Gaia—A Holobiont-like System Emerging From Interaction

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> "*I will sing of well-founded Earth, mother of all, eldest of all beings. She feeds all creatures that are in the world, all that go upon the goodly land, and all that are in the paths of the seas, and all that fly: all these are fed of her store. Through you, O queen, men are blessed in their children and blessed in their harvests, and to you it belongs to give means of life to mortal men and to take it away.*"
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> (Homeric Hymns, see Anonymous 1914).

Abstract The Gaia hypothesis has been heavily discussed ever since its first formulation in the early 1970s. While parts of the hypothesis can be accepted right away, the optimizing view of Gaia as stabilizing conditions on Earth to support life on the planet has raised several doubts. In particular, the evolutionary aspect of conditions evolving in such an optimizing way is hardly in line with classical evolutionary theory. Considering Gaia as a holobiont-like system allows to clarify these issues. Accepting that every form of life interacts in manifold ways with its biotic and abiotic environments and that these interactions form a multilevel network from which higher-level properties can emerge, the self-stabilizing effect of the interactions of the biosphere with the geosphere and the atmosphere can be explained. With viewing evolution as adaptation of interaction and fitness as a shift in probability distribution of the observable, even the optimizing interpretation of Gaia does make sense and leads to valuable insight.

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Nourishing Mother as a Provocative Scientific Metaphor

Gaia (Γαῖα), mother Earth has ever inspired mankind. Gaia feeds all creatures on land and in the sea, providing the basis of life for all living creatures on the planet. The metaphor of the mother comprises our interpretation of Gaia providing conditions for life on Earth in a supporting and comforting manner. As such, Lovelock and Margulis (1974) strikingly used the Greek notion of Gaia to coin a name for their hypothesis, known today as the *Gaia hypothesis* (Lovelock 1972). In its simplest form, the hypothesis states that the interactions of the biosphere with the atmosphere and the geosphere constitute a self-organizing system which optimizes conditions on Earth to support life on the planet. Taken in this form, the hypothesis comprises several concepts to be made explicit to serve a sound scientific discussion. The notion of the **biosphere**, as a first issue, relies on a suitable definition of life (see Lovelock 1988). Since it includes all forms of life on Earth, we need to focus on generic properties of life rather than explicit forms as being exemplified by specific organisms. Second, the hypothesis makes a statement about the **interactions** of the biosphere with other 'spheres'. Thus, we need to consider the set of interactions and focus on the potential of the biosphere to interact rather than any other property one might be interested in. Third, Gaia addresses the self-organizational nature of the system. We, therefore, need to consider **self-organization** contrasting any other, extrinsically controlled form of organization. Finally, the hypothesis characterizes the set of interactions as optimizing toward certain conditions. Clearly, speaking about **optimization**, we need to clarify in what sense optimization is to be understood. Before doing so, let us first recapture the history of the hypothesis and comment on some recent developments.

Soon after Lovelock's book (Lovelock 1979) was published, an intense debate started within the scientific community, splitting into those who consider Gaia as being an inspiring concept to think about Earth as basis for life, and others, quickly opposing by questioning the scientific nature of the hypothesis as being untestable, imprecise and not scientific in its core (see Doolittle 1981 for a summary). Kirchner (2002) opened-up grounds for an informed debate on the hypothesis by working out various variants showing-up in the discussion.

Undoubtedly, Earth's environment has been shaped by biotic interactions (Kasting and Siefert 2002), as well as it itself shapes conditions for all forms of life on Earth (see e.g., Beerling and Berner 2005; Berner et al. 2007) (see Fig. 1). In this sense, Earth as environment of life has coevolved with all forms of life, and both cannot be thought of without each other (*coevolutionary hypothesis*) (Kirchner 2002). The question remains to what extent this coevolutionary interaction can be understood as an optimization.

Matyssek and Lüttge (2013) provided several arguments for considering Gaia as an entity of interacting organisms being subject to selection in evolution. Their approach is based on the notion of a *holobiont*, which in its original form has been defined as "*the host organism and all of its associated symbiotic microorganisms*" (Rosenberg et al. 2007, p. 356). For illustrating this, Matyssek and Lüttge (2013) go through examples at increasing levels of scaling or spatial dimensions of biological

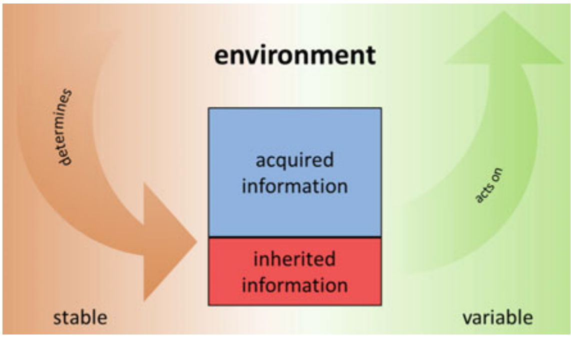

Fig. 1 The internal state of an agent reflects its environment. As there are (locally) stable factors in the environment and variable ones, the state consists of stable parts (inherited information) and dynamic parts (acquired information)

organization with the emergence of networks through integration of modules. This ladder starts with symbioses on cellular levels, including eukaryotic cells of animals and plants, where the organelles mitochondria and chloroplasts in the theory of endosymbiosis are considered as symbionts. It moves on to whole multicellular organisms, including man carrying a good kilogram of innumerable bacteria with him with 100–150-fold the number of genes of his own genome. It then arrives at habitats, biotopes, ecosystems, biomes, and eventually at the biosphere/Gaia as a supraorganism or the ultimate holobiont.

The central argument of the Gaia hypothesis can then be comprised in considering the biosphere as a dynamic system which self-organizes through feedback mechanisms keeping the system within a (pseudo-)stable state (Kirchner 2002; Lenton 2004). These feedback loops stabilize the system and thus provide the basis for the claim that at least within certain limits, the system maintains stability in a self-organizing manner and as such 'optimizes' conditions for life as such. The concept of the holobiont introduces the idea of evolution being the driving force of the observed 'optimization'.

Tyrrell (2013) objects to this point of view by pointing toward an apparent asymmetry in the argumentation. Without any doubt, the agents of the biosphere are subjected to natural selection, while neither atmosphere nor geosphere seem to adapt in an evolutionary sense. Taking a closer look, the difficulty in recognizing evolutionary forces acting on the abiotic components of Gaia is rooted in the gene-centric perspective of neo-Darwinism. In order to see evolutionary forces acting here, we need to broaden our view, looking for units of selection on all scales of biological organization. The idea of the holobiont already reflects the concept of multilevel selection (Theis et al. 2016). In this wider sense, geological formations retain historical information of the geosphere in the same way as, e.g., ice shelves preserve the history of past atmospheric events. Thus, abstracting from the gene as carrier of information, both, geosphere and atmosphere in their present form result from a developmental process and still provide informational content documenting their historic contingency. Note that it is not the presence of a specific mechanism of deciphering information which characterizes evolutionary development, but capability of utilizing stored information toward gaining 'knowledge' about the environment. This is indeed the case for geological formations being ‘utilized’ by mechanisms of Gaian self-control. For example, consider amplification of rock weathering (Schwartzman and Volk 1989) or the impact of arctic sea ice on stabilizing the global environment (Wadhams 2016). In its core, the theory of evolution describes the interacting forces of generation of information through random variation (mutation) and transmission of information (heredity) and their relation with respect to supporting some persistent organizational structure (selection).

Originally being introduced as the central unit of organization for the *hologenome theory of evolution* (Zilber-Rosenberg and Rosenberg 2008), the concept of the holobiont inherently carries a temporal and spatial dimension. Indeed, Zilber-Rosenberg and Rosenberg acknowledged the network of coenobiotic relations every animal and plant establishes, as well as the fact that associations with microorganisms can be transmitted to the next generation of the host organism. Nevertheless, through accentuating the role of a central host, the concept of the holobiont fixes the spatial dimension at the level of an organism. Likewise, temporal stability of the network of associations is located at the scale derived from generations in terms of the host. Note that these might comprise several ‘generations’ of microorganisms interacting with the same host individual.

On the other side, the concept of the holobiont emphasizes two important observations concerning living systems: (1) It is the network of interactions which is subject to natural selection rather than the individual organism on its own. Living systems exhibit themselves through their interaction with their environment (see Fig. 1) and, in particular, associated living systems. (2) The network of interactions as such comprises a level of information which can persist beyond the life span of a single agent participating in the network. Therefore, the network contributes to survival, i.e., stability of a level of organization beyond what can be expected from pure randomness.

The properties of systems leading to an observable characteristic pattern in both, spatial and temporal terms, has lead zu Castell et al. (2016) to generalize the concept of the holobiont, introducing a *holobiont-like system*. The central observation laying the foundation for the latter concept is the observation that life in its various forms on all scales of biological organization essentially deals with information, its generation, accumulation and transmission. A holobiont-like system is a conceptual model acknowledging these properties. It has been defined as a system of interacting biological agents developing through adaptation, the latter being a process generated by generic mutation, generic heredity and generic selection (cf. zu Castell et al. 2016). While utilizing notions from the classical Darwinian theory of evolution, the generalizing addition of the word ‘generic’ indicates that mutation, heredity and selection are understood in a broader sense, beyond their rather narrow definition derived from genetics. The concept of a holobiont-like system thus shifts the focus away from the *carrier of information*, as materialized in the structural bases of genes and other components, to the *process of information transmission*. As transformation of information can be termed *computation* (cf. Gershenson 2012), the shift therefore turns our focus away from the physical/chemical realization of an informational code in terms of DNA toward the computational processing of the code.

The second, important aspect being captured in the definition of a holobiont-like system is a definite choice of the type of algorithm being considered for developing the system of interacting agents. Adaptation describes a change in the informational representation of an entity in response to information being sensed from the environment of this entity. Gershenson (2012) calls such an entity an *agent*. The *environment* of an agent then consists of all the information an agent interacts with (Gershenson 2012).

Evolutionary Motivation for Holobiont-like Systems

Let us now take a closer look at evolution, i.e., the computational process driving adaptation. As mentioned, an organism's DNA is one way of coding information about the organism as a whole, its structure, its characteristics and its potential. Organisms interact with other organisms. At the level of habitats, in the sense of *biocoenosis*, this describes the network of interacting organisms within a certain habitat. Thus, organisms are agents, sensing their environment and reacting upon the sensed information. Thereby they alter their local environment. At large planetary scale this occurs to the extent that life has globally shaped the entire image of Gaia (Lüttge 2016). Life characterizes the large zonobiomes sensu Walter and Breckle (1984) from the equator to the poles of the planet with (1) the equatorial zonobiome with evergreen wet tropical forests, (2) the tropical zonobiome with summer rain and various types of tropical forests and savannas, with evergreen to deciduous vegetation, (3) the subtropical arid zonobiome with desert climate, (4) the mediterranian zonobiome with winter rain and evergreen laurel-like hard-leaf and deciduous forests, (5) the warm temperate zonobiome with temperate rainforests, (6) the temperate nemoral zonobiome (from latin *nemus* = grove) with summer-green deciduous broad-leaf forests, (7) the arid temperate continental zonobiome with steppes and prairies, i.e., grasslands subject to frost, (8) the cold-temperate boreal zonobiome (from latin *borealis* = northern) with the taiga of evergreen coniferous forests, and (9) the arctic and ant-arctic zonobiome with the tundra dominated by evergreen and deciduous shrub species. At smaller scales life actively changes the environment by niche construction (see below).

Taken together, a biocoenosis and its physical environment form an *ecosystem* in the sense of Tansley (1935). Being identifiable as a system, such a network of interactions carries characteristics which appear to persist longer than what we as an observer would expect from pure random choice. At the end, this is what makes us recognize a certain set of interactions as a system.

All the intrinsic properties being attributed to the set of interactions forming an ecosystem, such as waves of succession, trophic structure, or cycles of resources form an emerging characteristic, which we—again as being an observer—term an ecosystem. Organisms, being the central agents within the system, evolve from, adapt to and shape this ecosystem such that both are heavily affected by each other in an intertwined way (see Fig. 1). At the same time, an individual's life span within this system typically is much shorter than the period during which we can observe the level of organization characterizing the ecosystem. On the other side, the genetic information coded in DNA and as such, the blueprint for the interaction potential an individual is carrying, is bound to the one living representative. Thus, information has to be transmitted over time, being handed over to other individuals. The sum of these processes is what we call **heredity**.

The next observation which is crucial for the concept of a holobiont-like system is the fact that activity of an individual leaves an impact on the environment the individual is acting in. In this way, the network of interacting agents shapes its environment, leaving traces, which alter environmental conditions for the time to follow. These dynamic changes in the environment challenge all agents acting within it, being one factor that promotes adaptation in maintaining the agents' intrinsic level of organization. From an agent's point of view, these environmental changes are unforeseen as they integrate actions of all agents in the local environment. On top of that, there is a second source of change resulting from random fluctuations in the parameters of the environment. Summarizing, in order to persist, an agent has to deal with unforeseen changes in its environment and maintain its own stability. This is what we call *acclimation* when it is based on short-term plastic performance but **adaptation** when it is fixed long term through evolution.

The process of natural evolution uses random fluctuations as a source of creativity (in the sense of maintaining variability), from which ever new potential for reacting to this changing environment can evolve. The random seed being brought into the system results from incomplete transmission of genetic information. In combination with other sources of variation such as recombination, stability of interaction patterns being conserved by the genetic code (heredity) is paired with a source of change (**mutation**), creating variation in the gene pool of a biocoenosis. Both processes together provide a basis for adaptability. In order for these processes to work together, random changes in the informational representation of an agent (e.g., mutations) must be transmissible. Otherwise, they would just being wiped out at the end of life of the individual, leaving no persistent trace.

Darwin's theory of evolution now implies the presence of a third process, which acts above the level of the individual on the population as a whole. As such, **selection** is considered to be an autonomous process, i.e., not being directly driven by the agents in the system. The role of selection is to enhance subsets of genetic code while sorting out other sets and thus reducing variation. In a certain sense, mutation and heredity can be understood as active processes, being realized by the action of agents in their environment. In contrast, selection emerges in an indirect way. Selection as a process can be observed over time, although no agent can be identified which on its own selects in the sense of holding control over the system. We will dwell deeper on its characteristics in the following. For the moment being, let us assume that such an autonomous, variation reducing process exists.

Interestingly, mutation and heredity on the one side and selection on the other side do not act in parallel. Evolution proceeds through phases of development followed by phases of reproduction. Generations mark each such step, discretizing the continuous flow of time. Another view of the same alternation is that of phases of information transmission being followed by information encoding. The 'try-and-error' strategy of evolution might have a deeper reason we will come back to later on. Let us first return to our rather general point of viewing individual organisms as one form of representation of structured information.

Agents as being carriers of a certain informational representation, as well as the processes of mutation and heredity perfectly make sense when replacing the genome by any other means of coding information. **Generic mutation** thus means any form of randomly altering the informational state of an agent which is capable of persisting over longer periods of time. The boundary between alterations which prevent us from recognizing the agent as an entity and those which we consider as maintaining its essential characteristics is fuzzy. It reflects the role of the observer as being immanent in every definition of a system (Gershenson and Heylighen 2005). In a similar sense, **generic heredity** is understood as a process allowing for transmission of information such that emerging patterns, resulting from interactions of agents, can be observed longer than the individual life span of a single agent within the system. Adding **generic selection** in an analogous sense completes the triple generating adaptation of the holobiont-like system.

The advantage of using an abstract concept rather than a concrete biological representation, i.e., a given instantiation of these processes within the living world, lies in the possibility to transfer the concept to any level of biological organization. As such the concept of a holobiont-like system matches Bedau's *theory of supple adaptation* (Bedau 1998) which provides the basis for his perspective on a fundamental theory for life. Bedau postulates that the primary form of life is "*an automatic and continually creative evolutionary process of adapting to changing environments*" (Bedau 1998, p. 3). What distinguishes life from non-life "*is the way in which evolution automatically fashions and refashions appropriate strategies for coping as local contexts change*" (Bedau 1998, p. 3). In the same spirit, the concept of a holobiont-like system emphasizes the evolutionary process driving the system to continually adapt to an ever-changing environment.

Human experience clearly knows of several mechanisms which can be used to realize an adaptive process. Obviously, *learning from experience* provides one example. Nevertheless, our anthropocentric way of perception tends to be biased toward assuming teleological principles underlying suitable mechanisms of adaptation. For example, our common concept of learning assumes an intrinsic goal such that learning can be understood as a process of optimizing behavior toward achieving this goal. Scientifically, in epistemology, we clearly do not permit ourselves to assume the presence of any teleological principle underlying organization of nature. Although this might sound self-evident, it is a delicate issue when speaking about evolution in natural systems. Bedau, for example, purposely attributes a teleological notion of propriety as being part of supple adaptation (Bedau 1996). In the same way, Darwin's principle of 'survival of the fittest' carries an implicit goal of being 'fit'. In our understanding, such a teleological glimpse again reflects the role of the observer. On the long run, among the set of all possible networks of interactions, some managed to persist longer than what would be expected from random interaction. Observing these patterns, we tend to imply directedness in the evolution of such patterns, allowing for rational explanation. This *break of symmetry* as physicists call such phenomena (Hopfield 1994) can be understood by dismantling the steps leading to such a pattern and arranging them in a logically appealing order. As an ex post way of explaining the presence of breaks of symmetry, such a logically ordered chain of events is perfectly reasonable. On the other side, the existence of such a chain of events does not imply the influence of any directedness a priori during the evolution of the pattern. Therefore, natural selection is a statistical phenomenon capturing our ex post analysis of a set of natural patterns being observed. As a consequence, we cannot predict ex ante how selection will act in the future. We thus need to restrict ourselves to focusing on mechanisms providing the basis for future adaptability without relying on a concise model of the future environment.

The statistical nature of natural selection is well reflected in the commonly used way to measure selection in terms of an increase in allele frequencies within a given population. Doolittle (2014) is laying out the idea that increases in allele frequency can likewise result from an adoption of survival-enhancing, extinction-avoiding mutations. Obviously, mutants which are more likely to survive will last longer and therefore be more likely to be observed within a population. Second, acquiring survival-enhancing capabilities will, on the long run, effectively lead to more persistent individuals. At the end, differential selection of non-competing and non-reproducing individuals will also result in increasing allele frequencies (cf. Doolittle 2014). Thus, our commonly used practice to think of natural selection in terms of reproductive success should not blur the core of Darwin's theory explaining the observed likelihood of a certain stable configuration which results from the process of selection. In this sense, Darwin's theory of natural selection is indeed a special case of the more general principle of "*survival of the stable*" (cf. Dawkins 1976, p. 12). Indeed, the mere formation of stable patterns of atoms and molecules and their persistence beyond the duration of unstable configurations can be seen as the first steps of natural selection (cf. Dawkins 1976).

The question arises, whether such a form of persistence is the outcome of some lucky chain of events, only, or indeed more likely of being observed. Ulanowicz (1998, 2014) builds his theory of *autocatalysis* on the principle of self-enhancing reactions as given in many chemical reactions. Such autocatalytic configurations act in a growth enhancing way and thereby exhibit a tendency of *centripetality* since over time more resources will be brought into the autocatalytic cycle. Similarly, survival-enhancing adaptations will more likely be found in evolutionary lineages being observed later in their development compared to such being observed at an earlier state (Doolittle 2014). Therefore, the mere existence of a stable configuration over long periods of time already provides an indication that there are underlying mechanisms enhancing stability rather than observing a phenomenon purely resulting from chance.

Self-organization as Mechanism Driving Adaptation

The process of generating complex patterns from simple interactions with each of them not being able of capturing the pattern as a whole, is what is known as *self-organization*. Our way of understanding self-organization rests on two pillars. First, studying processes of self-organization in nature allows identifying common principles and underlying mechanisms. In particular, the study of self-organization in eusocial colonies with group members of different qualifications and specializations for social contributions leads to the unraveling of general principles resulting in emergent organizational patterns on the level of the group. Among those are *decentralization*, *stigmergy*,[1] *positive* and *negative feedback*, and *fluctuations* (cf. Garnier et al. 2007). The realization of such principles allows insect colonies to solve the problem of adaptation of the group to environmental changes. Interestingly, none of these general principles rests on altering the genetic state of the individual agent rather than utilizing modulation of an individual's behavior (e.g., via the hormone system). Thus, the risk of lethal consequences from random alterations of an individual's fundamental (genetic) code is being avoided by providing actions which can be fine-tuned upon sensing environmental signals. While this is not exclusively true (e.g., consider somatic hypermutation, e.g., Martin et al. 2015), this observation emphasizes the need for an adaptive system to find ways for transmission of such environmental modulation. Otherwise, adaptations upon environmental signals would not persist, since they cannot be passed on to the next generation. A growing body of knowledge sheds light on epigenetic mechanisms, which solve the problem even on the level of the genome (see, e.g., Allis and Jenuwein 2016) because by methylation/acetylation of nucleic acids and histone proteins they determine and thus modify the reading of the information inherent in a given structure (sequence of nucleotides) of the DNA (Grunstein 1997; Zhang and Reinberg 2001; Chinnusami and Zhu 2009; Yaish et al. 2011).

Consequently, in order to systematically understand the principles of self-organization, it is not sufficient to analyze the potential of action of all individual agents in the system (i.e., the genome). The emergent phenomena we observe on the level of the system of agents rather directly result from the interactions themselves and therefore are a matter of communication and information transfer among the members of the group (e.g., the *interactome*, see Aitchison and Rout (2015) on the cellular level).

The second pillar being used to study self-organization can be seen as the bottom-up approach complementing the study of self-organizing biological systems. Through actively modeling swarm intelligence in artificial systems, we have a tool at hand which allows analyzing the concepts underlying self-organization in a constructive way. Most importantly, in silico simulations allow us to experimentally test our hypotheses on interaction principles leading to emergent patterns of interaction. For example, in the first half of the last century, ornithologists still were look-

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[1] *Stigmergy* denotes the principle of "*indirect communication mediated by modifications of the environment*" (Marsh and Onof 2008, p. 137).

ing for the ‘common soul’ of a flock of birds, suggesting telepathy or yet unobserved forms of electromagnetic communication (Selous 1931). Detailed video analysis then led toward emergent properties such as self-generated synchrony (Davis 1980). Through computer simulations, Reynolds (1987) finally showed that flocking emerges from the local processes of cohesion, separation and alignment, all of which being explained on the level of a single bird.

Both pillars meet in the recent research field of *artifical life* (Gershenson et al. 2018). For our purpose here, it suffices to note that the concept of a holobiont-like system extracts the core of information processing from natural systems such as insect colonies.

Considering the above-mentioned principles underlying self-organization in swarm intelligence, the holobiont-like system provides a suitable conceptual framework. For example, decentralization matches the motivation for moving from the holobiont sensu stricto toward a holobiont-like system. There is no central host organism, providing ‘control’ on an overall level of organization for the system. Stigmergy inherently is a concept of information transfer. Adapting to actions of agents within the local environment reflects an individual’s way to capture information using a try-and-error strategy and thereby collecting information concerning its environment. Note that the concept of stigmergy builds on existing systems being used to sense the environment, rather than relying on specialized communication as for example given by human language. A similar concept can be found in *quorum sensing* as a principle of bacterial communication (Whiteley et al. 2017). Finally, positive and negative feedbacks in combination with fluctuations represent the core principles of the evolutionary process. Hereby, feedback acts as a mechanism of amplification, allowing small fluctuations to enfold impact on the level of the system as a whole. Thus, through feedback via transmission of hereditary information, fluctuations such as mutations can constitute phenotypic variation. The advantage of using the concept of a holobiont-like system in contrast to other, more genetically oriented concepts, again lies in the ability to study systems systematically at all levels of biological organization. For example, it can readily be used on the level of a collection of individuals.

Noble (2017) stresses the importance of interactions at all levels of biological organization as important factors for both, development and evolution of biological systems. “*Such interactions are also analogue in nature because they depend on constraints of lower (e.g., molecular) levels by higher-level processes that are formed as dynamic patterns. Those patterns represent continuous variation in expression levels of genes and many other factors.*” (Noble 2017, p. 127)

Self-organization of Control

For the purpose of this chapter, we are particularly interested in self-organization leading to self-stabilization. Reacting to criticism concerning the possible self-stabilizing interaction between the biosphere and the atmosphere, Watson and Lovelock (1983)

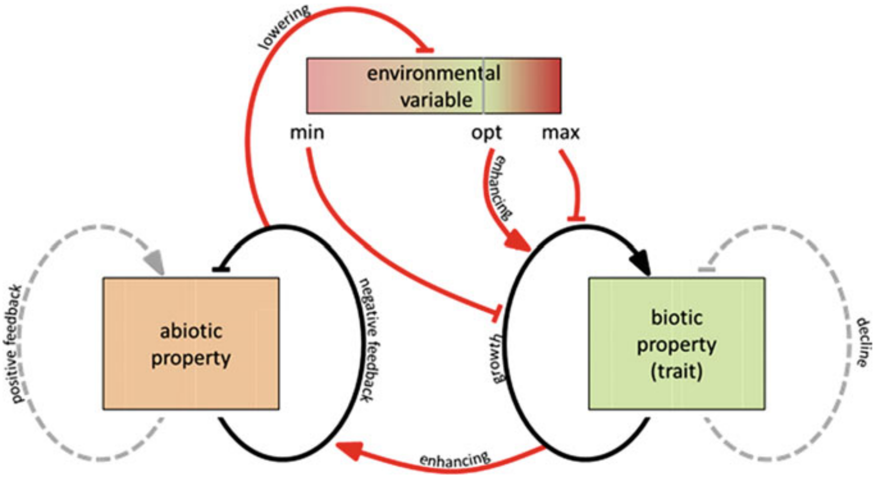

Fig. 2 Control of environmental variables can be achieved through the coupling of positive and negative feedback in both, the biotic and the abiotic 'sphere'

presented Daisyworld, a model of a planet covered with two species of daisy exhibiting different reflection properties due to different colors. Daisyworld provides an example of *rein control* (Dyke and Weaver 2013), the property of a system to regulate a set of variables in a homeostatic way (see Fig. 2). Daisyworld and successors of the model solve the problem of regulation through direct coupling between atmospheric variables and the biotic sphere reflecting the outcome of selection. In the original example, the plants reflect light and thus contribute to the thermal regulation of the atmosphere. While showing that self-regulation is possible in principle, the model nevertheless relies on very particular types of interaction and their immediate influence on the variables being controlled. Therefore, doubts have not been fully clarified since the presented coupling of life with environment appeared to be rather special.

Abstracting from the concrete example, Daisyworld exemplifies just one particular way of self-regulation. The process of evolution has led to a wealth of examples of biological systems stabilizing themselves (Lenton and Wilkinson 2003). Comparing stabilizing regulatory systems to destabilizing ones, the pure property of being stabilizing makes such systems more likely of being observed compared to destabilizing ones. Allowing for self-stabilizing interactions to emerge, the statistical nature of natural selection will make it more likely to observe more of them on the long run, given the potential that such systems manage to adapt to changing environmental conditions. Betts and Lenton (2008) argue that biotic regulatory feedback, only, can lead to the emergence of such self-stabilizing systems. The reason lies in the discrete progression of evolution already mentioned above.

Looking at evolution as a form of trial-and-error process, ever new strategies to adapt to environmental changes can be exploited as long as the creative potential of the pool of possible interactions has not been exhausted. With stabilizing mechanisms being as likely as destabilizing ones, just by chance, destabilizing biotic interactions tend to quickly lead to the extinction of the realizing biotic agents. Eventually, such biotic agents will deteriorate their conditions of existence. Thus, it is the capacity for death which allows evolution to advance, with less favorable trials diminishing themselves and the more favorable ones emerging and creating novelty. Combined with a capacity for change, the process of evolution on the long run will increase the likelihood of stabilizing interactions to be observed (see Betts and Lenton 2008).

Abiotic regulation does not have the same potential of supporting stabilizing systems since there is no way of stopping destabilizing interactions apart from them coming to a natural end due to physical or chemical constraints. Thus, the property of death on the one hand allows for unfavorable variants to deteriorate, while at the same time imposing the need for hereditary processes to help favorable ones to persist. Summarizing, self-regulation can indeed emerge through a process of evolution which is not optimizing for self-regulation per se, but effectively leading to a preference of self-stabilizing interactions as being a statistical outcome of a trial-and-error strategy.

Note that beside the possibility to create new trials as a result of chance, the process relies on some kind of memory. Without memory, a trial-and-error strategy would not much differ from pure random effects. Again, this is where generic heredity comes into play. The weakest form of information conservation can already be seen in the traces being left on the environment by an acting system. The process of fitness-enhancing environmental transformation is known as *niche construction* in ecological theory (cf. Krakauer et al. 2009). Thus, the existence of a niche can, if resulting from active transformation, already be interpreted as information transfer, since the niche lasts beyond the life span of a single occupant. Occupation of new niches can result from genetic mutations as well as from a subgroup of the population choosing the new niche (e.g., Skinner et al. 2014). Niche construction varies among genotypes. It rather establishes a correlation of the genotype with environmental conditions (Saltz and Nuzhdin 2014), although it depends on the functionality of the phenotypes emerging from the expression of information of genotypes. Similarly, there are many other ways of leaving traces of biotic action on the environment. Clearly, not all of them have the capacity of being used by further agents but undoubtedly, some of them have. For example, the sand-stabilizing effects of *Leymus arenarius* are assumed to contribute to the plants decline in dune habitats due to competition with other species (Greipsson and Davy 1994).

Longitudinal memory, i.e., preservation of information over longer periods of time and being derived from experience, can also actively be created by transfer of information from one generation to another. Such transfers need not necessarily be done in the sense of active teaching. To give an example, sodium derived from mud puddles by the moth *Gluphisia septentrionis* is transferred to the offspring, thus providing a fitness-enhancing advantage (Smedley and Eisner 1996). Multiple examples of such *parental effects* exist (Badyaev and Uller 2009), all of which can be seen as passing of information concerning the environment from the parents to their offspring. Epigenetic modifications in response to environmental cues can be stored and recalled and be also handed over to sexually produced subsequent generations (Molinier et al. 2006; Bond and Finnegan 2007; Adams 2010; Daxinger and Whitelaw 2010; Lüttge and Thellier 2016). This we name epigenetic memory (Thellier and Lüttge 2013; Lüttge and Thellier 2016).

Making use of information in an explicit way is given by *social learning* (e.g., Giurfa 2012). Social learning also produces information about the environment and thus, depending on the specific mechanism, provides a selective advantage being passed on to successive generations (van der Post et al. 2016). Furthermore, the actual process of learning itself can be supported by parental interaction with their offspring. Active teaching reveals fitness-enhancing effects since it speeds up individual learning and at the same time prevents erosion of traditions (see Thornton and Clutton-Brock 2011).

A third type of memory consists in community compositions. Albeit traditionally considered as originating from random circumstances, there is growing evidence, that certain aspects of community composition are the outcome of coevolutionary processes, leading to increased stability (Rosenberg and Zilber-Rosenberg 2018). The mere pool of possible associations might indeed be seen as random, while the results originating from interactions being created out of the pool typically show stable patterns. Random associations will originate during niche occupation with facilitation and competition between organisms establishing certain types of (bio-)diversity. Diversity establishes complexity, and this confers stability (Souza and Lüttge 2015).

For example, colonization of the volcanic island of Surtsey by vascular plants is the outcome of plant communities populating neighboring islands (Magnússon et al. 2014). From the potential brought in by wind and sea dispersal and, in addition, dispersal via birds, a widely observed association between the sea sandwort *Honckenya peploides* and costal grass *Leymus arenarius* started the formation of the plant ecosystem on the volcanic island (Fridreiksson 2005). This association between the deep-rooting dune grass and a salt-tolerant Caryophyllaceae has developed via coevolution in coastal regions of the northern hemisphere (Greipsson and Davy 1994). The information concerning this association has been carried over to the newly generated island via seed dispersal.

The amount of evidence showing transfer of microbial associations to the next generation in the holobiont sensu stricto is constantly growing. The well-known example of the maternal gut microbiome being transferred to the offspring passing through the birth canal endows the child with a first set of microbes, several of them being considered as beneficial for the development of the child (Kovatcheva-Datchary et al. 2013; van de Guchte et al. 2018). Similar examples can be found in plant systems (e.g., Vannier et al. 2018). The advantage of the host-microbe associations, providing a stable environment by the host on the one hand and a suite of quickly adaptable genomes by the high functional and species bio-diversity of the microorganisms, has been found to provide an efficient way to adapt to changes of the environment and thus providing stability of the system (Rosenberg and Zilber-Rosenberg 2018).

Return to Gaia as a Holobiont-like System

Being equipped with a solidly laid-out theoretical basis, we may now confidently ask to what extent Kirchner's form of coevolutionary Gaia carries properties of supple adaptation and thus, allows to consider Gaia as a holobiont-like system.

Koshland (2002) suggests the following **Seven Pillars of Life** being summarized in the acronym **PICERAS** to define the characteristics of life.
P—program. All forms of life follow some kind of internal program (e.g., the DNA).
I—improvisation. Living forms react to changes (unforeseen) in their environment.
C—compartmentalization. Living systems exhibit a boundary between the interior and the environment. At the same time, they make use of modularity, with modules also being compartmentalized.
E—energy. Living systems as ordered structure must be open systems and thus use energy and absorb entropy to the environment.
R—regeneration. Making use of catalysts and other chemical substances to transform energy, living systems have to cope with thermodynamic losses.
A—adaptability (which we would call acclimation). Improvisation alone is too slow. Therefore, living systems also reveal plasticity to react to environmental triggers on a short timescale.
S—seclusion. Living systems shield themselves to some extent from losing resources. For example, critical chemicals for one pathway may be prevented from being metabolized within another pathway.

As mentioned above, in order to discuss the hypothesis, we need to provide a proper basis of the concepts implicitly underlying the formulation of the hypothesis. First, there is the concept of the biosphere. It is commonly understood as the summary of all forms of life on Earth. From a broad perspective, life can be understood in terms of supple adaptation. But being an essential part of the concept of a holobiont-like system, adaptation has to be seen as a generic property. Do properties of the Earth allow us to identify adaptability of the system planet Earth? The fact that Earth adapts in a certain way seems to be widely accepted even among the most severe critics of Gaia (Kirchner 2002). The point of discussion is to what extent the biosphere and thus life per se is needed to drive adaptability of the system. We have already seen that life increases the probability of observing self-stabilizing systems, if not being an essential prerequisite (Betts and Lenton 2008).

There is an ongoing debate on the definition of life. We cannot arrive at a comprehensive definition (Lüttge and Scarano 2019, this book). Life appears more like a philosophical category than a natural-scientific one (Nachtigall 2010). We can only comprehend life by listing its essential characteristic properties. However, the discussion on a minimal set of characteristic properties is far from being settled. On the other hand, several suggestions are available for sets of characteristics, which, if being all present in a given system, allow the conclusion that we consider the system as being living. One of those sets is PICERAS (Koshland 2002) (see Textbox). Checking this list against Gaia, some characteristics appear to be obvious and commonly accepted. For example, no one would doubt the Earth being a compartmentalized system, i.e., one planet (C), transforming solar energy (E) into various forms of entropy being released to space (R), and improvising in the sense that the system adapts to environmental changes such as the increase of solar energy, or cosmic impact (I). Furthermore, Lovelock (1979) presents a careful analysis of global processes, maintaining a quite unlikely state, considered form the point of view of thermodynamic stability. Yet, we must remember that all living systems are open systems through which a continuous flow of matter and energy is occurring (Netter 1959) and this includes Gaia composed of living subsystems. These systems are thermodynamically not in steady state but in a kind of dynamic pseudo-steady state in terms of irreversible thermodynamics. Thus, with stability, we mean maintenance and sustainment of the characteristics of the dynamics as will be dealt with in more detail below in relation to homeostasis. Also seclusion is somewhat of a void condition in the context of Gaia with the Earth being the only system carrying life within a reasonable vicinity of the planet (S).

The essential argument raised by opponents of Lovelock's theory is that Gaian and anti-Gaian feedback mechanisms are likewise likely to evolve by natural selection and thus, there is no process of selection driving the evolution of Earth (Kirchner 2002). The core of this criticism is tightly linked to what essentially is the unit of selection. Opposing Gaia, Doolittle (1981) argues that natural selection always has to operate in a way, such that the unit of selection is more capable of maintaining long-term persistence than its competitors. Thus, selection is operating on a set of representatives of a certain genetic type, i.e., the population. While Charles Darwin considered selection to act on individual organisms, Stephen Jay Gould argued that selection is also acting on entire species (Gould 2002). Following Noble (2017), we need to consider multilevel interactions reflecting the life-environment relationship. We, therefore, have to search for persistence of information being stored in some way within a system. Koshland demands the presence of a program which can be adjusted through mechanisms of adaptability (Koshland 2002). In order to facilitate discussion, let us call the program—in the sense of Koshland—giving rise to the performance of a system within its environment the *infotype*. The classical genotype can therefore be seen as a subset of the infotype of a given organism. We thus have to ask: What is Gaia's infotype (P) and how does it relate to Gaia's 'fitness' (A)?

Broadening our view, selection should be interpreted as a statistical property, leading to deviations from an initial distribution of infotypes, which are perceived as being non-random (i.e., some kind of bias). *Fitness* thus is an ex post property, being attributed to a system after observing that the system outcompeted its competitors. As such, fitness is intrinsically bound to the realization of a certain infotype (e.g., the phenotype) within the context of given environmental conditions. Considering fitness as being the property optimized through the process of natural selection, selection consequently combines the phenotype and its specific environmental conditions in an intrinsic way. Being laid-out symmetrically, the concept allows to be adjusted on either side. Fitness of a system can thus change by either changing the properties of the system, or altering its environmental conditions. The gene-centric interpretation of population genetics captures fitness through the adaptation of the genotype by measuring the number of offspring. However, we need a more general view on fitness. For example, clonal growth of plants in habitats may cover large areas and thus demonstrates obvious fitness in the absence of any sexual reproduction (Kempermann and Barnes 1976; Grant 1993; Brulheide et al. 2004). Fitness might likewise arise from the ability of the phenotype to change its environmental conditions in a favorable way, e.g., as revealed by successful niche construction (see above). Thinking of anthropogenic traits, our ability to build houses guarantees *Homo sapiens* a higher level of survivability providing locally stable climatic conditions. The basis for this specific advantage leads to higher fitness which is not being stored primarily in the genotype of the organism, rather than within its cultural heritage. Summarizing, we need to uncover processes of information storage, i.e., memory, and change of information, i.e., novelty, characterizing the homeostatic processes of planet Earth. The characterizing property of Gaia is its set of interactions among the various 'spheres'. Thus, we need to focus on infotypes representing these interactions.

Hopfield (1994) described biology as the study of meaningfulness of information in natural systems contrasting the passive role information plays in physical systems. Following von Uexküll information is "*anything that an agent can sense, perceive or observe*" (von Uexküll 1957; cited in Gershenson 2012). Being a generic concept, information allows to consider interaction among agents as transfer of information. Clearly, this is a very broad definition. From a cybernetics perspective, we aim at studying those interactions which are capable of maintaining the characteristics of the system. Note that the latter is an essentially observer-dependent property (Gershenson and Heylighen 2005). Through observing a system, we as an observer are implicitly defining the system's characteristics. For example, we can consider an enterprise from an economical point of view, studying its action as player in an economic environment. We might also consider the same enterprise as a social system, aiming at its inner functioning, its management system and its way to communicate with customers. Neither one of these perspectives is right or wrong. It is the perspective of the observer giving a system its identity, i.e., the set of properties which make the system appear as an entity in the view of the observer.

In the same way, Gaia comprises a certain view of planet Earth as being a cybernetic system controlling certain global physical, chemical, geological, and biological properties. A central theme in Lovelock's work is the network of bio-/geo-chemical processes, maintaining control of the system. His hypothesis is based on the observation that conditions on Earth are highly unlikely from the point of view of thermodynamics, and at the same time surprisingly constant over the course of time. These two properties lead to the question of (1) how such conditions emerge from interactions among the various 'spheres', and (2) how homeostasis in a dynamic sense of stable open systems (see above) has been maintained over eons. Thus, we are being faced with an instantiation of emergence of control via self-organization and the question of the extent to which adaptation plays a role in maintaining such a system of control.

Coming back to the interactions, Lovelock (1979) considers three major factors being controlled by Gaia: surface temperature, chemical composition of the atmosphere, and salinity of oceans. He then discusses several processes which contribute to homeostasis of these factors. In what sense can information, needed to maintain control loops for these three factors, be found on Earth, and how is this information being stored and transmitted? These sound like unfeasible questions from a neo-Darwinian perspective, since Gaia is not captured in a single genotype. To answer the questions, let us start with the observation that living systems are open systems, taking up energy from their environment in exchange of entropy. Persistent life has to sustain homeostatic control of the energy-entropy cycle. Thus, living systems have developed processes maintaining the internal stability of the organisms in the presence of environmental fluctuations. Homeostatic control is realized through the coordinated interaction of positive and negative feedback loops. In accordance with Kirchner's objection (Kirchner 2002), initially, stabilizing and destabilizing feedbacks are equally likely to evolve. Nevertheless, in an a posteriori analysis stabilizing feedbacks have a greater chance of being observed since destabilizing components will lead to obliteration of the systems carrying them (see Betts and Lenton 2008). Torday suggests that "*moving in a prograde direction, by thinking about the evolutionary adaptations in the context of the ever-changing environment, the causal relationships become clear*" (Torday 2015, p. 580). Homeostasis can be seen as one characteristic of evolutionary adaptation. It "*can act simultaneously as both a stabilizing agent and as the determining mechanisms for evolutionary change*" (Torday 2015, p. 575). A convincing example is given by the evolution of the lung, which shows how ontogeny and phylogeny are playing together in order to master major transitions resulting from ocean-salinity and land-transition (Lane and Martin 2012).

Initially, random interactions lead to feedback cycles which in some cases might have enhanced a system's capability of maintaining internal homeostasis, while in others deterioration was the consequence. Once being in place, feedback cycles will lead to changes of the environment through action of the system. These changes will then be reflected by adaptations of other systems, also altering environmental conditions. Progressing, fluctuations occur, which the initially considered feedback system will have to compensate. From this perspective, *homeostatic control* is a mechanism to reduce noise in perception of information from environmental sensors (cf. Woods and Wilson 2013). Under changing environmental conditions, systems utilizing mechanisms to adjust their homeostatic control will have a better chance to persist. Interestingly, the latter development seems to depend on predictability of noise. While predictable noise tends to be integrated within the system's function, unpredictable noise leads to emergence of mechanisms of noise exclusion (see Stern 1999).

Evolution through homeostatic control also provides an explanation for major transitions in evolution, in particular via 'coupling of forces'. Through combining control systems which might have evolved separately, new features can emerge and higher-order control levels can be reached. The importance of pairing as driving evolutionary change has been highlighted by Lynn Margulis (then L. Sagan) supporting the theory of endosymbiosis (Sagan 1967). Clear parallel developments can be seen in Torday's study of embryogenesis and physiology of the lung. "*Perhaps the reason why we go through the life cycle from zygote to zygote is to acquire epigenetically-heritable information from the environment and selectively integrate it into our genome. The 'filtering' mechanisms are those of ontogeny and phylogeny, providing both the short-term and long-term 'histories' of the organism as a means of monitoring the homeostatic relevance of the acquired mutations.*" (Torday 2015, p. 579).

Summarizing, Gaia is represented by the set of interactions of the communities of living organisms, the ecosystems they create and the modulation of environmental processes they generate, as well as the buffers they maintain. All of them comprise an infotype of interactions which develops and adapts. Such an *integrative view* of evolution (Noble 2017) has no privileged level of causation (Noble 2012). But as an observer, we perceive the set as a self-regulatory system leading to unexpected stability over eons.

Gaia as Optimizing for Interaction

In its strongest form, the hypothesis concludes that self-organization of Gaia is optimized toward maintaining conditions for life on the planet. As mentioned before, we are far from assuming the existence of any extrinsic principle providing the basis for the criterion according to which optimization might be driven. Thus, we have to explain, how optimization can occur in absence of an a priori given functional to be optimized. We will built up the argumentation by the following thought experiment. At the end, it will follow that optimization can be seen as an ex post property being generated by a shift in probability.

Let us begin with assuming that an agent has a finite set of options for interactions. At first, the probability for choosing any one out of this set is uniform, i.e., every interaction has the same probability of being chosen. Picking one, the agent experiences the outcome of the chosen action evaluating it by mapping it onto its internal state. For the sake of simplicity, assume the result of this evaluation being either positive or negative. Hereby, *positive* is understood in the sense of helping the agent to maintain its current state of organization. In the opposite case, the chosen interaction will lead to a decrease of the agent's potential for self-maintenance (*negative*). Recall that the constant flow of entropy in the universe forces the agent to invest energy in order to perform work being needed to maintain its state of low entropy.

On the long run, negative actions will lead to a decreasing likelihood of observing such an agent, due to its increasing need of energy to work against the current break of symmetry. Recall that every form of organization does need to invest in work to resist the tendency of increasing entropy. On an average basis, over time, agents having predominantly chosen negative interactions will vanish. In the other case, the probability of observing agents which (randomly) chose several positive interactions accumulating in a net increase of their capability for self-maintenance

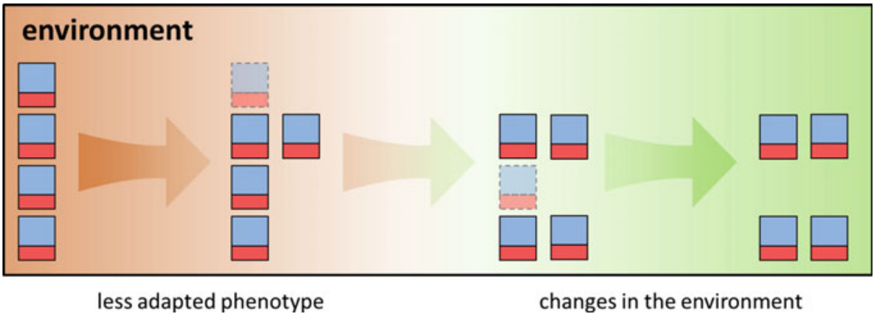

Fig. 3 Negative selection of less adapted phenotypes eventually leads to a distribution of phenotypes which retrospectively is interpreted as adaptation

will display a higher likelihood of being observed over longer time periods. Summarizing, starting with a population of agents being equal with respect to their ability for self-maintenance, successive interactions will shift the probability distribution toward agents exhibiting higher potential. This is what is called *sequential selection* (Fig. 3, Betts and Lenton 2008).

Our thought experiment rests on a critical assumption. In order to be able to accumulate an increase in the potential for self-maintenance, the agents need to have the capability to preserve the outcome of the previously chosen interaction. In a wider sense, we can call such a capability '*being able to learn from experience*'. If the population misses this capability, the results of positive and negative interactions would average out on the long run. Thus, we have found a first crucial ingredient for being able to observe organization being generated through interactions. The system must have the possibility to allow for *positive feedback*.

As mentioned before, the increasing need of energy to maintain the organizational state in the case of unfavorable interaction creates a *negative feedback* eventually leading to the situation where loss of energy exceeds energy uptake. Being less effective in using its resources, such configurations will have less likelihood of being observed over longer periods of time.

Having identified positive feedback, the question arises why evolution does not stop, i.e., converge to the ultimate, i.e., an optimal agent. The answer lies right at the start of our thought experiment. Recall that the seed for producing organization was a random selection from an initial set of options. Being crucial for the start of the process, these random seeds also play a crucial role in driving evolution. In practical terms, no system of storing and transforming information is perfect. There is always a chance of error. There is always a chance of random alteration of the 'chosen' action as there is a chance of error in the observation of its consequences. Both sources of error generate a source of novelty, producing new, not yet tested actions and not yet observed reactions. Taking into account that every action is reflected in a resulting change of the environment the latter also carries a source of random change. In consequence, the resulting source of variability leads to ever-changing conditions the agent has to cope with. As long as the agent manages to maintain its capability to react to such changes, i.e., as long as there also is an internal source of variability (e.g., plasticity), the agent will be able to persist. This property of an agent is termed *autopoiesis* by Maturana and Varela (see, e.g., Varela et al. 1974). Altogether, this creates what we observe as adaptation. Adaptation thus rephrases the observation that self-sustaining organization on the long run is more likely of being observed. In the same sense, selection means the long-term observation of change in probability distribution from a (theoretical) uniform distribution over the set of all possible interactions toward higher likelihood of interactions maintaining self-organization.

Ulanowicz' theory of autocatalysis (Ulanowicz 1998) leading to increasing ecosystem *ascendency* argues along these lines, postulating that positive interactions tend to create a self-supporting feedback. Can these arguments also be lifted to the global scale? Indeed, there is no theoretical reason for stopping us from doing so. In the same way as we have argued earlier that the integrative view of evolution relies on multilevel interactions, the biosphere–geosphere–atmosphere interactions driven by actions of living agents accumulate to Gaian interactions at the global scale. Modeling approaches have shown that Gaian self-organization, including principles of rein control, can indeed emerge from individual-based interaction (see Downing and Zvirinsky 1999). Thus, at least the *lucky version of Gaia* can be brought in line with evolution and natural selection. In their assessment of arguments, Free and Barton (2007) come to the conclusion that biotic feedback on the environment should tend to stabilize the interaction system leading to greater stabilization of the biosphere. This exactly matches our thought experiment. Hereby, stability must clearly not depend on the presence/absence of a particular species or a particular ecosystem. In this sense, we can think of **selection for stabilization** rather than selection of traits or particular genotypes.

Betts and Lenton, go further, arguing that it is the property of life itself which makes the trial-and-error strategy of evolution work. With regulatory and anti-regulatory feedback being likewise probable, the temporal boundedness of life allows anti-regulatory mechanisms to destroy themselves leading to a 'reset of the system' (cf. Betts and Lenton 2008). The difficulty of missing a population of examples to act on for selection is solved by considering advantages vs. disadvantages in a sequential order. Thus, in terms of sequential selection, Gaia is a valid perspective coming to terms with the principles of Darwin's theory. In this sense, Gaia's optimizing property results from the self-stabilizing feedback of the biotic–abiotic interaction systems. Clearly, Gaia is not competing with other comparable systems for limited resources. But as we have pointed out, competition for space and resources is not sufficient to be claimed as being the sole driving force of evolution. As has already been shown by the Baldwin effect (Simpson 1953), the outcome of natural selection also reflects choices individuals have taken. Popper (2013) has been led to formulate a concept of *active Darwinism*. In this context, the current version of the system Gaia as we observe it today is the one which evolved out of several other versions before. Obviously, none of the precursors 'survived' (e.g., the Hadean, the Archean, the Proterozoic, etc.), since the atmosphere–geosphere–biosphere interactions constantly forced Gaia to adapt (see, e.g., Wassenburg et al. 2016).

One point of criticism remains to be eliminated. While Downing and Zvirinsiky's guild model (1999) showed that self-regulation might emerge from individual-based natural selection, the actual nature of the interaction between life and its environment remains predefined in their model. This condition has been released by the Flask model (Williams and Lenton 2007). The model shows nutrient recycling and stable ranges of abiotic factors emerging from a microbial-interaction model without referring back to an explicit assumption on the nature of the life–environment interaction.

A purely interaction-based approach not even using interpretations such as nutrients or biotic/abiotic factors is given by the Tangled Nature Model (Christenssen et al. 2002). Arthur and Nicholson (2017) used a modified version of the Tangled Nature Model to allow for effects of the individuals on the physical environment of another individual. While the original version of the Tangled Nature Model only considered direct interaction among individuals, this generalization reflects both, direct and indirect effects of action by an individual on neighboring individuals. The essential features of the Tangled Nature Model remain, i.e., quasi-stable evolutionary states emerge, in which a network of species forms a *stable core* which eventually breaks down if a new species evolves, which destabilizes the existing core via *parasitic* or *symbiotic quakes*. Over time, it gets more and more difficult for a newly generated species to induce such quakes, leading to increasing, so-called *entropic barriers*. The alternation of periods determined by self-stabilizing interactions with shorter periods of destabilizing interactions confirms the pattern of sequential selection. Through the coevolution of the species with their environment, stability again increases as a consequence of increasing entropic barriers. The life–environment interaction in this model does not necessarily improve conditions for life, but makes them more probable (cf. Arthur and Nicholson 2017). Thus, at the end, it is the more likely we observe, leading us to accept Gaia even in its optimizing version.

Conclusions

The Gaia system being defined as the sum of all interactions of life with its environment on planet Earth thus forms a holobiont-like system with many processes of processing information in both, the biotic and the abiotic 'spheres'. These processes undoubtedly have led to conditions which support life on Earth through a network of positive and negative feedbacks. Self-stabilization of this network can indeed arise from action of individual agents. In this sense, Gaia has evolved over eons of time. The outcome of a sequential process of selection for stabilization has led to the interpretation of Gaia as optimizing conditions for life on Earth.

Gaia cannot be understood from one level of biological organization alone. It is a system of multilevel interaction. And we must keep in mind that no single organism, no single ecosystem and no single interaction can be considered as a must. The history of planet Earth has shown several quakes, both, parasitic and symbiotic. Superplume eruptions leading to changes in the atmosphere with mass extinctions being the consequence (Matyssek and Lüttge 2013) might be considered as example of the first, the development of vascular plants as an example for the second type. Either way, Lovelock has been misinterpreted early on as risking that based on his hypothesis men would resist from taking action to stop threatening the global ecosystem due to human perturbation (Doolittle 1981). But this conclusion does not hold. The optimizing view of Gaia is acceptable, indeed, but with stabilizing Gaia being more probable, it does not follow that the improbable is not possible. Gaia does not hold up as an excuse not to carefully study the sensible interactions of feedbacks stabilizing every complex system and base ones decisions to interact on the fact that every action in such a system leads to counter-action.

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