of the modern genes for the terpenes is simplified. This is because all terpenoids originate from only two biochemical building blocks – isopentenyl diphosphate and dimethylallyl diphosphate (Hoshino and Gaucher, 2018).

Five genes associated with metabolic pathways involving one or both of these building blocks are reported in LBCA (Coleman, 2021):

1. The *lldD* gene: This generates type II isopentenyl diphosphate isomerase. This has the role of converting isopentenyl diphosphate from one physical form (isomer) to the form used as the terpenoid building block;
2. The *miaA* gene: This generates dimethylallyl transferase. As for *LldD*, *miaA* has the role of converting dimethylallyl diphosphate to the isomer used as the terpenoid building block;
3. The *ispG* gene: The 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway for isoprenoid biosynthesis is essential in most bacteria and plants (Campos et al., 2001). Campos et al. identified *gcpE* as a novel gene of the MEP pathway. The distribution of this gene in bacteria and plants strictly parallels that of the gene encoding 1-deoxy-D-xylulose 5-phosphate reductoisomerase, which catalyses the first committed step of the MEP pathway. Their data demonstrated that the *gcpE* gene is essential for the MEP pathway in *E. coli* and indicated that this gene is required for the trunk line of the isoprenoid biosynthetic route;

4. The *ispH* gene: The *ispH* gene product has a role in a step of the non-mevalonate biosynthetic pathway leading to the universal terpenoid precursors, isopentenyl diphosphate and dimethylallyl diphosphate; and
5. The *xyfB* gene: D-xylulokinase specified by the *xyfB* gene catalyses the phosphorylation, converting unphosphorylated 1-deoxy-d-xylulose to terpenoids (Wungsintaweekul et al., 2001).

Of these, two are terpenoid precursor genes: *lldD* and *miaA* (Coleman,2021).

In addition to the above role of terpenes in plant defence, we note that there is evidence for terpene emissions by trees being the most significant contributor to the formation of secondary organic aerosols, which act as cloud condensation nuclei increasing cloud cover (Oku et al., 2024). In this connection Leggett and Ball (2021) showed a Granger causal link from increased cloud cover to the global environmental regulation outcome of reduced global atmospheric temperature.

With terpenoids providing the means for such joint action in the present day, it can be inferred that a similar process has been available since the time of LBCA.

The foregoing cases provide repeated examples of modern genes for control systems in individual organisms involved in environmental regulation and joint action between so-equipped individuals. Further, these modern genes are also shown to have existed in LUCA or LBCA.

4. Discussion

The present study began by exploring the question of what might comprise the necessary attributes of Gaia. The case was made that operating at planetary scale was one necessary attribute of Gaia. Two further core attributes were proposed for Gaia – (i) the presence of control systems involved in environmental regulation in sufficient of the biological individuals contributing to Gaia, and (ii) a sufficient number of these individuals carrying out joint action in environmental regulation, such that results beneficial to life are produced with an impact that is discernable at global scale.

We then sought representative examples of each of the control system and joint action attributes of environmental regulation in operation in individual organisms in present-day life. Representative genes necessary to the genetic specification of each example were identified. These same genes were then sought in the earliest examples of life that have been genetically characterised in empirical terms – the Last Universal Common Ancestor (LUCA) and/or the Last Bacterial Common Ancestor (LBCA).

Using this approach, empirical evidence was found and presented for the existence of a number of separate specific genes contributing to the functioning of examples of

environmental regulation near the start of life (in LUCA and/or LBCA), and the same genes carrying out the same role for the same attributes in individual organisms today.

The range of physical scales where these results were presented started from the level of the single cell, with both control system and joint action functionality for environmental regulation being found there.

The evidence presented was of the flagellum control system being involved in providing external functionality to the cell via chemotaxis motility, including motility for individual prokaryotes coming together to regulate their environment by means of the creation of the protective biofilm. Such coming together is mediated by quorum sensing. Genes for both this and flagellar control were shown to be present in LBCA or LUCA.

Finally, for the most recent, multicellular, stage of life, examples were provided of both control systems and joint action core attributes of environmental regulation. The modern example of joint action that was presented involved woody trees utilising terpene emissions to coordinate response to pest attack in order to achieve better outcomes for the group of organisms. This process was shown to involve both control system action for environmental regulation and joint action for that function. Some of the genes involved in this process in modern trees are also found in LBCA.

We have shown that certain specific genes found both in LUCA or LBCA and subsequently in modern individual organisms and groups of such organisms enable environmental control operations. These processes include that right up to the scale of groups of trees, a scale that approaches to the level of Gaia itself.

We stress that we do not claim that those genes exist at Gaia level or produce the specific Gaia-level effects on global atmospheric temperature observed in Leggett & Ball (2020; 2021). (It is, however, conceptually only a small step to see that those processes already involving groups of trees using some control system and joint action processes that were present in LBCA could coherently integrate to produce a global group of organisms using control system and joint action processes to produce many global effects, including the effects on atmospheric temperature observed in Leggett & Ball (2020; 2021). Seeking such processes is potentially a subject for further research.)

What we do claim is genes for processes like the proposed Gaia core attribute processes are present in life and have been for a very long time. Hence these Gaia genes could be used to produce a planetary Gaia.

Dawkins (1982), defining Gaia in terms of its planetary attribute, which posits that there is *one* Gaia on Earth, pointed out that neo-Darwinian natural selection requires competition between *multiple* units of selection. Given the absence of such multiple units of selection, (i) Dawkins claimed that Gaia could not come into being by neo-Darwinian natural selection; and (ii) others interpreted this as Gaia could not, and did not, exist.

With regard to this claim, the present study has provided evidence that genes for the processes of control systems and joint action – the same processes making up the core attributes of Gaia – have been available at least at lower scales from near the start of life (in LUCA and/or LBCA). With respect to the chronological time period in which ancestral life such as LUCA might have appeared, Betts et al. (2018) date the emergence of LUCA to not later than 3.9 Ga.

With such genes being a unit of selection, we believe that we have identified genes for environmental regulation which are ancient, and therefore that the components for operationalising environmental regulation on the planet have been available from early in life's history. These could over time become present in groups of organisms conducting environmental regulation at a range of scales of biological organisation, even up to planetary scale.

Doolittle (1981) and Dawkins (1982) as quoted at the outset wrote of the impossibility of imagining any evolutionary way in which Gaia could have arisen. We submit that the scenarios above (involving nothing but standard – that is, gene-based – Darwinian natural selection) provide a range of such ways.

Data Availability

All data underlying the study are available from the references cited.

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