



Principles of Information Processing and Natural Learning in Biological Systems

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Abstract

The key assumption behind evolutionary epistemology is that animals are active learners or ‘knowers’. In the present study, I updated the concept of natural learning, developed by Henry Plotkin and John Odling-Smee, by expanding it from the animal-only territory to the biosphere-as-a-whole territory. In the new interpretation of natural learning the concept of biological information, guided by Peter Corning’s concept of “control information”, becomes the ‘glue’ holding the organism–environment interactions together. The control information guides biological systems, from bacteria to ecosystems, in the process of natural learning executed by the universal algorithm. This algorithm, summarized by the acronym IGPT (information-gain-process-translate) incorporates natural cognitive methods including sensing/perception, memory, communication, and decision-making. Finally, the biosphere becomes the distributed network of communicative interactions between biological systems termed the interactome. The concept of interactome is based on Gregory Bateson’s natural epistemology known as the “ecology of mind”. Mimicking Bateson’s approach, the interactome may also be designated “physiology of mind”—the principle behind regulating the biosphere homeostasis.

Keywords Evolution · Cognition · Information · Epistemology · Bacteria · Biosphere

1 Introduction

The universal capacity of organisms, from bacteria to animals, to actively sense their local environments and adjust to them intelligently, reflects the universal capacity to learn (Plotkin 1982; Bradie 1986; Gontier 2006; Watson et al. 2015; Watson and Szathmáry 2016; Bradie and Harms 2017). In the evolutionary sense, all organisms are active learners or ‘knowers’. The processes behind natural learning are at the heart of evolutionary epistemology. According to the branch of evolutionary epistemology known as EEM (evolutionary epistemology mechanisms): (1) organisms are knowledge systems, (2) evolution is the

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process of knowledge acquisition and (3) there are features shared by all forms of the evolutionary knowledge acquisition (Plotkin 1982).

Learning enables organisms to intelligently adjust to local environments and calls for further learning and further adjustments—organisms are engaged in an endless process of natural epistemology or biological intelligence (Slijepcevic 2018). Furthermore, the process of learning is not one sided. As organisms learn about their local environments and adjust to them, local environments become their learning partners (Lewontin 1978; Oka-sha 2005). Local environments, represented by diverse groups of organisms, learn about adjusting actions of their organismal partners and intelligently adjust to their partners' adjustments. This is the biosphere-wide cybernetic process that includes all species and all organisms (Bateson 1979). In this process, organisms of the same species communicate with each other through natural languages (Ben-Jacob 1998; Ben-Jacob et al. 2004) and different forms of semiosis (i.e. habits, codes), as they are at work in ecological systems and explored by contemporary biosemiotics (Kull et al. 2008). On the other hand, organisms from different species communicate through the process of cross-kingdom communication based on biosemiotics (McFall-Ngai et al. 2013; Jarosz et al. 2014).

Given that the nature of communicative interactions is cybernetic or informational, biological information becomes an essential ingredient in the process of natural learning. The role of information in natural learning featured prominently in writings of EEM proponents (e.g. Plotkin 1982; Plotkin and Odling-Smee 1982). However, very little can be found in the EEM literature about the actual concept of biological information and how this concept integrates into the process of natural learning.

The aim of the present paper is to integrate the original EEM's understanding of natural learning by Plotkin (1982) and Plotkin and Odling-Smee (1982) with cybernetic, information theory and systems theory views, using bacteria as a model system. I start by presenting the EEM's take on the concept of information and the role of information in natural learning (Sect. 2). I then outline the concept of biological information that combines information theory and its more recent derivatives appropriate for biological systems, in particular, "control information" of Corning (2007) (Sect. 3) and information processing by bacteria (Ben-Jacob 1998, 2009; Ben-Jacob et al. 2004) (Sect. 4). In the final part of the paper (Sect. 5), I present a synthetic outlook of information processing and natural learning in biological systems.

2 Information and Natural Learning According to Plotkin and Odling-Smee as Representatives of Early EEM

This section is an overview of how Plotkin (1982) and Plotkin and Odling-Smee (1982) understood the concept of information and natural learning. In brief, their view deviated from the mainstream neo-Darwinian ideas. In neo-Darwinian terms, organisms behave as biological machines controlled by genes (Dawkins 1976; Futuyma 1998). Organisms with random genetic changes survive and propagate in those environments whose properties are compatible with the properties of biological machines brought about by random genetic changes. This scenario is almost mechanistic: organisms fit pre-existing environments. Furthermore, environments are unresponsive and largely immune to influences by organisms.

By contrast, organisms internalize environmental features in the process of natural learning. Given the organic constitution of all environments inhabited by animals (e.g. the atmosphere is the product of the living world etc.) environments are their learning

partners because they consist of organisms of different kinds (microorganisms, fungi, plants) (Lewontin 1978; Okasha 2005; Holland 2006). Thus, natural learning is interpreted as a form of adaptation—the process of knowledge acquisition about the environment and subsequent adjustment to the environment guided by the new knowledge. In this process genetic determinism is not the only factor influencing adaptations. An important role is played by the concept of information. Adaptations are interpreted as processes of information gain, subsequent storage of information, and translation of information into phenotypic traits (Plotkin 1982). Interestingly, the concepts of information and knowledge are often taken to mean the same:

The terms information and knowledge are used interchangeably. They refer to coherent and conserved patterns of order in the environment and the corresponding organization of the phenotype whose end-directedness relates to those particular patterns of environmental order. (Plotkin 1982, 6)

However, equating the concepts of information and knowledge may be imprecise for two reasons. First, the entire field of cybernetics, concerned with the information theory, is ignored. Second, there is no attempt to make a distinction, if any, between the concept of information in physicalist sense (original information theory) and biological sense (organisms may be different from machines in terms of information processing).

The imprecise treatment of information is somewhat softened in a detailed outline of the concept of natural learning. Here is the definition of natural learning in the style of evolutionary epistemology (Plotkin and Odling-Smee 1982), which contains parallels to modern niche construction and ecological inheritance theories (e.g. Laland et al. 2014):

Learning is acquisition by an individual animal of information about some aspects of that animal's world, the storage of that information, and its integration into pre-existing behaviour patterns such that it is potentially capable of changing the behaviour of that animal in the future. Like any other form of information or knowledge gain, learning is a dynamic, dialectical process involving a changing world and a changing learner. (Plotkin and Odling-Smee 1982, 443)

The processes behind natural learning are further elaborated and explained using the framework (Plotkin and Odling-Smee 1982) briefly outlined below.

1. Living systems are knowledge systems. This is the key principle of evolutionary epistemology attributed to writings of earlier evolutionary epistemologists.
2. The world, as perceived by organisms, is constantly changing. An important source of change are organisms themselves “whose teleonomic goal is to bring about some change in the world”.¹
3. “Change is the engine that drives the evolution and the formation of adaptation”. The concept of “change” is probably closest the framework comes to explaining the concept of information in functional or biological sense (see next section).
4. Learning is a process that enables organisms to obtain knowledge about the changing world (their immediate environment). There are four levels of learning. Level 1 is genetic (allele frequencies and reproducing populations). Level 2 is epigenetic (“the flexible translation of a genotype into a phenotype”). Level 3 is physiological (organ or organ-

¹ All citations in parts 1–7 (all pieces of text in inverted commas) are from Plotkin and Odling-Smee (1982, 450–451).

- system specific: e.g. immune system or brain). Level 4 represents cultural processes (learned information transmission among a group of learners in a non-genetic fashion). This is similar to the concept of evolution in four dimensions (E4D) by Jablonka and Lamb (2007).
5. There is no sharp distinction between individual organisms and social groups in terms of their properties as biological systems. This means that a group of organisms may acquire a form of intentional behaviour resembling that of an organism (superorganism).
 6. Learning is hierarchical and always proceeds in direction from Level 1 towards higher levels.
 7. All processes of natural learning share a universal algorithm. Thus, the explanatory power of evolutionary epistemology rests with this universal algorithm for natural learning.

The intention behind the above framework was to use it as the basis for a universal biological theory (Plotkin 1982). There was an attempt to describe the universal algorithm for natural learning. It consisted of integrating four levels of learning into a wide-ranging framework (theory) in which diversity of learning forms in animals was confronted and controlled by their environments, thus creating the unity of learning as the product of the organism–environment interactions (Plotkin and Odling-Smee 1982).

Judging the above framework from a >35-year distance, it certainly remains plausible provided that deep updates are carried out to bring the framework in line with numerous research avenues initiated and developed since then. For example, the assumption that natural learning is restricted to animals makes the theory untenable from the perspective of universality.² Organisms that dominate the planetary biomass are microorganisms and plants (Whitman et al. 1998; Mancuso and Viola 2015). They must be incorporated into the framework because there is an emerging large set of data supporting the notion of microbial and plant capacities to learn (e.g. Lyon 2015, 2017; Trewavas 2017) (see also Sect. 4). In addition, independent concepts of natural learning have been articulated by a number of authors (Bateson 2000; Lyon 2015, 2017; Watson et al. 2015; Watson and Szathmáry 2016). Finally, a relatively superficial treatment of the concept of information, and the field of cybernetics and systems theory, makes the framework seriously outdated. The aim of the next section is to focus on the concept of biological information with a view to generating a more comprehensive and up to date framework for natural learning from the perspective of evolutionary epistemology.

² Strictly speaking, it is not true that evolutionary epistemology (EE) is based on the assumption that natural learning is applicable only to animals. For example, Campbell (1974), in his ten stages of knowledge argued that the first stage is the “non-mnemonic problem solving” used by protists (“paramecium, stentor”). However, Campbell wrongly interpreted protists as animals. Furthermore, Campbell’s “non-mnemonic problem solving” stage appears outdated in light of recent advances in bacterial and protist cognition which recognize mnemonic problem solving in these organisms. For details of bacterial mnemonic problem solving (memory) and communication (stage 7 in Campbell’s scheme) see Sect. 4 of this article. On the whole, early EE writings focused overwhelmingly on animal cognition. Only rarely EE researchers ventured outside the kingdom Animalia. When this happened, as in the case of protists, the explanatory narrative suffered from taxonomic inaccuracies.

3 Information Theory

The birth of information theory in 1948 was one of the landmark events in modern science. Two key figures of cybernetics, or communication theory, were Shannon (1948) and Wiener (1948). They viewed the concept of information as an engineering problem. According to Corning (2007) the mechanistic attitude of early cybernetics—information as a purely engineering issue—resulted in a failure to understand information in the functional sense. The functional side of information relates to how living systems interpret and utilize information.

The only person in the early cybernetic circles who attempted to explain information in the functional sense was Gregory Bateson (Harries-Jones 2017). His famous dictum that information is “the difference that makes a difference” (Bateson 1979, 1991, 2000) still resonates well with natural system theorists. In spite of a reasonable explanatory power of Bateson’s ideas, they lacked the mathematical rigour present in writings of Shannon and Wiener. More recently, Corning (2007) provided a useful scientific and mathematical grounding of information in the functional sense that may overcome shortcomings of Shannon’s and Wiener’s concepts. I will next briefly outline the development of cybernetic ideas from Shannon and Wiener to Bateson and Corning.

The fundamental problem of communication, according to Shannon, is how to transmit messages (information) from a sender to a receiver through a communication channel and avoid corruption by noise. Even though most messages have meanings, semantic aspects of communication are irrelevant to the engineering side of things. From the perspective of evolutionary epistemology, this is a significant problem because the content of messages (semantic side of biological information) is essential to organisms as active learners. Thus, Shannon interpreted information as the capacity to reduce statistical uncertainty (noise). If the information is measured in binary bits, the informational uncertainty may be expressed in a number of bits required to eliminate uncertainty. Mathematician John von Neuman suggested to Shannon that he should use the thermodynamic term “entropy” to express statistical uncertainty.

However, Corning (2007) argued that physicalist interpretations of statistical equations for entropy by Boltzman and Gibbs in the nineteenth century, and Schrödinger in his legendary book *What is life?*, although extremely useful to physicists, engineers, chemists and molecular biologists, started to blur a distinction between entropy in the thermodynamic sense (as governed by energy) and how physical order/disorder is created in the world. Entropy refers to the availability of energy to carry out work. However, information in the functional or biological sense may have nothing to do with work potential (Bateson 2000; Corning 2007; Harries-Jones 2017). Information is “the capacity to control the capacity to do work” (Corning 2007, 303, original in italics; see also below).³

Wiener’s interpretation of information did not exactly match that of Shannon. Similarly to Schrödinger, Wiener argued that information represents negative entropy or negentropy. Wiener also introduced biological systems in his elaboration of cybernetic ideas. He interpreted capacities of biological systems and their components, such as enzymes and cells, as metastable Maxwell’s Demons capable of reducing entropy. He viewed entropy in biological systems as a form of entropic anomaly—an anomaly of

³ Other authors who attempted to address the concept of biological information include Pattee (2001) and Deacon (2012). However, their works (semantic closure by Pattee; the notion of constraint in the context of biological information by Deacon) are beyond the scope of this study.

living systems relative to physical ones. For Bateson and Corning, Wiener's explanation addressed only part of the problem. To make up for the missing part, Bateson introduced the term "bioentropy". A detailed explanation of bioentropy can be found in Harries-Jones (2010). In brief, "bioentropy focuses on the ability of organisms to create pattern from noise in a systemic informational context" (Harries-Jones 2010, 2373–2374).

In his mathematical analysis Wiener did not differ significantly from Shannon. Instead of formalizing the functional understanding of information, he was more concerned with measuring amount of information. Thus, in the early days of cybernetics, the balance was tipped in favour of engineering and physics—precise measurements of information (syntax) rather than focus on the informational content of messages (semantics). The consequence was that the concept of information was reified—from the engineering and physicalist points of view, it is legitimate to regard information in material terms. In other words, information is an independent entity that can be measured. This remains the mainstream view in spite of some serious objections. For example, Rapoport thought it is misleading to view information as a concrete physical entity "that can be poured into an empty vessel like liquid" (cited in Corning 2007, 300). Similarly, Heinz von Foerster argued that information is a purely relational concept that can be actualized only when it is related to cognitive systems (cited in Corning 2007). Thus, information does not have an independent existence. This is in line with Bateson's arguments according to which information has no dimensions. "The difference that makes a difference"—biological information as understood by Bateson—must have a receiver at the end interested in the information content which will guide the receiver to adjust behaviour accordingly (Bateson 1979).

The apparent lack of a proper scientific grounding of information in functional or biological sense prompted Corning (2007) to propose a new concept he termed "Control Information" or I_c . Here is the definition of control information:

The capacity (know how) to control the acquisition, disposition and utilization of matter/energy in purposive (teleonomic) processes. (Corning 2007, 302)

He also presented a simple mathematical formalism that takes account of all relevant parameters including: energy, entropy, Shannon information termed I_s etc. In brief, Corning argued, similarly to Bateson, that information is not a thing or mechanism. It can only be defined as a relationship between an organism (living cybernetic system) and its environment. The environment contains a variety of latent or potential control information designated I_p (p for potential). The informational potential of the environment is only actualized when purposeful cybernetic systems (organisms) make use of it. Thus, in the functional sense information is entirely context-dependent and user-specific. For example, pheromones emitted by ants cannot be registered by human senses.

Furthermore, control information causes purposeful work to be done by biological systems. The key point here is that control information allows the separation of biology from mechanics of physics and engineering. Control information as a biological concept is "the capacity to control the capacity to do work". Bateson (1991) similarly argued that "the difference that makes a difference"—the equivalent of control information—"does not provide the energy, it only triggers the expenditure of energy". Thus, the difference leads to "transform of difference". In contrast to physical equilibrium systems, organisms are non-equilibrium open systems that require constant structural adjustments in order to survive. Control information or "transform of difference" thus becomes an ordering principle—a form of bioentropy in which ecological waste (entropy) created by one species becomes an essential metabolite for survival of another (Harries-Jones 2010, 2017).

Corning provided a number of examples to illustrate control information in practice and also to put it in a wider context. For example, he attempted to explain the relationship between control information on one side and feedback, semiotics and biosemiotics, second-order cybernetics and sociological theory of communication on the other. Instead of presenting his illustrations, I will next explore the interpretation of information theory in the context of microbiology that yields a remarkable similarity to Corning's concept of control information.

4 Natural Information Processing in Bacteria

A wide range of experimental studies, accumulated over the last several decades, indicate that the origin of natural learning can be traced to bacteria,⁴ first living organisms (e.g. Lyon 2015, 2017). This is particularly important from the perspective of evolutionary epistemology—the concept of natural learning is not restricted to animals. Therefore, it is appropriate to use bacteria to demonstrate Corning's concept of control information as a component of natural learning. The main proponent of natural learning in bacteria, or “natural cognition” as he called it, was Eshel Ben-Jacob. In a series of papers he presented principles of natural intelligence and natural information processing in bacteria and described how bacterial colonies create a collective “mind” by exchanging information between individual members. Below is the summary of his thinking based on several key papers (Ben-Jacob 1998, 2009; Ben-Jacob et al. 2004).

The first thing to note is that bacteria are not solitary organisms. Overwhelming evidence suggests that bacteria, through social cooperation, become multicellular organisms (superorganisms) consisting of 10^9 – 10^{12} individual members. Bacterial colonies show cell differentiation, a division of tasks and, in some cases, the existence of modules resembling reproductive organs. However, for the sake of demonstration let us first explore information processing in the single bacterial cell using the well-known phenomenon of bacterial chemotaxis, before exploring information processing by bacterial colonies.

Each individual bacterial cell is a complex system capable of exploring thermodynamic imbalances in the environment for its own survival. From the perspective of thermodynamics, a bacterial cell can be viewed as a three-component system. One component of the system is its “engine”, the function of which is to explore thermodynamic imbalances in the environment to carry out work (Fig. 1a).

The second component of the system is the “machine” (Fig. 1a). Its function is to use the energy obtained by the engine to maintain the structure of the cell (synthesis of organic components required for the maintenance and survival of the bacterial body). By doing this, the machine acts against disorder within the cell or the natural course of entropy increase. The third component of the system is the information-processing module, which coordinates and synchronizes actions of the engine and the machine (Fig. 1a). The information-processing module consists of the cell sensing system integrated with the cell genome and the cell molecular network that transmit signals from the sensing system to the genome.

⁴ Whatever applies to bacteria, in terms of natural learning, it is also applicable to archaea, the second domain of life. The reason I singled out bacteria in this article is that almost all studies of natural learning in prokaryotes rely on bacteria.

Chemotaxis is usually defined as the cell movement that occurs in response to gradients in concentration of a chemical agent present in the environment. Chemotaxis can be positive (attraction) or negative (repulsion). In attractive chemotactic movement, a bacterium swims in a slow tumbling fashion and measures concentration of a relevant chemical along the way. The process of measurement involves the sensing of chemical gradients, the recollection of previous measurements (memory), and information processing (genome plus molecular network) to detect potential differences between measurements. When the analysis is completed, in a remarkable feat of natural learning, a bacterium makes a decision whether to continue slow tumbling movements (no difference between measurements) or change the swimming style into long and fast movements towards higher concentration (a significant difference in measurements).

We can now put control information in the context of chemotaxis. The information processing module of the bacterium serves to sense the environment and extract latent information from it. The latent information is Corning's I_p —gradients of concentrations of various chemicals in the local environment inhabited by the bacterium (Fig. 1a). Thus, the concentration of chemicals in the environment, as a form of latent information (I_p), does not have independent existence—it is simply a part of the physical properties of the environment. Furthermore, the concentration of a chemical in the environment is not a thing or

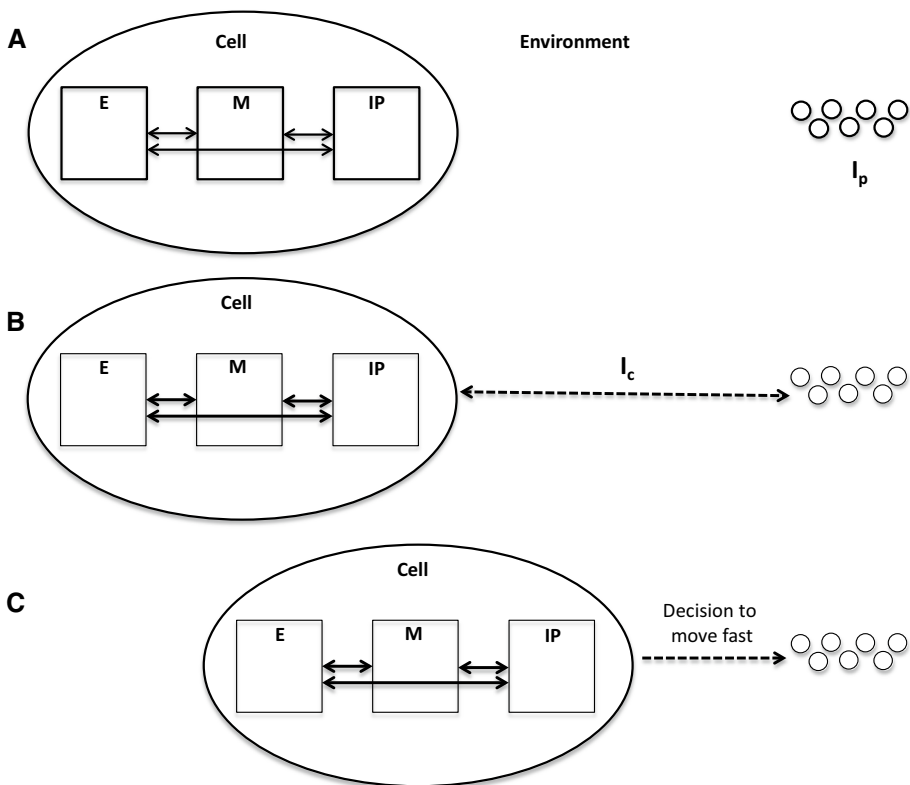


Fig. 1 Information-processing in bacterial chemotaxis. **a** A bacterial cell contains engine (E), machine (M) and information-processing module (IP). I_p is latent information in the environment. **b** When the latent information is sensed it becomes control information or I_c . **c** Decision is made based on natural computation (learning) prompted by I_c . For details see the text

mechanism. It represents a non-homogeneous distribution of sugar in the watery solution of the bacterial swimming environment. Only when the relationship between a particular cybernetic system, in this case the bacterium, and its environment is established via the information-processing module, I_p becomes actualized and turns into I_c (Fig. 1b). This, in turn, prompts the bacterial cell to undergo the analytical episode of natural computation after which a proper decision (natural learning) is made with regard to “[t]he capacity (know how) to control acquisition, disposition and utilization of matter/energy in a purposive (teleonomic) process” (Corning 2007, 302) (Fig. 1c).

In the bacterial act of natural information processing, there is neither a formal sender, nor a formal communication channel, nor even a message, like in the case of Shannon’s understanding of information. But, there must always be a user, in this case the bacterium. Furthermore, the episode of bacterial chemotaxis is in line with Bateson’s definition of information: “The difference that makes a difference”. In this case, the difference is the actual difference in the concentration of a chemical between the past measurements performed by the bacterial natural computation and the current measurement. This difference leads to “transform of difference”—a decision of the bacterium to change the swimming style if the concentration of sugar is high enough (Fig. 1c). This new swimming style leads to “expenditure of energy” as the capacity to adjust to its local environment.

Let us now consider how bacterial colonies behave in the process of natural information processing. There is one crucial difference between the colony and a single cell—the emergence of communication between individual cells. Individual cells communicate through various forms of chemotactic signalling and quorum sensing (bacterial natural language). Thus, for individual cells, the colony becomes their natural environment. As a result, individual cells begin to respond to the colony itself—the information flows from the colony to the individual. This results in the emergence of the colonial identity with different modules for distributed information processing (Fig. 2a).

The result is that the combined action of the internally stored information (e.g. the genome of each bacterium) and the information extracted from the environment by the society of bacteria that form the colony, turns the colony into a brain-like entity capable of performing collective acts of natural learning. The colony acquires a form of memory that consists of the information stored in individual genomes and the information collectively extracted from the environment and memorized by the structure of the colony (natural mind). Genetic memory per se is not sufficient for adaptation. Thus, the genetically stored information in individual bacteria serves only to initiate more complex collective information processing faculties that in turn generate new knowledge required to adapt to new conditions in the environment. It can be argued that chemotactic signalling at the level of the colony represents a form of social intelligence consisting of the exchange of messages loaded with meaning (semantics and pragmatics) resulting in the self-organization of the colony as a product of current and past environmental conditions. The mechanisms behind all biological functions discussed in this paragraph are explained by Ben-Jacob (2009).

In the context of the colony, which now represents an integrated society of 10^9 – 10^{12} bacteria, the concepts of I_c and I_p become multitudes. For the colony, the territory of I_p becomes the society of individual bacteria (internal I_p) but also the external environment (source of external I_p) (Fig. 2a). The “collective mind” of the colony transforms two sources of I_p (internal and external) into I_c (Fig. 2b). This initiates the process of contextual natural computation that eventually results in the collective decision-making (Fig. 2c). For example, when the colony encounters a dry and hard surface, individual bacteria begin excreting a lubricating layer of fluid to create the swimming medium for other bacteria. Thus, the learning capacity of the colony is reflected in the ability to perform collective

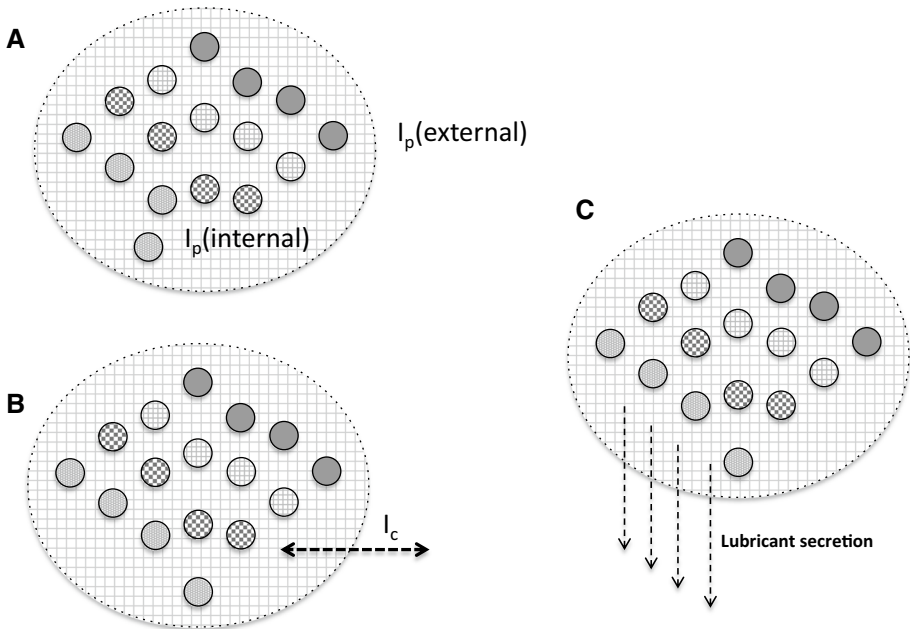


Fig. 2 Information-processing by a bacterial colony. **a** The population of bacterial cells (small circles) unified by the colonial identity (an ellipsoid shape containing all cells). Different patterns in individual bacterial cells indicate division of tasks within the colony. Sources of I_p are the colony and the external environment. **b** Collective sensing of the environment by the colony turns I_p into I_c . **c** (for details see the text). The collective decision is made by the colony based on natural computation (learning) prompted by I_c . Mechanisms behind colonial identity, division of tasks, collective sensing, natural “mind” and natural computation are described in Ben-Jacob (2009)

sensing of the local environment and make a decision as to how to appropriately adjust to it.

Taken together, the above two examples of information processing and natural learning (Figs. 1, 2) illustrate the concept of Corning’s control information in the simplest living organisms—bacteria. Similarly to Corning, Ben-Jacob argued that “[b]y latent information we refer to data embedded in the environment that, once processed cognitively, initiates change in the organism’s function or behavior” (Ben-Jacob 2009, 79). It is thus clear that Corning’s components of control information, I_p and I_c , have their equivalents in Ben-Jacob’s interpretation of bacterial cognition. Ben-Jacob’s “latent information” is equivalent to Corning’s I_p ; Ben-Jacob’s “cognitive processing” is equivalent to Corning’s I_c .

Thus, the principles of control information may be applicable to all living systems, from single cells to societies and ecosystems (see below). Corning’s control information is a form of ‘glue’ that holds together organism–environment interactions. Control information, thus, forms the basis for the universal algorithm for natural learning. In line with this possibility, the emerging field of biosemiotics views information exchange as an indispensable feature of life (e.g. Kull et al. 2008). Importantly, semiosis cannot exist without interpretability. The biosemiotic concept of “interpretability” is strikingly similar to the concept of “actualization” in control information (see above).

5 Synthesis

In the final part of the paper, I will present a synthetic overview of information processing and natural learning in biological systems by updating the old framework of Plotkin and Odling-Smee (1982) with the concept of control information (Corning 2007). The overview will address the principles of natural learning, categories of biological systems involved in it, the methodology behind natural learning and the emergence of the biosphere as the communicative network of biological systems.

5.1 Principles of Natural Learning

Early proponents of EEM were concerned exclusively with the cognitive structure of animal intelligence. However, animals constitute a minority of biological forms. If the biosphere is viewed as the biomass comprised by living systems that make it up, then plants and microbes dominate (Whitman et al. 1998; Mancuso and Viola 2015). Also, in terms of species number bacteria dominate the biosphere (Larsen et al. 2017). Numerous publications in the last couple of decades show that plants (reviewed in Trewavas 2017) and bacteria (Ben-Jacob 1998, 2009; Ben-Jacob et al. 2004; Lyon 2015, 2017) possess natural learning capacities. Thus, evolution may represent a continuous learning process (Watson and Szathmary 2016) which appears to follow algorithmic principles (Watson et al. 2015). In this process organisms are not passive evolutionary objects shaped by the interaction between the genes (internal structures) and the environment (external conditions), but instead, they act as natural agents actively involved in creating conditions for own evolution (Walsh 2018).

In line with the above arguments, I suggest that the new definition of natural learning should take account of all organisms and serve to extend the original and narrow framework of Plotkin and Odling-Smee (1982). Thus, *in the process of natural learning biological systems acquire information about their local environments, process that information by own internal structures, and translate processed information into phenotypic traits*. The universal algorithm for natural learning can be described by the acronym IGPT (information-gain-process-translation). IGPT represents a multi-stage process of natural learning derived from an older concept by Plotkin (1982) and Plotkin and Odling-Smee (1982), and now enriched with the concept of control information (I_p and I_c) (Corning 2007). Examples of IGPT in action are given in Figs. 1 and 2. The IGPT algorithm can be expressed as:

$$I_p \rightarrow I_c \rightarrow IG \rightarrow IP \rightarrow IT$$

where *IG* (Information Gain) represents information gathering about the environment by the biological system using its own sensory-motor apparatus; *IP* represents processing that information by the internal structure of the biological system (natural computation); and *IT* represents translation of the processes behind *IG* and *IP* into structural changes of the biological system. Thus, the environmental features represented by $I_p \rightarrow I_c$ are internalized by biological systems in a multi-stage IGPT process. I_p and I_c represent (1) a form of ‘glue’ that holds together organism–environment interactions and (2) a guiding principle behind natural learning (Figs. 1, 2).

5.2 Categories of Biological Systems Involved in Natural Learning

Natural learning is an essential feature of biological systems. One way of categorizing biological systems, relative to their capacities to learn, may be SET (serial endosymbiosis theory) (Sagan 1967; Margulis 1998, 2004). The key principle behind SET is “individuality by incorporation”—“all organisms large enough for us to see are composed of once-independent microbes teamed up to become larger wholes” (Margulis 1998, 43–44). I propose seven categories of biological systems based on how the most fundamental units of natural learning, bacteria, are distributed throughout the biosphere as building blocks for more complex systems for natural learning.

All seven categories of biological systems involved in natural learning are summarised in Fig. 3, together with their evolutionary timeline and some other parameters that will be addressed in the next section.

The fundamental unit of natural learning is a single cell prokaryote—a bacterium. Therefore, I term the most fundamental unit of natural learning a “Simple Cell” or SC (Fig. 3). (However, it must be acknowledged that biological systems below SC, such as viruses, may be capable of natural learning (Villareal 2015)). All other systems for natural learning are derived from SC by two biological processes: multiplication and merger. The process of multiplication produces populations of SCs (e.g. bacterial colony) unified into single functioning systems by the process of communication (bacterial

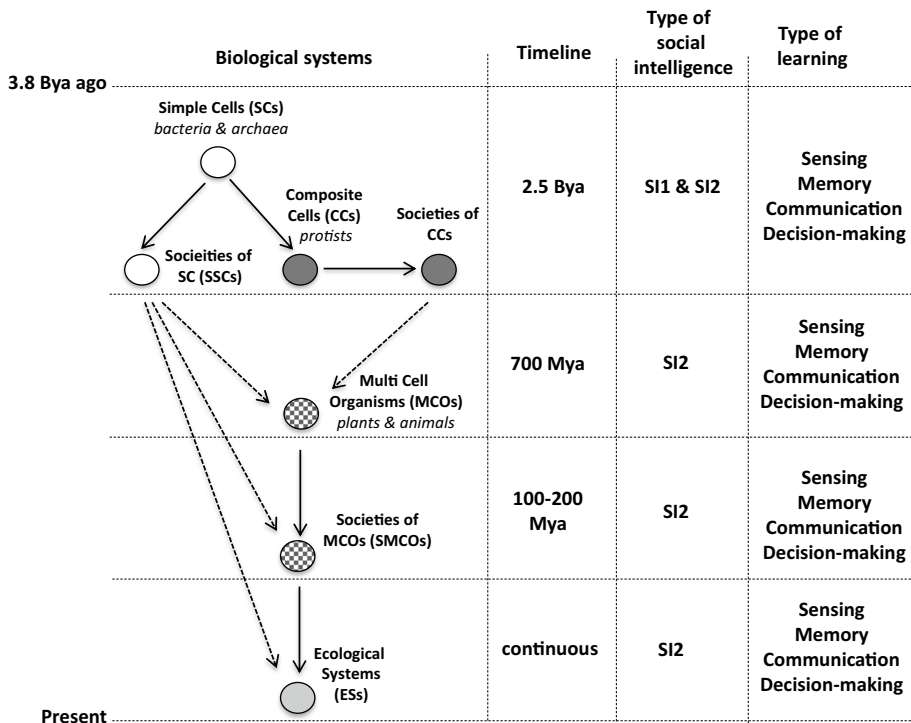


Fig. 3 Categories of biological systems involved in natural learning based on SET. For abbreviations and explanation see the text. Types of social intelligence (SI) are SI1 (communication between conspecifics) and SI2 (cross-kingdom communication)

language) (Ben-Jacob et al. 2004). I term populations of SCs “Societies of SCs” (SSCs) (Fig. 3).

On the other hand physical mergers between two or more SCs generates a more complex system I term CC (Composite Cell) (Fig. 3). CC is equivalent to various types of the eukaryotic cell as elaborated by SET. All single cell protists, single cell fungi and algae belong to this category. Their populations, integrated into more complex systems by the communication process, lead to the next category: “Societies of CCs” or SCCs (Fig. 3).

The above four categories, SCs, SSCs, CCs and SCCs, dominated the biosphere for 3.2 billion years (since the origin of life 3.8 Bya to roughly 600–700 Mya) (Fig. 3). The transition to true multicellularity required a hierarchical shift in which loosely organized SCCs sacrificed their individuality in deference to that of a tightly organized corporate body (a cell-based superorganism). Thus, the next category of biological systems involved in natural learning is the Multi-cell Organism (MCO) displaying cell specialization and division of labor, and developmental processes—all plants and animals (Fig. 3). They emerged in the evolution 600–700 Mya. MCOs cannot function without accompanying microbiota. MCOs are meta-organisms, also called holobionts, consisting of two sets of cells: tightly integrated eukaryotic cells forming the corporate body and populations of loosely integrated microbial cells present inside and outside the corporate body (Margulis 1993; Zilber-Rosenberg and Rosenberg 2008).

Populations of MCOs exhibit varying degrees of sociality leading to the next category, “Societies of MCOs” (SCMOs) (Fig. 3). The highest form of sociality is known as eusociality. It is recognized by the emergence of tightly organized collectives of MCOs called “superorganisms” in the case of social insects such as ants, termites and bees (Crespi and Yanega 1995; Wilson and Hölldobler 2005). Human beings are also eusocial (Wilson 2012).

The final category of biological systems involved in natural learning is termed ESs or “Ecological Systems” (Fig. 3). These include biomes such as mature forests in which all previous six categories of biological systems are integrated. For example, plants have the capacity to control nitrogen-fixing bacteria and through this control, they strategically influence entire biomes with the final outcome being the resilience of their environment (Sheffer et al. 2015). Some animal-built and human-built structures can be loosely classified into this category including the ecological collectives involved in the practice of agriculture. For example, ant agriculture involves plants, bacteria and fungi (Wilson and Hölldobler 2005; Wilson 2012).

In summary, seven categories of biological systems involved in natural learning are prokaryotes and their societies (SCs and SSCs), protists, fungi, algae and their societies (CCs and SCCs), plants and animals and their societies (MCOs and SMCOS) and biomes integrating all lower systems (ESs) (Fig. 3).

5.3 The Methodology of Natural Learning

To complete this general outline of natural learning it is important to identify the cognitive methodology behind it. In other words, which cognitive methods are used universally by all categories of biological systems in their quest for new knowledge? Before exploring the methodology of natural learning it is important to precisely define biological systems as users of cognition in the evolutionary process.

Biological systems are purposive teleonomic systems or natural agents (Walsh 2018) that become cognitive agents in the context of evolutionary epistemology. According to

Ernst Mayr, “[a] teleonomic process or behavior is one that owes its directedness to the operation of a program”. He defined a program “as coded or pre-arranged information that controls a process (or behaviour) leading it toward a given end”. Genetic programs that control organisms are “closed programs”, meaning they are entirely deterministic. However, according to Mayr, organisms also possess “open programs” that allow them to acquire additional information through “learning, conditioning, or through other experiences” (all Mayr 1974, 99).

Some biologists, including Lewontin (1978), argued against the concept of the biological program as a form of a deterministic Darwinian machine. Instead, organismal forms are under-determined by the action of the genes and environment because organisms are active natural agents involved in creating conditions for evolution of biological forms. The notion of organisms as natural or cognitive agents is similar to Robert Rosen’s theory of anticipatory systems (Rosen 1985). Anticipatory systems contain internal predictive models of themselves and of their environments. According to Rosen, every organism, from a bacterium to an elephant, must contain information about self, about species and about the environment (an internal model), encoded into the organization of the living system. This modelling relation between organisms and their internal structures is primarily epistemological. Thus, the behaviour of Rosen’s anticipatory systems at any present instant involves aspects of past, present and future, because the internal model serves to pull the future into the present resulting in the natural act of anticipation.

Assuming that biological systems are natural agents (Walsh 2018) or anticipatory systems (Rosen 1985), there are four universal cognitive methods used by all of them in the process of natural learning⁵:

- *Sensing/perception* The capacity to collect information about the environment.
- *Memory* The capacity to store collected information into system’s own internal structure. The genetic storage (DNA as a storage medium) is only one layer of biological memory. The other layer of biological memory is the entire system’s structure.
- *Communication* Capacity to communicate with conspecifics (natural languages and biosemiotics), and non-conspecifics (cross-kingdom communication as a form of biosemiotics).
- *Decision-making* The final product of all cognitive methods and anticipation leading to the action of the system relative to its environment. If the action is retained by the ecological filter of natural selection it becomes epistemologically successful leading to its storage into the systems’ structure. If not, it becomes an epistemological error, which is eliminated by natural selection.

5.4 Biosphere as the Communicative Network

The final task is to put all categories of biological systems in the context of the biosphere. Heinz von Foerster argued that information is a purely relational concept that can be actualized only when it is related to cognitive systems. If we accept his dictum and assume that the biosphere is the supersystem that accommodates all seven categories of biological systems and their environments (Fig. 3), the biosphere becomes the network of communicative interactions between them (Fig. 4). In this network the IGPT algorithm guided by

⁵ Behaviour, as a cognitive method, is replaced by anticipation; see definition above.

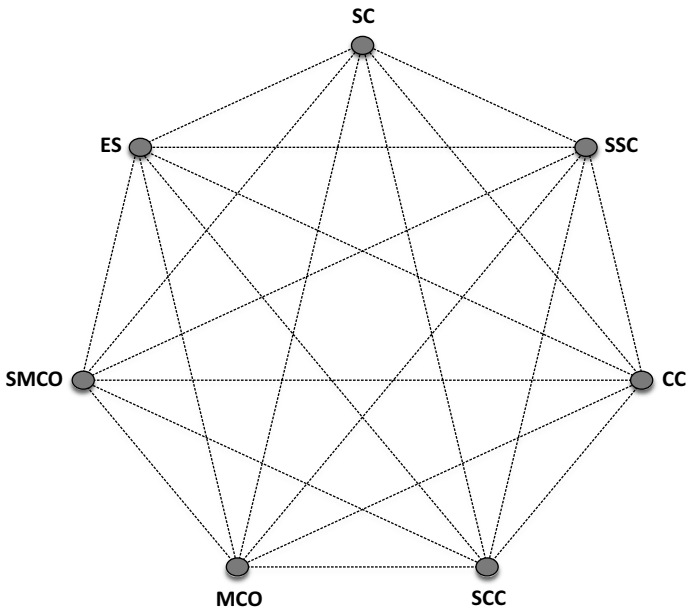


Fig. 4 The interactome—the biosphere-wide distributed network of communicative interactions (for abbreviations see Sect. 5.2). Dashed lines represent the ‘glue’ holding organism–environment interactions together. For details see Sect. 5.4. The interactome should be viewed as a distributed rather than centralized system. For example, Fig. 4 may represent an ecosystem such as a mature forest (Ulanowicz 2002). The interactome represents a holarchy of all ecosystems that comprise the biosphere

I_c and I_p (Sect. 5.1) and the universal cognitive methods (Sect. 5.3) become the means by which biological systems (Sect. 5.2) internalize their environments (Fig. 4).

Thus, concepts of organisms and environments are relative concepts. From the dawn of life, when first bacteria internalized a small inorganic part of the planet Earth, there is no hard distinction between organisms and their environments. Organisms create their environments (Laland et al. 2014). A suitable analogy for the relativity of the organism–environment complex is the holon concept of Arthur Koestler. Organisms are two-face entities like the Roman god Janus—part internal structures (organisms in true sense) and part external structures projected by their internal models (environments) (Fig. 4).⁶

The totality of all communicative interactions in the biosphere may be termed the “interactome”⁷—the biosphere-wide distributed network of biological information that holds organism–environment interactions together (Fig. 4).

The biosphere, as the supersystem accommodating all biological systems and their environments, possesses the capacity to self-regulate (homeostasis) (Lovelock and Margulis 1974). The concept of the “emergent homeostasis” (Turner 2004) provides some

⁶ This is equivalent to Rosen’s modelling relations between organisms and their internal models (see above). A similar but older idea of Umwelt (surrounding world) was elaborated by Jakob von Uexküll. Charles Sanders Peirce entertained a similar idea. A modern term is “niche construction” (Laland et al. 2014).

⁷ My term “interactome” is different from the same term used in biochemistry that refers to the totality of protein interactions in the cell.

support for the notion that interactome may contribute to the biosphere homeostasis. The idea behind the emergent homeostasis is that genetically diverse organisms pursue common physiological interests resulting in the local or distributed homeostasis. Thus, the idea of interactome serves to add a different dimension to the emergent homeostasis: the informational or biosemiotic dimension. For example, there is evidence that the mutualistic symbiosis between leafcutter ants (genera *Atta* and *Acromyrmex*) and fungi (genera *Leucoagaricus* and *Leucocoprinus*) (ant agriculture) may involve some form of chemical communication or biosemiosis, which is informational in nature (Vasse et al. 2017).

The best example of interactome in action is a climax forest containing all seven elements shown in Fig. 4. Ulanowicz (2002) introduced the concepts of “mutual information” and “infodynamics” into ecology. These concepts represent a measure of the interconnectedness of the energy flow in the ecosystem. The ecosystem is most interconnected (information-rich) in its mature stage (e.g. climax forest in a steady state). The concept of interactome is compatible with, and it may help the analytics of ecological “infodynamics” (Ulanowicz 2002). Furthermore, the biosphere-scale homeostasis may also be viewed as the synergy between ecosystems that make it up. It is important to stress that the biosphere should not be viewed as a single cognitive system, but rather a super-system, or the synergy (holarchy) of all systems that make it up—interactome is a distributed rather than centralized regulator of homeostasis.

If interactome indeed contributes to biosphere homeostasis, this possibility would open some interesting questions. Is the biosphere a form of anticipatory system? Does the biosphere possess a form of memory? These questions are legitimate, but probably unanswerable at present.

However, some bold speculations may help to define the research direction that could enable us, at the minimum, to ask appropriate questions. In this regard it is worth remembering Bateson's (1979) concept of mind. He proposed six criteria of mind including (1) that mind is an aggregate of interacting parts and (2) that the interaction between parts is triggered by difference (see Sect. 3), which is “a non-substantial phenomenon not located in space or time” (Bateson 1979, 92); in other words, biological information. Bateson persuasively argued that human subjectivity and consciousness are limited as forms of natural epistemology.

In line with Bateson's thinking, the interactome may also be called “physiology of mind”. The term is derived from Bateson's concept “ecology of mind”. Bateson's “ecology of mind” was a form of natural epistemology driven by bio-cybernetics (Harries-Jones 2017). The term “physiology of mind” refers to the *milieu intérieur* concept of Claude Bernard, as the capacity of a given biological system to regulate its own stability or homeostasis, applied to the biosphere as a whole (Turner 2017).

6 Concluding Remarks

In this paper I updated the 35-year-old framework for natural learning, which served as the basis of EEM. The update consisted of integrating the concept of control information and expanding the territory of evolutionary epistemology from the animal-only territory to the biosphere-as-a-whole territory based on recent advances in bacterial and plant cognition. I proposed a new definition of natural learning and attributed natural learning to seven types of biological systems involved in natural learning. Finally, I outlined the universal algorithm for natural learning and suggested that the biosphere contains a multitude

of communicative interactions, or the interactome, between biological systems that make it up, guided by the universal algorithm. Finally, I identified a similarity between Bateson's concept of "ecology of mind" and the concept of interactome. The similarity is contained within the new term "physiology of mind", as the ability of interactome to regulate the biosphere homeostasis.

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References

- Bateson, G. (1979). *Mind and nature: A necessary unity*. New York: Bantam Books.
- Bateson, G. (1991). *A sacred unity: Further steps to an ecology of mind*. New York: HarperCollins.
- Bateson, G. (2000). *Steps to an ecology of mind*. Chicago: University of Chicago Press.
- Ben-Jacob, E. (1998). Bacterial wisdom, Gödel's theorem and creative genomic webs. *Physica A*, 248(1–2), 57–76.
- Ben-Jacob, E. (2009). Learning from bacteria about natural information processing. *Annals of the New York Academy of Sciences*, 1178(1), 78–90.
- Ben-Jacob, E., Becker, I., Shapira, Y., & Levine, H. (2004). Bacterial linguistic communication and social intelligence. *Trends in Microbiology*, 12(8), 366–372.
- Bradie, M. (1986). Assessing evolutionary epistemology. *Biology and Philosophy*, 1(4), 401–459.
- Bradie, M., & Harms, W. (2017). Evolutionary epistemology. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2017 Edition). <https://plato.stanford.edu/archives/spr2017/entries/epist-emology-evolutionary/>.
- Campbell, D. T. (1974). Evolutionary epistemology. In P. A. Schlipp (Ed.), *The philosophy of Karl Popper* (pp. 413–463). LaSalle, IL: Open Court.
- Corning, P. (2007). Control information theory: The "missing link" in the science of cybernetics. *Systems Research and Behavioral Science*, 24(3), 297–311.
- Crespi, B. J., & Yanega, D. (1995). The definition of eusociality. *Behavioral Ecology*, 6(1), 109–115.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Deacon, T. (2012). *Incomplete nature: How mind emerged from matter*. New York: W. W. Norton & Company.
- Futuyma, D. J. (1998). *Evolutionary biology* (3rd ed.). Sunderland, MA: Sinauer Associates.
- Gontier, N. (2006). Introduction to evolutionary epistemology, language and culture. In N. Gontier, et al. (Eds.), *Evolutionary epistemology, language and culture: A non-adaptationist systems theoretical approach* (pp. 1–29). Berlin: Springer.
- Harries-Jones, P. (2010). Bioentropy, aesthetics and meta-dualism: The transdisciplinary ecology of gregory bateson. *Entropy*, 12(12), 2359–2385.
- Harries-Jones, P. (2017). "Steps" to agency: Gregory Bateson, perception and biosemiotics. *Biosemiotics*, 10(2), 211–228.
- Holland, J. H. (2006). Studying complex adaptive systems. *Journal of Systems Science and Complexity*, 19(1), 1–8.
- Jablonka, E., & Lamb, M. J. (2007). Précis of evolution in four dimensions. *Behavioral and Brain Sciences*, 30(4), 353–365.
- Jarosz, D. F., Brown, J. C. S., Walker, G. A., Datta, M. S., Ung, W. L., Lancaster, A. K., et al. (2014). Cross-kingdom chemical communication drives a heritable, mutually beneficial prion-based transformation of metabolism. *Cell*, 158(5), 1083–1093.
- Kull, K., Emmeche, C., & Favareau, D. (2008). Biosemiotic questions. *Biosemiotics*, 1(1), 41–55.
- Laland, K., Uller, T., Feldman, M., Sterelny, K., Müller, G. B., et al. (2014). Does evolutionary theory need a rethink? Yes: Urgently. *Nature*, 514(7521), 161–164.

- Larsen, B. B., Miller, C. E., Rhodes, M. K., & Wiens, J. J. (2017). Inordinate fondness multiplied and redistributed: The number of species on Earth and the new pie of life. *The Quarterly Review of Biology*, 92(3), 229–265.
- Lewontin, R. C. (1978). Adaptation. *Scientific American*, 239(3), 212–230.
- Lovelock, J. E., & Margulis, L. (1974). Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis. *Tellus*, 26(1–2), 2–10.
- Lyon, P. (2015). The cognitive cell: Bacterial behavior reconsidered. *Frontiers in Microbiology*, 6, Article 264. <https://doi.org/10.3389/fmicb.2015.00264>.
- Lyon, P. (2017). Environmental complexity, adaptability and bacterial cognition: Godfrey-Smith's hypothesis under the microscope. *Biology and Philosophy*, 32(3), 443–465.
- Mancuso, S., & Viola, A. (2015). *Brilliant green*. Washington: Island Press.
- Margulis, L. (1993). *Symbiosis in cell evolution: Microbial communities in the Archean and Proterozoic eons* (2nd ed.). New York: W.H. Freeman and Co.
- Margulis, L. (1998). *The symbiotic planet: A new look at evolution*. London: Phoenix.
- Margulis, L. (2004). Serial endosymbiotic theory (SET) and composite individuality: Transition from bacterial to eukaryotic genomes. *Microbiology Today*, 31(4), 172–174.
- Mayr, E. (1974). Teleological and teleonomic: A new analysis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Methodological and historical essays in the natural and social sciences. Part of Boston Studies in the Philosophy of Science* (Vol. 14, pp. 91–117). Berlin: Springer.
- McFall-Ngai, M., Hadfield, M. G., Bosch, T. C., Carey, H. V., Domazet-Lošo, T., et al. (2013). Animals in a bacterial world, a new imperative for the life sciences. *Proceedings of the National Academy of Sciences*, 110(9), 3229–3236.
- Okasha, S. (2005). Multilevel selection and major transitions in evolution. *Philosophy of Science*, 72(5), 1013–1025.
- Pattee, H. H. (2001). The physics of symbols: Bridging the epistemic cut. *BioSystems*, 60(1–3), 5–21.
- Plotkin, H. C. (1982). Evolutionary epistemology and evolutionary theory. In H. C. Plotkin (Ed.), *Learning, development and culture: Essays in evolutionary epistemology* (pp. 3–16). Chichester: Wiley.
- Plotkin, H. C., & Odling-Smee, F. J. (1982). Learning in the context of a hierarchy of knowledge gaining processes. In H. C. Plotkin (Ed.), *Learning, development and culture: Essays in evolutionary epistemology* (pp. 443–471). Chichester: Wiley.
- Rosen, R. (1985). *Anticipatory systems: Philosophical, mathematical and methodological foundations*. Oxford: Pergamon Press.
- Sagan, L. (1967). On the origin of mitosing cell. *Journal of Theoretical Biology*, 14(3), 225–274.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27(3&4), 379–423, 623–656.
- Sheffer, E., Batterman, S. A., Levin, S. A., & Hedin, L. O. (2015). Biome-scale nitrogen fixation strategies selected by climatic constraints on nitrogen cycle. *Nature Plants*, 1, Article 15182.
- Slijepcevic, P. (2018). Evolutionary epistemology: Reviewing and reviving with new data the research programme for distributed biological intelligence. *Biosystems*, 163, 23–35.
- Trewavas, A. (2017). The foundations of plant intelligence. *Interface Focus*, 7(3). <https://doi.org/10.1098/rsfs.2016.0098>.
- Turner, J. S. (2004). Gaia, extended organisms, and emergent homeostasis. In S. H. Schneider, J. R. Miller, E. Crist, & P. J. Boston (Eds.), *Scientists debate Gaia. The next century* (pp. 58–70). Cambridge, MA: The MIT Press.
- Turner, J. S. (2017). *Purpose and desire: What makes something "alive" and why modern Darwinism has failed to explain it*. New York: Harper Collins.
- Ulanowicz, R. E. (2002). Information theory in ecology. *Computers & Chemistry*, 25(4), 393–399.
- Vasse, M., Voglmayr, H., Mayer, V., Gueidan, C., Nepel, M., Moreno, L., et al. (2017). A phylogenetic perspective on the association between ants (Hymenoptera: Formicidae) and black yeasts (Ascomycota: Chaetothyriales). *Proceedings of the Royal Society B: Biological Sciences*, 284(1850). <https://doi.org/10.1098/rspb.2016.2519>.
- Villareal, L. P. (2015). Force for ancient and recent life: Viral and stem-loop RNA consortia promote life. *Annals of the New York Academy of Sciences*, 1341(1), 25–34.
- Walsh, D. M. (2018). Objectivity and agency: Towards a methodological vitalism. In D. J. Nicholson & J. Dupre (Eds.), *Everything flows: Towards a processual philosophy of biology* (pp. 167–185). Oxford: Oxford University Press.
- Watson, R. A., Mills, R., Buckley, C. L., Kouvaris, K., Jackson, A., et al. (2015). Evolutionary connectionism: Algorithmic principles underlying the evolution of biological organisation in evo-devo, evo-eco and evolutionary transitions. *Evolutionary Biology*, 43(4), 553–581. <https://doi.org/10.1007/s11692-015-9358-z>.

- Watson, R. A., & Szathmáry, E. (2016). How can evolution learn? *Trends in Ecology & Evolution*, *31*(2), 147–157.
- Whitman, W. B., Coleman, D. C., & Wiebe, W. J. (1998). Prokaryotes: Unseen majority. *Proceedings of the National Academy of Sciences*, *95*(12), 6578–6583.
- Wiener, N. (1948). *Cybernetics: Or control and communication in the animal and the machine*. Cambridge, MA: MIT Press.
- Wilson, E. O. (2012). *The social conquest of earth*. Chennai: Liveright.
- Wilson, E. O., & Hölldobler, B. (2005). Eusociality: Origin and consequences. *Proceedings of the National Academy of Sciences*, *102*(38), 13367–13371.
- Zilber-Rosenberg, I., & Rosenberg, E. (2008). Role of microorganisms in the evolution of animals and plants: The hologenome theory of evolution. *FEMS Microbiology Reviews*, *32*(5), 723–735.

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