Shaping Theoretic Foundations of Holobiont-Like Systems

Wolfgang zu Castell, Frank Fleischmann, Tina Heger, and Rainer Matyssek

Contents

1 The Holobiont Sensu Stricto 220
2 Defining a "Holobiont-Like" System 223
3 Theoretical Foundation 226
4 Arguing for an Extension Beyond the Holobiont Sensu Stricto 231
5 Hypotheses for Experimental Analysis 236
6 Conclusion 239
References 240

Abstract Acknowledging the fact that organisms never evolve in isolation, Zilber-Rosenberg and Rosenberg emphasized the concept of the holobiont, comprising a host organism together with all of its associated microorganisms. Considering the holobiont as being a unit of selection, the hologenome theory of evolution then leads to incorporate Lamarckian aspects into the cycle of adaptation and selection. Nevertheless, the concept of the holobiont carries an implicit temporal dependency. Similar contingencies can be identified for other ideas, e.g., the notion of a supraorganism. Building on ideas from computational thermodynamics and information theory leads to the concept of a holobiont-like system. This notion aims at

---

W. zu Castell (✉)
Scientific Computing Research Unit, Helmholtz Zentrum München, German Research Center for Environmental Health GmbH, Ingolstädter Landstraße 1, 85764 Neuherberg, Germany

Department of Mathematics, Technische Universität München, München, Germany
e-mail: castell@helmholtz-muenchen.de

F. Fleischmann
Section Pathology of Woody Plants, Center of Life and Food Sciences Weihenstephan, Technische Universität München, München, Germany

T. Heger
Restoration Ecology, Center of Life and Food Sciences Weihenstephan, Technische Universität München, München, Germany

R. Matyssek
Technische Universität München, Hans-Carl-von-Carlowitz-Platz, Wissenschaftszentrum Weihenstephan, 85354 Freising, Germany

U. Lüttge et al. (eds.), *Progress in Botany*, Progress in Botany 77,
DOI 10.1007/978-3-319-25688-7_7

capturing the essentials of a system of interacting biological agents, being driven by an evolutionary algorithm. The concept can be applied upon several scales, allowing to consider the holobiont sensu stricto as well as full ecosystems. It nicely frames within the metaphor of the adaptive cycle and, thus, leads to deeper insights into sustainability of biological systems.

1 The Holobiont Sensu Stricto

Natural organisms never evolve in isolation. Every individual is part of a rich network of interacting organisms determining the course of the individual's development. In particular, higher plants and higher animals are accompanied by an enormous variety of microorganisms which altogether form a coenobitic (i.e., symbiotic[1] sensu stricto) association. In the diversity of living organisms, we observe results from adaptation to a dynamically changing environment. The process realizing adaptation in natural systems is evolution taken in an algorithmic sense (see Dennett 1996). Evolution as a process is anchored in three crucial components: variation, heredity, and differential reproduction (Mayr 2002). Thus, evolution inherently operates on multiple scales ranging between the level of genes, being the carrier of heritable information, and that of populations of phenotypes unfolding the information. Although it is widely accepted that natural selection is intrinsic to evolution, there is quite some debate on what is the effective biological level of selection. Growing insights into epigenetic mechanisms reveal a deeper interrelationship between genes as one mode of coding information combined with environmental specifications (Goldberg et al. 2007).

Acknowledging the observation that selection extends beyond the level of the individual within coenobitic associations, Zilber-Rosenberg and Rosenberg (2008) formulated the hologenome theory of evolution. The central concept within this theory is the holobiont, originally defined as close association, temporal or permanent, of members of different species of organisms (Margulis 1993). Through the later use of the term by Rosenberg et al. (2007), a holobiont today is to be understood as the functional entity consisting of a "host organism" with all its associated symbiotic microorganisms (cf. Rosenberg et al. 2007). Hereby, Zilber-Rosenberg and Rosenberg deliberately advance beyond the conventional concept of coevolution. It is the genetic potential of the full association (see Fig. 1) which is subject to selection, and this potential changes throughout the life cycle of the host, i.e., via amplification or acquisition of microorganisms. Note that the classical definition of a holobiont focuses on host-microbe interactions, thereby neglecting

---

[1] We use the word "symbiotic" in the original sense of de Bary, i.e., in a neutral sense. Thus, symbiotic relations include mutualistic, commensalistic, and parasitic relationships.

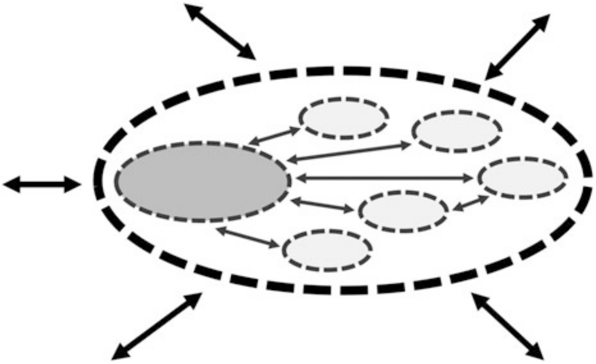


Fig. 1 The holobiont sensu stricto being defined as a host organism (*larger ellipse*) and all its associated microorganisms (*smaller ellipses*) together with all their interactions. Note that the boundary defining the system is contingent on the perspective of the observer

other associations, which also shape the host organism, particularly when considering plants.

According to Zilber-Rosenberg and Rosenberg (2008; Rosenberg et al. 2010), the hologenome theory is based on four general principles:

1. All animals and plants establish symbiotic (sensu coenobitic; see above) relationships with microorganisms.
2. Associated microorganisms are transmitted across developmental stages of the holobiont.
3. The association between host and microorganisms as an entity determines the fitness of the holobiont within its environment.
4. The hologenome is subject to variation through changes in the host and/or its microbial associates.

Interestingly, the last principle carries some Lamarckian aspects since variation in the holobiont can occur via additional mechanisms which operate beyond the level of the gene. These are amplification of existing microorganisms within the holobiont and acquisition of novel strains from the environment as well as abandonment of strains through horizontal drift (Rosenberg et al. 2009) as a consequence of information gained (i.e., “experience learnt”) from environmental stress, just to name some examples.

Considering the three basic components of mutation, heredity, and selection, the four stated principles are well rooted in evolution theory, addressing the question of the representative unit of selection. Starting with neo-Darwinism, the gene-centered perspective on selection (Dobzhansky 1937; Mayr 1942; Dawkins 1976) aimed at explaining evolutionary adaptation solely on the level of the gene, since this is the level at which heritable information is transmitted to the next generation through the gametes. Somewhat more precise, adaptation is considered as a process changing the frequency of genetic alleles—more general chromosomal DNA—within a population. Opposing the gene-centric view, Wilson and Sober (1994) introduced a theory of multilevel selection, embracing the debate on group selection (Wynne-Edwards 1962, 1986; Wilson and Wilson 2008) versus kin selection (Fisher 1930;

Haldane 1955; Hamilton 1963, 1964). Both approaches aim at clarifying the puzzle of explaining cooperative behavior of social insects via Darwinian selection. Whereas kin selection is based on the concept of inclusive fitness, expanding the notion of fitness beyond the individual by taking fitness of related individuals into account, critics argue that the phenomenon could likewise be explained by accepting the point of view that natural selection reinforces traits that are favorable for a group of organisms in general. In some sense, the hologenome theory follows the gene-centric paradigm, considering the hologenome as the sum of inheritable information of the holobiont. Since associations among individuals, however, incorporate associations among individuals of the same kind, the concept of group selection is included to some extent.

Although being compelling, the hologenome concept raises questions. One of them results from the conceptual challenge regarding heredity. For example, the life cycles of eukaryotic and prokaryotic associates typically vary, proceeding at different timescales. Hence, what are the generations being addressed in the second principle stated above? The obvious answer, i.e., generations being defined by the host sensu Zilber-Rosenberg and Rosenberg, reinforces a bias already immanent in the definition of the holobiont. The so-called host, i.e., the dominant eukaryont, would be singled out from the association. This is an arbitrary choice made by the observer studying a particular type of complex system. Considering plants and associated mycorrhizal fungi, there is no logical necessity to rule out one over the other. Changing perspective in host-mycorrhiza interaction supports our view. While originally mycorrhiza has been considered to mainly unlock soil resources for the plant, there is growing evidence that the plant plays a major role in shaping the mycorrhizal community (Rennenberg et al. 2009; Pena et al. 2010).

Second, there is another inherent dependency on timescales. What exactly is considered as being an association—and what is “one generation” of an association? Do we enclose short-term events, e.g., infections through bacterial pathogens? We probably should, because if exemplifying the human immune system, being strongly path dependent, i.e., contingent on a unidirectional cause-effect chain, its development results from all contacts with microbial components (Eberl 2010).

Thus, we argue that the host-centric view within the common definition of the holobiont (sensu Zilber-Rosenberg and Rosenberg) is a choice made by the observer, resulting from the paradigm of observer dependence. The latter is an inherent property of any complex system (see Kay 2008) and, thus, conceptually unavoidable. Second, widening the concept of heredity beyond transmission of information across discrete generations (typically defined by meiotic cycles of individuals, maybe synchronized within populations), in particular through the incorporation of Lamarckian aspects (Rosenberg et al. 2009; Gilbert 2011; see above), there is no need to restrict the concept of the holobiont to the level of organisms. Such a claim gains further support by the argument that the notion of an organism is an intrinsically human concept, in particular when considering microorganisms (Ruse 1989; Rosselló-Mora and Amann 2001; Pepper and Herron 2008).

Similarly, other concepts of multi-organisms also carry intrinsic scale dependencies. A supraorganism[2] is defined as "a collection of single creatures that together possess the functional organization implicit in the formal definition of organism" (Wilson and Sober 1989, p. 339). The definition implicitly refers back to the scale of the organ level. Although there might be no consistent definition of an organ (see Ruse 1989), the commonly accepted concept of an organ implies some kind of local boundary. Thus, individuals comprising an organ-like component of a supraorganism are intrinsically assumed to be within spatial vicinity.

Both objections, i.e., the host-centric view and the gene-centric concept of heredity, thus are particular instances of scale dependency, scale being taken here in a spatiotemporal sense. Contrasting with both approaches, i.e., holobiont and supraorganism, we aim for a concept which is scale invariant, both in the temporal and spatial sense. It is through implicit scale dependency that difficulties arise which lead to controversy and conflicting debate. In order to derive such a scale-invariant concept, we employ ideas from information theory and computational thermodynamics. Neither aspect is new in ecology (see, e.g., Jørgensen and Svirezhev 2004). Through employing abstraction, we are able to extract essential characteristics of biological processes. Abstraction creates the grounds to us for recognizing relevant characteristics at various scales and in different scenarios, i.e., irrespective of scale-related process specificities.

After presenting a formal definition of our concept, we will introduce the major biological definitions needed from the perspective of computational thermodynamics in the following section. We will then proceed with arguing in favor of the suitability of the proposed concept. Finally, we will provide some hypotheses and show how they can be deduced from the theoretical foundations laid out in the preceding sections.

2 Defining a "Holobiont-Like" System

We propose the concept of a **holobiont-like system**, an evolving system of interacting agents. Agents are understood to be biological units (e.g., organs, individual organisms, or populations) that interact with each other and their (local) environments (e.g., soil structure, chemical neighborhood, other organisms within close vicinity). It is assumed that no single agent or group has a controlling function or "full view" of the system. It is through the interactions that the association of agents becomes observable as a system (see Fig. 2). Although, from the point of view of the observer it might seem like one associate or group

---

[2] Note that etymologically, the Latin word "supra" means "higher" in the sense of ordination, whereas "super" implies a spatial order. Thus, in contrast to the mainly used notion of "superorganism," we prefer to stay with the notion of a "supraorganism."

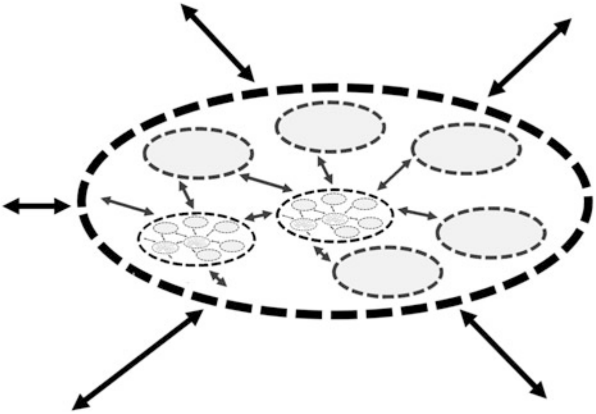


Fig. 2 The holobiont-like system as being defined as a system of interacting biological agents (*ellipses*) adapting through generic evolution. In contrast to the holobiont sensu stricto, no agent is singled out. The concept naturally allows being applied recursively, leading to a nested set of systems

is controlling the system, we consider systems lacking the prescribed role of a central conductor.

The second characteristic property of a holobiont-like system is its ability to adapt within a dynamic environment. We will consider evolution in a rather abstract, algorithmic sense. Hereby, adaptation is understood to be the generic property of a system to internally capture information (i.e., experience) and adopt actions based on the derived state of information. Therefore, adaptation is to be understood as the generic property of the system to react upon changes in its environment.[3] Generally speaking, adaptation of a system “may be at the individual level through learning, or it may be at the population level through differential survival and reproduction of the more successful individuals” (Axelrod 1997, p. 4). The kind of adaptation we are interested in is adaptation through evolution in a generic sense. In order to be able to consider evolution in a generic way on multiple scales, we employ the concept of information, being a measure for the internal entropy of the system. Information can be coded in various ways, e.g., within genes, structures, community composition, more generally any kind of pool, or in form of epigenetic modifications, and can be passed on through varying time resolution. **Generic evolution** then is the process of adaptation resulting from the interaction of three subprocesses:

1. **Generic mutation**: a process leading to transmissible random changes in the informational representation of a system, e.g., mutation or changes in the abundances of agents.
2. **Generic heredity**: the process of transmission of information over time, e.g., in genomes of agents through reproduction, in the abundances of agents, or structure.

---

[3] Therefore, “natural adaptation” in the genetic context of the theory of evolution is one example of adaptation of a system.

3. **Generic selection**: an autonomous process that uses the outcomes of local interaction to enhance a subset of components.

Clearly, this definition needs some explanation. The process of evolution of a holobiont-like system can be built on a reformulation of Lewontin's conception of the principles underlying evolution (Lewontin 1970):

1. Interacting agents in a population have different morphologies, physiologies, and behaviors, thus comprising phenotypic variation.
2. Different phenotypes have different rates of survival and different mechanisms to persist in variable and dynamic environments, leading to differential fitness.
3. The correlation between the predecessors and successors of individual agents in the contribution of each to future generations of the system, i.e., fitness (expressed through the proportion of the number of offspring within a population), is heritable.

Note that information can be transmitted through various channels, e.g., spatiotemporal fluxes of matter or energy between pools, signaling, reproduction, and organismic diversity. Within a dissipative system, any type of pattern, i.e., information, has a certain likelihood to emerge from pure noise (i.e., transmission without net outcome of informational structure). Hence, some patterns persist longer than what can be expected by randomness. Such persistence above random average can be observed. Heredity describes the process which leads to persistence of certain patterns. In the interesting case of genetic heredity, information stored in the gene code of a genome can persist beyond the life cycle of the individual and thus pass on to future generations. Thus, on the level of genes, information persists, both within the gene code as well as in epigenetic modifications, while on the level of the individual information, i.e., structure, resolves into entropy.

In a similar way, we are forced to carefully rethink our concept of fitness. A posteriori, we are able to observe persistence of a certain clustering of genes longer than what would be expected from random fluctuations. In biological terms, we are talking about the persistence of genetic traits over generations. Fitness is then often measured in terms of success of reproduction, i.e., success in preserving certain clusters of genes and hereby overcoming the spatiotemporal constraints of the individual. Similarly, fitness in asexual reproduction might be quantified via the amount of propagules being produced. Fitness thus turns into a characteristic of a group of genes. Dealing with groups of agents, with every agent carrying its own genetic information, we do not have such an obvious gene versus individual hierarchy anymore. Therefore, we cannot exploit the time discretization given through the life span of an individual in order to define fitness, e.g., in terms of frequency of a certain trait within generations. Fitness thus becomes the integration of system properties that allow the consortium to maintain its internal structure beyond the random fluctuation of entropy.

The core of Darwin's idea of evolution through natural selection is thus conserved in the proposed conceptual framework. Variation among the agents constituting a holobiont-like system gives rise to variation in the degree of interaction among the individuals. At the same time, variation of agents allows for the initiation of differing phenotypes with differential reproductive success. Hence, also another fundamental component of Darwin's idea is fulfilled. Both components give rise to diversity in network interaction, both internally and externally with the environment (Holland 1995; Levin 1998). As such, the potential for internal variability gives rise to the plasticity of the system in its ability to adapt to dynamically changing environmental conditions (Levin 1998).

Conversely, external variations—via selection—shape the ability of the associate network to persist longer than possible by pure chance. From the point of view of information, the system builds up regularities based on its "experience," i.e., preceding history in the flow of information. The selectively derived regularities then impact the future performance of the system, which feeds back into the system as the environment continues to pass through dynamic changes (see, e.g., Gell-Mann 1994). It is the persistence of the system over a certain period of time which gives the system its specific "character." Note that this again involves the observer. Recognizing a system as functional entity relies on our modes of perception which are highly scale dependent and intrinsic to human perception capacities, both in spatial and temporal terms (Kay 2008). Survival of a system then means that the functional entity we are observing manages to persist both spatially and temporally above the level of noise (with also the latter being defined by the perception of the observer).

Finally, adaptation within a persistent functional entity needs mechanisms to capture information within the system (Gell-Mann 1994). In principle, this can be achieved directly via some recognition process of factorial alterations, e.g., learning, or indirectly through reinforcement by repeated action. The classical concept of heredity refers to persistence of an organism as a type, not as an individual. This means, the captured information can be passed on, overcoming the temporal limits of the individual while guaranteeing system persistence on the level of its conceptual type, e.g., the species. It is the interplay of prevalent long-term patterns on various levels of biological organizations which the debate on the level of selection is all about. As such, there is further accordance with driving questions of ecological theory, although the latter are typically considered at short-term timescales.

3 Theoretical Foundation

Let us start with discussing some fundamental concepts of biological sciences within the framework of computational thermodynamics. Living systems clearly persist in a state of lower entropy compared to their environment. Thus, according to the second law of thermodynamics, such systems cannot exist without a flow of energy, which allows the system to establish and maintain its lowered internal entropy. The continuous flow of energy on Earth allows for the existence of structures, which consume energy, while augmenting the entropy of the universe. Schrödinger coined the notion of "feeding through negentropy" (Schrödinger

1944). Therefore, living systems locally alter the flow of energy within their environment and thus create an impact on other living systems in their vicinity. As such, any form of interaction influences the local energy landscape. Organisms persisting within this continuous energy flow are phenotypes expressing features which optimize some implicitly given function[4] of the local energy flow (Bar-Yam 1997). In this way, living organisms create what is called the *coupled fitness landscape*[5] (Kauffman and Johnsen 1991).

The potential of an organism to survive in a dynamically changing environment depends on its ability to utilize the local nonequilibrium conditions within its environment for maintaining its state of low entropy. Evolution on Earth has resulted in a variety of ways that make energy available to organisms, so that the informational content of the system may be sustained, e.g., upon fixation of energy from solar energy by means of photosynthesis. Following Bar-Yam (1997), living organisms reflect a local optimization of their usage of the variation in energy flow. It is not the absolute amount of free energy being used which determines the level of adaptation of the system, but the capability of the system to deal with dynamic variation of the local energy flow. Thus, fitness can be interpreted as the cost function resulting from the various optimizations performed by the organisms within a given proximity in the space-time continuum. Note that through this interpretation, fitness is a local concept. It cannot be decoupled from the spatio-temporal vicinity of the acting system.

Such a physical interpretation of fitness also decouples natural selection from the mechanism of organismic replication and, in particular, from any quantitative description of reproduction. Conserved information is one particular instance of order. Thus, conserving information means maintaining the state of low entropy. Therefore, fitness also depends on the ability of a system to adaptively persist through mechanisms of conserving information beyond the reproductive mechanisms, e.g., through ecologically successful niching. It is in this latter sense that heredity matters across all levels of biological organization.

With the given interpretation in mind, evolution can be understood as being a computational process (see Dennett 1996). Evolution is “a theory of information transfer, describing the process of transmitting messages containing biological information, with mutation a phenomenon of information change and a source of variation” (Zenil et al. 2012, p. 2174).

As mentioned above, persistence is ultimately linked to structural and temporal patterns constituting the entities we observe as being persistent. Patterns emerging from interaction of agents can have several sources. For example, nonlinear

---

[4] “Function” to be understood in the (abstract) mathematical/physical sense not as biological function. To be precise, the term “function of a variable” is used for a mapping of the variable into some space, without the need to further specify the concrete nature of the mapping.

[5] The landscape is “coupled” since it results from the superposition of the local fitness landscapes of each individual organism.

dynamics commonly leads to structures of self-similarity.[6] Similarly, patterns of coherence emerge from autonomous interaction in complex systems. However, as being local, patterns are contingent on a certain temporal and spatial scale. Thus, using the notion of a pattern implies observer dependency.

Following the ideas of generative science (Epstein 1999), we can take on a modeling perspective providing analytical tools to study nature. Therefore, in order to provide a formal definition of the systems we aim to analyze, we employ concepts from computational theory. A multi-agent system (MAS) is defined as the collection of a set of autonomous agents which interact through a set of rules, which is defined for each agent independently, thus implementing a local view for each agent (Wooldridge 2002). An agent itself is a persistent[7] object carrying a state. What exactly the state consists of results from the act of modeling. As such it depends on the observer or—more precisely—on whatever is considered worth of being represented.

MAS have been introduced to study decentralization in decision making and bottom-up solution strategies (Wooldridge 2002). Through their interactions, the agents change their states. The rules of the system as a whole result from the interaction of the agents. MAS have shown to produce complex interaction patterns (see, e.g., Hogeweg and Hesper 1983; Reynolds 1987; Palmer et al. 1994; Helbing et al. 2000). Within this context, complex can be defined in an etymological way as being hard to separate into parts (see Gershenson and Heylighen 2005). The essential characteristic of MAS is self-organization. Since each agent only has a local perspective, there is no governing system, determining the behavior of the system as a whole. Thus, the functionality and, as such, the character of the system as an entity emerges via self-organization through the interactions of its agents (see Heylighen 2013). "Self-organization establishes a relation between the behavior of the individual components and the structure and functionality of the system as a whole: simple interactions at the local level give rise to complex patterns at the global level. This phenomenon is called *emergence*" (Heylighen 2013, p. 121; highlighted in the original).

Note that in classical MAS, the rules of its agents are fixed (e.g., Conway's Game of Life, see Gardner 1970 for further details; swarm robotics, Şahin and Winfield 2008). Once we allow the rules of the agents to change through, e.g., some process of learning (i.e., in a sense of recognizing environmental change and storing recognition), we obtain a complex adaptive system (CAS). Holland (1992, 1995) defines a complex adaptive system[8] as a (typically large) collection of agents that interact and adapt. Through the possibility of the agents to adapt, the system shows self-similarity.[9] However, by doing so, the system inherently shows path

---

[6] Note in passing that self-similarity is one of the defining properties of fractals.

[7] In contrast to volatile.

[8] Holland uses the notion of *constrained generating procedures*.

[9] "Self-similarity" in the sense that the agents in both their states and their rules adapt as well as the system as a whole adapts in its composition of agents and their interactions.

dependency, i.e., the state of the system depends on the states the system has been going through in the past. Path dependency clearly can be conserved in the agents' memory, if they have anything like memory (i.e., in physical terms, not necessarily consciousness). For the particular example of plant memory, the reader is referred to Thellier and Lüttge (2013), Lüttge and Thellier (2016). Memory merely may be conserved in the system's structure. For example, the morphology of the skeleton of vertebrates results from their common evolutionary ancestor and, thus, conserves the lateral symmetries and essential characteristics resulting from the selection process the ancestor has been subject to. It is important to note that path dependency thus introduces a concept of memory which can be passed on during the further development of the system. We note in passing that path dependency comes along with intractability (Nikolic and Kasmire 2013). This means that the shortest model describing the system is the system itself. From intractability then follows unpredictability at least for all purposes of prediction and controllability.

Holland (1995) summarizes four basic properties which complex adaptive systems are showing:

1. Complex adaptive systems develop inhomogeneities in the way their basic elements are organized. Thus, aggregation can be observed, leading to patterns in space and time.
2. Complex adaptive systems evolve.[10] Through the process of adaptation, chance events are reinforced leading to nonlinearity.
3. The capability of responding to unforeseen changes in the environment is only possible if diversity is maintained.
4. Since interactions are commonly instantiated through energy flows, complex adaptive systems exhibit a homeostatic nature, in particular keeping flows of energy in balance.

As adaptation obviously is the key feature within the idea of a CAS, we need to take a closer look at this concept in the context of biological systems. Adaptation can be realized through several mechanisms, one of which is evolution. As mentioned above, the key components of evolution are mutation, heredity, and selection. Applying the abstract framework, we consider (**generic**) **evolution** in a broad sense, comprising three generic subprocesses. Evolution is based on variation which is provided by the diversity of agents comprising a system. Additional variation within the system is created through transmissible random changes in the informational representation of the system. This process is called (**generic**) **mutation**. While in classical neo-Darwinism chance has been claimed to be the major source of variation, recent contributions stress a dualism of chance and determinism (Buiatti and Buiatti 2008). Therefore, variation can be generated both through deterministic and random processes. For example, we have Mendel's Laws of Inheritance explaining frequencies of alleles in populations in a deterministic way. To generate variation within the genetic potential of a population, chance

---

[10] In the sense of adaptation through absorption of information (i.e., experience).

acts via mutation or sexual reproduction. The importance of chance results from the necessity to stabilize the system and counterbalance effects from energy dispersal (cf. Buiatti and Longo 2013).

(**Generic**) **heredity** describes a process of transmission of information over time. Thus, heredity leads to temporal persistence which can be observed. But heredity is more than just an occasional, temporal persistence. In order for an algorithm to optimize through variation and selection, information gained through the interaction of the system with its environment has to be captured within the system. Evolution on Earth resulted in highly optimized organisms which managed to adapt to specialized ecological niches. The successful "strategy" for searching through the virtual space of possible solutions requires a mechanism of maintaining information and thus introducing directedness in time. Without heredity, the simple trial-and-error strategy would be highly inefficient. However, through the transmission of information over time, "experience" gained through exploring the consequences of recent adaptations in the informational representation of the system will increase overall adaptiveness. The idea of generalizing the neo-Darwinian concept of heredity has gained growing interest with recent work in molecular biology, in particular in epigenetics (Bossdorf et al. 2008; Richards 2006; Lüttge and Thellier 2016). Jablonka and Lamb (2005) introduced the concept of evolution in four dimensions. Next to genetic evolution, comprising the classical neo-Darwinian concept, epigenetic inheritance, social learning, and symbolic communication are added as additional dimensions of transmission of information (cf. Jablonka and Lamb 2005)—with the last two dimensions representing outcome from the cultural evolution.

The third subprocess is selection. We can consider (**generic**) **selection** as an autonomous process that uses outcomes of local interaction to enhance a subset of components. Being an autonomous process, selection emerges from the interaction of systems with each other.

Note that the algorithmic nature of evolution does not lead to explanations why things are the way we see them. But the algorithm allows us to understand how things evolved over the course of time (Nikolic and Kasmire 2013). The gain in using an algorithmic approach lies in the ability to define essential biological concepts independent of temporal or spatial scales (see also Zenil et al. 2012), rather than giving an interpretation in a teleological sense. Thus, the interpretation of evolution as an algorithmic concept within the framework of adaptation in systems of interacting agents provides a conceptual definition conducive to analyzing holobiont-like principles on various scales.

4 Arguing for an Extension Beyond the Holobiont Sensu Stricto

Let us recall the definition of the holobiont as the functional entity of a “host organism” together with all its associated microorganisms (Sect. 2). Clearly, such an entity is a system of interacting agents, each of which acts without external control. Interactions can be manifold. There is no a priori assessment concerning the nature of the coenobitic relationships. Which of the interactions we consider as being part of the holobiont is up to the choice of the observer. The subjective perspective extends to the nature of the relationship between host and microbes. Whether a certain relationship can be termed mutualistic or parasitic, it “requires a clear appreciation of the spatial, temporal and taxonomic context in which these systems operate” (Herre et al. 1999, p. 49). Altogether, it is the observer assigning some purpose to the system (see also Gershenson and Heylighen 2003).

The holobiont operates within a certain environment which the entity of agents is exposed to. As such, the system is subject to adaptation. To give an example, consider vertebrates. There are many examples of species-specific bacteria which are essential for the maturation of the immune system (e.g., Mazmanian et al. 2005; Weiss et al. 2011; Buffie and Pamer 2013). Even parasites can contribute to increasing fitness (e.g., Herre et al. 1999). Thus, coenobitic relations affect the fitness of the system, i.e., the “holo-immunome” (cf. Dheilly 2014). Analog mechanisms also exist for plants, e.g., priming (Pozo and Azcón-Aguilar 2007) and induced resistance (Jung et al. 2012; Zamioudis and Pieterse 2012). Therefore, variation in abundances of microbiota through amplification and acquisition/abandonment and variation in the modes of interaction (altogether promoting ecological niching) have an effect on the ability of the holobiont to keep its overall level of internal entropy, i.e., its organization. “The theoretical framework provided by considering not only the host but also the parasite as a holobiont revealed that some interactions have been underestimated and others have not yet been explored” (Dheilly 2014, p. 1). For the example of the holobiont sensu stricto, classical selection leads to the enhancement of holobiontic associations. Concerning heredity, we should consider the broader setting of generic heredity. As mentioned in the introduction, the holobiont shows, next to genetic inheritance, additional modes of transmission of information, e.g., the community assembly as such. Information can be passed on vertically to the next generation, e.g., via gametes, as well as horizontally to accompanying individuals through interaction. For bacteria this could be quorum sensing, the capability of bacteria to sense their local cell density (Bassler and Losick 2006), just to give an example. Both vertical and horizontal transmissions thus change the informational representation of the holobiont. This can also be traced on an evolutionary timescale. For example, genome reduction may result from long-term symbiosis of bacteria with their symbiotic host (McCutcheon and Moran 2012) or the development of a highly specialized metabolic repertoire as in the case of the human gut commensal *Bacteroides* *thetaiotaomicron* (Benjdia et al. 2011). Summarizing, the holobiont can be seen as the prototype of a complex system adapting through an evolutionary process.

The general observations in the previous section clarified holobiont characteristics to be twofold: (1) On the ontological side, there is an association of biological agents together with their biotic–abiotic interactions. The association is taken to be a functional entity within a certain environment. (2) On the epistemological side, the evolutionary process drives the development of the system within its environment. The essential principles underlying this process can be directly deduced from the hologenome theory. Furthermore, interaction with microbes can affect epigenetically induced plasticity of plants on an evolutionary scale, although not being the only factor shaping epigenetic plasticity. Intrieri and Buiatti (2001) claim that introgression of genes from *Agrobacterium rhizogenes* had a major impact on the development of the genus *Nicotiana*. Thus, compared to the holobiont sensu stricto, the perspective of a holobiont-like system opens up a broader context. Buiatti concludes that the "data from plants suggest that selection operates at several levels of the hierarchical organization of life, and that fitness is determined by the effects of both epigenetic and genetic factors. I suggest that, since at every level (cell, organism, population, species, ecosystem) there are internal and external factors that affect fitness, there is a need for organisms to coordinate the networks of interactions that occur at the different levels" (Buiatti 2011, p. 257). Again, we stress that neither genetic nor epigenetic mechanisms provide the only modes of transmission. We deliberately aim to transcend beyond both of these dominantly gene-oriented modes.

Let us consider a second example. An ecosystem is the prototype of a complex adaptive system. The system is defined through a network of organisms as interacting with their biotic and abiotic environment at a denoted spatial location (cf. Tansley 1935). Current extensions include further aspects which are characteristic for a holobiont-like system. For example, Ellenberg et al. (1986) additionally concede to the system a limited capacity of self-regulation. Furthermore, some authors claim that emergent properties have to be viewed as characteristic for an ecosystem (see, e.g., Jørgensen and Müller 2000; Matyssek and Lüttge 2013; Lüttge 2016).

Coming back to the thermodynamic approach to ecosystem theory (see, e.g., Jørgensen and Svirezhev 2004), Aoki (1995) interprets ecological succession of a lake as evolution from oligotrophy to eutrophy and approaches succession via studying an increase of entropy. The entropy principle in living systems he proposes claims that entropy production in biological systems passes through at least two phases. An early phase in which entropy production increases over time is followed by a later period, where production decreases (cf. Aoki 1995). The concept has been picked up later, adding approaches to estimate entropy production in ecological systems such as food webs (Meysman and Bruers 2007).

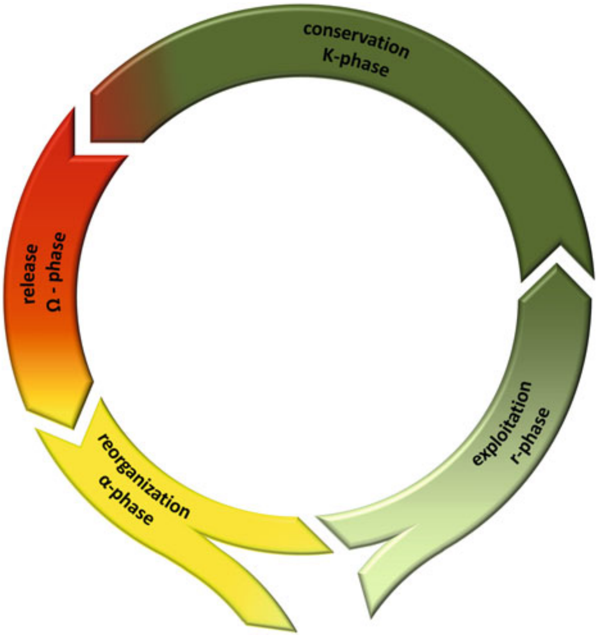
Through the utilization of natural resources, organisms within an ecosystem interact, leaving an impact on the space of possible actions of neighboring species. Independently of being limiting or upon excess, changing resource availability implies interaction. Food webs constitute one example of structure emerging from the interaction of species within an ecosystem.

Species composition itself is capturing information about the ecosystem. Evolving from selection, speciation, dispersal, and drift (Vellend 2010), the community conserves information about the evolution of the system. "Experience" is preserved in existing ecological niches created through the actions/interactions of the individuals comprising the system. Adaptive fitness of the ecosystem as an entity depends, among others, on the species diversity the system attained to maintain as a result of successful ecological niching. Also other environmental aspects, e.g., spatial fragmentation, are captured within species composition. The latter aspect has been described by metapopulation theory (Hanski 2004; Alexander et al. 2012), although not without debate (Baguette 2004). It is the ability of an ecosystem to make natural resources available for the species constituting the system, which creates variation within the set of existing ecosystems. The Lamarckian aspects of transmission (Rosenberg et al. 2009) inherent in the hologenome theory will apply at the general ecosystem level. Microbial systems provide a particularly instructive example, since horizontal gene transfer and hereditary symbioses in eukaryonts provide mechanisms reaching beyond classical neo-Darwinian heredity (cf. Sapp 2011).

In contrast to standard definitions of an ecosystem, the view of the entity as a holobiont-like system includes the aspect of adaptation and/or evolution of the system as a whole. Thus, we emphasize the characteristics of the system to enhance its adaptive abilities and thus, contrasting more traditional, static perspectives. Dennett's view of evolution as an algorithm has deep consequences. Through generic heredity, i.e., transmission of information, the system evolves over time, allowing to build on gained "experience." As such, evolution is a realization of the principle of *competence without comprehension* (Dennett 2009). It defeats the traditional concept that any higher competence cannot be achieved without an a priori understanding. Evolution as an algorithm has been powerful enough to create all complex life on Earth through the combination of simple subprocesses. As such, the evolution of ecosystems has a direction, too. Ecosystem development moves on in cycles which proceed toward higher modes of "order" and complexity. Succession of pioneer species toward climax species reflects an increasing level of organization from rapid capturing toward retaining of resources, as reflected by refined ecological niching and increasing specialization (see Burkhard et al. 2011).

Let us briefly come back to the scale independency inherent in the definition of a holobiont-like system. There is system nestedness in multiple ways. Patterns emerging from the interaction of agents lead to structure on the level of the system and thus create the suite of actions for the behavior of the system as an entity. While providing stability, structure also limits the behavior of the agents on lower levels (*downward causation*) (see Gershenson and Heylighen 2003). Additionally, the choice of the observer to define the system boundaries creates dependencies in a horizontal sense. Boundaries of open systems need to be delimiting and penetrable at the same time. Therefore, there is always some fuzziness, since precise, (eco-) physiological boundaries can hardly ever be defined. Such kind of fuzziness is a prominent ecosystem feature. This feature is innate to the fact that systems need to be open in their energy exchanges with their environment, which forms the prerequisite for confining entropy.

Fig. 3 The adaptive cycle (according to Gunderson and Holling 2002) consisting of a phase of exploitation (r-phase), followed by conservation (K-phase). Once the effort to sustain the state of high-level order raises too much, the system will switch into a phase of release (Ω-phase) followed by a period of reorganization (α-phase)



Systems provide context for other systems. Thus, systems form nested sets with vertical as well as horizontal relationships. Classically, ecosystem theory knows two phases of system development. First, there is an r-phase of exploitation of resources (where r stands for the rate in the standard model of population dynamics) followed by a K-phase of specialization and conservation of the attained structure and order (K refers to the capacity constant in the population dynamical model). The idea of an r-/K-phase generalizes the concept of r-/K-strategies, as introduced by MacArthur and Wilson (1967) in a natural way. Gunderson and Holling (2002) added two additional, typically shorter phases leading to an *adaptive cycle* of exploitation (see Fig. 3), conservation, release, and reorganization. Cells divide and die, individuals grow and vanish, species appear and disappear, and ecosystems evolve, persist, and collapse. Holling (2001) coined the notion of *panarchy*[11] as a metaphor to describe such interrelated sets of adaptive cycles (Fig. 4; see also Gunderson and Holling 2002). Through their development over time, systems pass through a sequence of *adaptive cycles* of exploitation. Evidently, cycles on hierarchically low levels are running on faster timescales compared to cycles on high levels of system organization. This conceptual background clearly applies to the

---

[11] The authors argue for the invention of a new term: “Since the word hierarchy is so burdened by the rigid, top-down nature of its common meaning, we prefer to invent another term that captures the adaptive and evolutionary nature of adaptive cycles that are nested one within the other across space and time scales. We call them panarchies, drawing on the image of the Greek god Pan—the universal god of nature” (Gunderson and Holling 2002, p. 74).

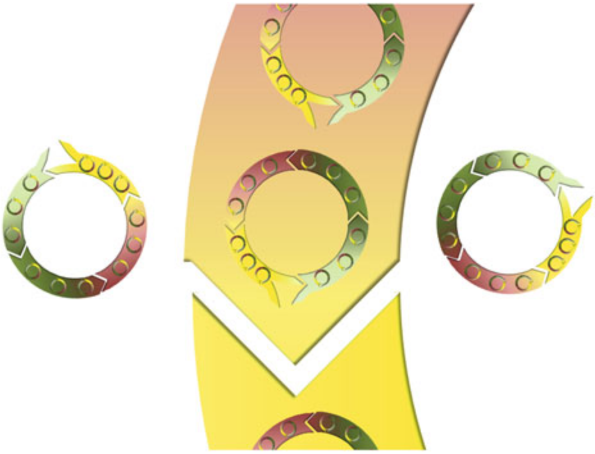


Fig. 4 The panarchy metaphor (Gunderson and Holling 2002) builds on the idea of the adaptive cycle. Systems passing through the cycle interact with other systems (horizontally) which might be within a different phase of the cycle. At the same time, systems are parts of other systems and consist of systems on a lower scale (vertical interaction). Thus, a nested set of horizontally and vertically interacting systems arises, forming a panarchy

concept of holobiont-like systems. Emerging through the interaction of agents, adaptive cycles of the holobiont-like system are determined by the adaptive cycles of the agents, which themselves constitute holobiont-like systems, too. It is interesting to note that through the association between eukaryotes and prokaryotes, these cycles become interlinked, reflecting a continuum in time and space for holobiont-like systems to exist (see Holling 2001).

It is thus reasonable to analyze a given holobiont-like system as being part in a panarchy of other systems. Disregarding these dependencies leads to skewed argumentation and debates hard to settle. Considering ecosystems as holobiont-like systems emphasizes the dynamic evolution of the system. The need to go through the full adaptive cycle follows from the algorithmic principle of evolution. In order to evolve, i.e., search through the (hypothetical) space of conceivably stable ecosystems, the evolutionary algorithm needs to instantiate examples and expose them to the process of selection. The collapse of the ecosystem ends this exposure. The information being transmitted to the "next generation," i.e., along the dimension of time, through generic heredity guarantees the evolutionary "experience" (see above) to be captured. Thus, a new status or even variant of ecosystem can develop through building up on the functions and performances being captured in previous rounds of the adaptive cycle (see also Burkhard et al. 2011).

Going downward on the biological scale, we can consider holobiont-like systems on the organ level. A prototype would be the human immune system. It is indeed questionable to consider the immune system as being an organ, since it is hard to localize the immune system within an organism. On the other side, the immune system has organ-like properties. It is built up from various cell types of different speciation, e.g., phagocytes, natural killer cells, lymphocytes, or T cells.

Through those cells, tasks are shared, e.g., building the innate and the adaptive immune system. Information is passed along through the system by direct cell–cell communication, the development of pattern recognition receptors and antigens, all reflecting the interaction of the immune system with its environment. The immunological memory is conserved in the diversity of B and T cells (Janeway et al. 2001). Persistent differences in adaptability of the system provide the foundation for current hypotheses in the development of autoimmune diseases, e.g., the *Hygiene Hypothesis* (Okada et al. 2010) or the *Old Friends Hypothesis* (Rook and Brunet 2005). Mutation is directly evoked through mechanisms such as *somatic hypermutation* (see, e.g., Janeway et al. 2001). Furthermore, the complex interplay of the innate with the adaptive immune system provides further sources of variation via proliferation of immune cells. Selection is also immediately present due to the interplay of inflammatory and anti-inflammatory mechanisms.

Another informative example can be a branch of a tree. The agents are given by different tissue types and/or microorganisms being present. As for generic mutation, we have classical genetic mutation within cells, as well as drift and dispersal of microorganisms. Furthermore, phenotypic modifications, e.g., plant gall, introduce further variation. Apart from the obvious modes of transmission, generic heredity at the organ level in this example includes spatial persistence through morphological structure. In a similar way, morphology adds to selection through, e.g., shading or restriction of water supply.

Although all classical modes of evolution on the genetic scale are still applicable within the context of holobiont-like systems, the generic counterparts of the evolutionary subprocesses typically comprise further modes of biological interaction. Thus, the concept of the holobiont-like system does not render the traditional neo-Darwinian concepts dispensable, but reaches beyond the gene-centric perspective, embracing a wider range of nongenetic mechanisms.

5 Hypotheses for Experimental Analysis

After all, do we actually need another concept? Focusing on both, system properties and scale independency opens a new view onto biological systems. In particular, the characteristic property of adaptation inherent in the definition of the holobiont-like system incorporates a perspective of evolutionary theory into ecological analysis. Conversely, the idea of nested adaptive systems developing and evolving over space and time allows explicitly addressing the different scales involved in common evolutionary theory and ecology.

An overarching hypothesis thus states that the view of plants as parts of holobiont-like systems improves the possibilities for explanation and prediction of ecological and evolutionary patterns and processes. Following the scale-independent view, we expect this hypothesis to hold across spatial and temporal scales. A gene-centered, evolutionary approach falls short in addressing the complexity of processes and mechanisms, determining the effectiveness of the phenotype when being confronted with the competitive situation within an ecosystem of interacting organisms. Improved knowledge in molecular biology has elucidated a variety of interacting functions, enfolding the potential lying in the gene. “No longer can the gene be thought of as inherently stable, discrete stretch of DNA that encodes information for producing a protein, and is copied faithfully before being passed on. [. . .] The stretch of DNA that is a ‘gene’ has meaning only within the system as a whole. And because the effect of a gene depends on its context, very often a change in a single gene does not have a consistent effect on the trait that it influences” (Jablonka and Lamb 2005, p. 7).

Theory building in plant sciences has traditionally been rooted in an autecological perspective. Shortcomings of, e.g., the *Growth-Differentiation-Balance Theory* (Herms and Mattson 1992; Matyssek et al. 2012a), address plant-internal resource allocation as a trade-off between the demands of growth versus stress defense. More precise, the trade-off between investments in primary versus secondary metabolism is associated with ecological costs. The latter might differ with changing environmental conditions. In contrast, experiments demonstrate the plant to possess enormous plasticity in regulating its resource allocation under dynamically changing ecological scenarios (Matyssek et al. 2012b). The concept of a holobiont-like system naturally frames the conceived plant system within a hierarchy of interactions, thus incorporating a systems biology perspective. Hereby, there is no limit on the considered level of biological organization. The panarchy metaphor locates adaptive cycles of proteins within cells, life cycles of cells within tissue, tissue within organisms, and the life span of the organisms itself within an ecosystem. The mechanisms shaping these adaptive cycles, enabling to preserve released free energy within the supra-system, will be different on each level. Nevertheless, generic factors driving the mechanisms as well as underlying principles are anticipated to be universal. Preservation of free energy may even appear as one thermodynamic reason in evolution toward advancing complex adaptive systems in biology, eventually linked within horizontally and vertically nested hierarchies.

Pattern organization within a hierarchy is a natural consequence of self-organization of systems of autonomously interacting agents: “Aggregation and hierarchical assembly are not imposed on complex adaptive systems, but emerge from local interactions through endogenous pattern formation” (Levin 1998, p. 432). Essential ingredients to enable self-organization within dissipative systems are a certain level of diversity, dynamically adapting interactions among agents, as well as effectiveness of an autonomous process counterbalancing the creation of diversity through selection (cf. Levin 1998). Thus, the subprocesses defining generic evolution within the holobiont-like system provide the basis for emerging patterns of self-organization. The perceived directedness of system development, passing through the adaptive cycle from the simple to the more complex, i.e., from an r-phase of exploitation toward a K-phase of specialization and conservation (cf. Gunderson and Holling 2002; Burkhard et al. 2011), can be explained through the action of an underlying evolutionary algorithm. Via hereditary processes, information is kept within the system. It is accumulated during various runs through the adaptive cycles on lower levels. Being embedded within a hierarchically upper adaptive cycle, information is persistently transmitted within the system. Various indicators and *ecological orientors* (Fath et al. 2004) can be employed to identify the state of the system at the various scales (see, e.g., Burkhard et al. 2011).

The idea of transmission of information both horizontally among biological units and vertically within the system is deeply rooted in biological theory. In particular, "change through use and disuse" (cf. Jablonka and Lamb 2005) is not foreign to Darwin's theory of evolution via natural selection. Although the historical development has defeated Lamarckism on the basis of lack of grounds for an hereditary mechanism transmitting acquired information, recent insights in, e.g., epigenetic functions, horizontal gene transfer, transmission of microorganisms, etc., have led to reconsider inheritance beyond the single gene (see, e.g., Jablonka and Lamb 2005; Zilber-Rosenberg and Rosenberg 2008).

Likewise, ecological theory has adopted a more dynamical perspective. Considering an ecosystem to be an adaptive system shifts the focus from individual organisms to organismic interactions. Thermodynamic ecosystem theory (Prigogine et al. 1972; Jørgensen and Svirezhev 2004) has been proposed as well as approaches based on network analyses (Fath and Patten 1999), just to give some examples. The aspect of adaptation across scales has been presented, among others, by Aoki (1995), who uses the term "evolution" to denote the development of ecosystems. Holling (1986) and Gunderson and Holling (2002) considered directedness in the evolution of ecosystems across scales while introducing their panarchy concept.

Acknowledging directedness in ecosystem development will also provide new perspectives. For example, the consideration of ecosystem maintenance has to be modified (see also Lüttge et al. 2016). Considering an ecosystem as proceeding through the adaptive cycle from less organized to higher complexity, the system cannot be maintained in a highly evolved state forever. The longer the system remains in a low-entropy state, vulnerability will rise under small, unforeseen perturbations, shifting the system into the following phase of release (cf. Burkhard et al. 2011). Thus, maintenance of ecosystem functions needs to warrant the constant flow of entropy at any level of self-organization.

Through the systems perspective, ecosystem functions emerge from the interaction of the organisms forming the system. One level further down the scale, these interactions are subject to dynamic change, too. The *Stress-Gradient Hypothesis* (Bertness and Callaway 1994; Brooker et al. 2008) postulates that beneficial organismic interaction increases along gradients of progressively limiting abiotic stress. On a broader perspective, interactions among certain organisms take place within the concerted action of many organismic associations. Maintenance of system functionality on the larger scale, however, imposes selective pressure on single interactions. Further on, selective pressure enforces a dynamic process on the set of interactions which might change the character of a particular single interaction, e.g., from mutualistic to parasitic. Thus, qualifiers such as "mutualistic" or "parasitic" might change during system development just because of the dynamic change of the state of the system.

From the overarching hypothesis stated at the beginning of the section, several sub-hypotheses can be deduced. First of all, we can study the holobiont-like system as a conceptual model and analyze its suitability in fostering ecological or evolutionary understanding. An important aspect of the model is the claim that emergent properties can be observed on the system level. Generic properties of complex adaptive systems can thus be studied in a scale-independent manner. We anticipate properties such as resilience, redundancy, or robustness to be universal on all scales. The holobiont-like system provides straight forward hypotheses for these functions to be realized. For example, resilience is postulated to be the consequence of the diversity of agents, buffering the system against various types of stress. In addition, agents might be partly exchangeable, allowing system functionality to remain unchanged although single agents might be lost. Accordingly, robustness is expected to result from the network of interactions, increasing beyond the robustness of the single agent.

Studying holobiont-like systems as evolutionary systems, multilevel selection theory is intrinsically integrated. Interactions are expected to be found within one level as well as among levels. Processes of selection acting upon those interactions comprise a conceptual part of the definition. Appealing to the panarchy of system nestedness, it might be speculated that positive feedback of selection at a lower level relates to adaptation on the higher level. General principles like the one just stated are claimed to be scale independent.

We have already highlighted ecological hypotheses to be addressed through the concept of holobiont-like systems. Abstracting from the *Stress-Gradient Hypothesis* (SGH), we claim that dynamic rather than static environments favor holobiont-like systems. Whereas the SGH postulates a change in the characteristics of interactions along a stress gradient, we can generally ask for determinants of the set of interactions of a holobiont-like system. Generally, it is the dynamic interaction of the agents as well as with their environment which forces each agent to constantly adjust its rules of involvement and adapt upon gained experience. Without dynamics in the environmental processes, stable trajectories will be found, leading the system to rest in its current state. In contrast, within dynamically changing environments, the autonomous process of selection will enfold its selective potential on the set of interactions which currently define the system. Counterbalancing the selective pressure, variation created within the system will lead to new potential, providing the basis for evolution to occur.

6 Conclusion

Timely developments both in ecological theory and in the theory of evolution have reached a state of maturation which begins to overcome the initially separating, apparent exclusiveness of each theory. In parallel, advancing insight into biological mechanisms and functioning has never ceased to unveil an ever growing richness and diversity. Historical claims that life on Earth may eventually be fully understood and ready for control and maintenance by man have turned out repeatedly to be falsified soon after being postulated (see, e.g., the 1988 fires in Yellowstone National Park, Turner et al. 2003, or the Exxon Valdez oil spill, Harwell and Gentile 2006). As the concept of the organism still has its scientific value in systemizing and classifying the richness of life on Earth, it encompasses limits of understanding as we leave the autecological perspective, which indeed is needed when striving for comprehension of the complex ecological cause-effect relationships as the mechanistic drivers of evolutionary processes. Evidently, ecology and evolution are intrinsically woven. In fact, such a move opens the conceptual dimension for grasping intellectually the ways in which life is actually self-perpetuating.

Various theoretical tools have in the meantime been introduced to ecological theory, enhancing insights into ecosystem functioning. Nevertheless, we are still far from understanding critical states in ecosystem functioning to an extent that may enable us to sustain such systems as well as their ecological services to mankind with its various perspectives and demands. We must learn that ecology and evolution represent dynamic and, hence, “progressive” rather than “conservative” phenomena. Such a perception imperatively requests the observer—in the shape of a researcher—to conceive crucial functionality of any kind of biotic systems in terms of multiply nested interaction networks.

We propose merging two conceptual frameworks so far mostly associated either with ecological or evolutionary research by introducing the integrative concept of holobiont-like systems. Reaching beyond the scale-limiting definition of the holobiont sensu stricto, we still adopt its natural focus on the interaction of autonomous agents as well as its implicit concept of hereditary transmission. As advancement, we gain scale independency, which allows incorporating evolutionary development as driven by ecological mechanisms into all levels of biological organization. The holobiont-like system thus becomes the conceptual core for exploring scale independency of biotic interaction networks. As a result, revelation of the multiple nestedness of informational control cycles is approached as envisaged by the panarchy metaphor. The latter allows comprehension of the operational grounds by which systems ensure persistence while allowing for advancement. On such grounds, hypotheses can be posed, as pointed out in this account, the assessment of which through empirical evidence and informational analysis will help to functionally explain the integrated “eco-evo” foundations of biotic interaction networks.

References

Alexander HM, Foster BL, Ballantyne F IV, Collins CD, Antonovics J, Holt RD (2012) Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. J Ecol 100:88–103

Aoki I (1995) Entropy production in living systems: from organisms to ecosystems. Thermochim Acta 250:359–370

Axelrod R (1997) The complexity of cooperation. Princeton University Press, Princeton, NJ

Baguette M (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. Basic Appl Ecol 5:213–224

Bar-Yam Y (1997) Dynamics of complex systems. Addison-Wesley, Reading, MA

Bassler BL, Losick R (2006) Bacterially speaking. Cell 125:237–246

Benjdia A, Martens EC, Gordon JI, Berteau O (2011) Sulfatases and a radical S-adenosyl-L-methionine (AdoMet) enzyme are key for mucosal foraging and fitness of the prominent human gut symbiont, *Bacteroides thetaiotaomicron*. J Biol Chem 286:25973–25982

Bertness MD, Callaway R (1994) Positive interactions in communities. Trend Ecol Evol 9:191–193

Bossdorf O, Richards CL, Pigliucci M (2008) Epigenetics for ecologists. Ecol Lett 11:106–115

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JM, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Porey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34

Buiatti M, Buiatti M (2008) Chance vs. necessity in living systems, a false antinomy. Biol Forum 101:29–66

Buiatti M (2011) Plants: individuals or epigenetic cell populations? In: Gissis SB, Jablonka E (eds) Transformations of Lamarckism. From subtle fluids to molecular biology. MIT Press, Cambridge, MA, pp 251–260

Buiatti M, Longo G (2013) Randomness and multilevel interactions in biology. Theory Biosci 132:139–158

Buffie CG, Pamer EG (2013) Microbiota-mediated colonization resistance against intestinal pathogens. Nat Rev Immunol 13:790–801

Burkhard B, Fath BD, Müller F (2011) Adapting the adaptive cycle: Hypotheses on the development of ecosystem properties and services. Ecol Model 222:2878–2890

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Dennett D (1996) Darwin's dangerous idea: evolution and the meanings of life. Simon & Schuster, London

Dennett D (2009) Darwin's "strange inversion of reasoning". Proc Natl Acad Sci USA 106:10061–10065

Dheilly NM (2014) Holobiont-holobiont interactions: redefining host-parasite interactions. PLoS Pathog 10, e1004093

Dobzhansky T (1937) Genetics and the origin of species. Columbia Press, New York, NY

Eberl G (2010) A new vision of immunity: homeostasis of the superorganism. Mucosal Immunol 3 (5):450–460

Ellenberg H, Mayer R, Schauermann JH (eds) (1986) Ökosystemforschung—Ergebnisse des Sollingprojekts 1966–1986. Ulmer Verlag, Stuttgart

Epstein JM (1999) Agent-based computational models and generative social science. Complexity 4(5):41–60

Fath BD, Jørgensen SE, Patten BC, Straškraba M (2004) Ecosystem growth and development. Biosystems 77:213–228

Fath BD, Patten BC (1999) Review of the foundations of network environ analysis. Ecosystems 2 (2):167–179

Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford

Gardner M (1970) Mathematical games—the fantastic combinations of John Conway's new solitaire game "life". Sci Am 223:120–123

Gell-Mann M (1994) Complex adaptive systems. In: Cowan G, Pines D, Mellzer D (eds) Complexity: metaphors, models, and reality. SFI Studies in the sciences of complexity. Proc Vol XIX. Addison-Wesley, Boston, MA, pp 17–45

Gershenson C, Heylighen F (2003) When can we call a system self-organizing? In: Banzhaf W, Ziegler J, Christeller T, Dittrich P, Kim JT (eds) Advances in artificial life. Springer, Heidelberg, pp 606–614

Gershenson C, Heylighen F (2005) How can we think the complex? In: Richardson K (ed) Managing organizational complexity: philosophy, theory and application. Information Age Publishing, Charlotte, NC, pp 47–61

Gilbert SF (2011) Symbionts as an epigenetic source of heritable variation. In: Gissis SB, Jablonka E (eds) Transformations of Lamarckism. From subtle fluids to molecular biology. MIT Press, Cambridge, MA, pp 283–293

Goldberg AD, Allis CD, Bernstein E (2007) Epigenetics: a landscape takes shape. Cell 128:635–638

Gunderson L, Holling CS (2002) Panarchy: understanding transformations in human and natural systems. Island Press, Washington, DC

Haldane JBS (1955) Population genetics. New Biol 18:34–51

Hamilton WD (1963) The evolution of altruistic behaviour. Am Nat 97:354–356

Hamilton WD (1964) The genetical theory of social behaviour I, II. J Theor Biol 7:1–52

Hanski I (2004) Metapopulation theory, its use and misuse. Basic Appl Ecol 5:225–229

Helbing D, Farkas I, Vicsek T (2000) Simulating dynamical features of escape panic. Nature 407:487–490

Harwell MA, Gentile JH (2006) Ecological significance of residual exposures and effects from the Exxon Valdez oil spill. Integr Environ Assess Manag 2(3):204–246

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335

Herre EA, Knowlton N, Mueller UG, Rehner SA (1999) The evolution of mutualisms: exploring the paths between conflict and cooperation. Trends Ecol Evol 14:49–53

Heylighen F (2013) Self-organization in communicating groups: the emergence of coordination, shared references and collective intelligence. In: Massip-Bonet À, Bastardas-Boada A (eds) Complexity perspectives on language. Communication and society. Springer, New York, NY, pp 117–149

Hogeweg P, Hesper B (1983) The ontogeny of the interaction structure in bumble bee colonies. Behav Ecol Sociobiol 12:271–283

Holland JH (1992) Adaptation in natural and artificial systems. MIT Press, Cambridge, MA

Holland JH (1995) Hidden order. How adaptation builds complexity. Addison-Wesley, Reading, MA

Holling CS (1986) The resilience of terrestrial ecosystems: local surprise and global change. In: Clark WC, Munn RE (eds) Sustainable development of the biosphere. Cambridge University Press, Cambridge, MA, pp 292–320

Holling CS (2001) Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390–405

Intrieri MC, Buiatti M (2001) The horizontal transfer of *Agrobacterium rhizogenes* genes and the evolution of the genus *Nicotiana*. Mol Phylogenet Evol 20:100–110

Jablonka E, Lamb MJ (2005) Evolution in four dimensions. MIT Press, Cambridge, MA

Janeway CA, Travers P, Walport M, Shlomchik MJ (2001) Immunobiology: the immune system in health and disease, 5th edn. Garland Science, New York, NY

Jørgensen SE, Müller F (eds) (2000) Handbook of ecosystem theories and management. CRC Publishers, New York, NY

Jørgensen SE, Svirezhev YM (2004) Towards a thermodynamic theory for ecological systems. Elsevier, Amsterdam

Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming of plant defenses. J Chem Ecol 38(6):651–664

Kauffman SA, Johnsen S (1991) Coevolution to the edge of chaos: coupled fitness landscapes, poised states, and coevolutionary avalanches. J Theor Biol 149:467–505

Kay JJ (2008) Framing the situation: developing a system description. In: Waltner-Toews D, Kay JJ, Lister NME (eds) The ecosystem approach. Complexity, uncertainty, and managing for sustainability. Columbia University Press, Chichester, NY, pp 15–35

Levin AS (1998) Ecosystems and the biosphere as complex adaptive systems. Ecosystems 1:431–436

Lewontin RC (1970) The units of selection. Annu Rev Ecol Syst 1:1–18

Lüttge U (2016) Plants shape the terrestrial environment on Earth—challenges of management for sustainability. In: Cánovas FM, Lüttge U, Matyssek R (eds) Progress in botany, vol 77. Springer, Heidelberg

Lüttge U, Souza GM, Bertolli SC (2016) Hierarchy and information in a system approach to plant biology. In: Cánovas FM, Lüttge U, Matyssek R (eds) Progress in botany, vol 77. Springer, Heidelberg

Lüttge U, Thellier M (2016) Roles of memory and the circadian clock in the ecophysiological performance of plants. In: Cánovas FM, Lüttge U, Matyssek R (eds) Progress in botany, vol 77. Springer, Heidelberg

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

Margulis L (1993) Symbiosis in cell evolution: microbial communities in the Archean and Proterozoic Eons. W.H. Freeman, New York, NY

Matyssek R, Gayler S, zu Castell W, Oßwald W, Ernst D, Pretzsch H, Schnyder H, Munch JC (2012a) Predictability of plant resource allocation: new theory needed? In: Matyssek R, Schnyder H, Osswald W, Ernst D, Munch JC, Pretzsch H (eds) Growth and defence in plants—resource allocation at multiple scales, vol 220, Ecological studies. Springer, Berlin, pp 433–449

Matyssek R, Koricheva J, Schnyder H, Ernst D, Munch JC, Osswald W, Pretzsch H (2012b) The balance between resource sequestration and retention: a challenge in plant science. In: Matyssek R, Schnyder H, Osswald W, Ernst D, Munch JC, Pretzsch H (eds) Growth and defence in plants—resource allocation at multiple scales, vol 220, Ecological studies. Springer, Berlin, pp 3–24

Matyssek R, Lüttge U (2013) Gaia: the planet holobiont. Nova Acta Leopoldina NF 114 (391):325–344

Mayr E (1942) Systematics and the origin of species from a viewpoint of a zoologist. Harvard University Press, Cambridge, MA

Mayr E (2002) What evolution is. Orion Books, London

Mazmanian SK, Liu CH, Tzianabos AO, Kasper DL (2005) An immunomodulatory molecule of symbiotic bacteria directs maturation of the host immune system. Cell 122:107–118

McCutcheon JP, Moran NA (2012) Extreme genome reduction in symbiotic bacteria. Nat Rev Microbiol 10:13–26

Meysman FJR, Bruers S (2007) A thermodynamic perspective on food webs: quantifying entropy production within detrital-based ecosystems. J Theor Biol 249:124–139

Nikolic I, Kasmire J (2013) Theory. In: Dam KH, Nikolic I, Lukszo Z (eds) Agent-based modelling of socio-technical systems. Springer, Dordrecht, pp 11–71

Okada H, Kuhn C, Feillet H, Bach J-F (2010) The 'hygiene hypothesis' for autoimmune and allergic diseases: an update. Clin Exper Immun 160:1–9

Palmer RG, Arthur WB, Holland JH, LeBaron B, Tayler P (1994) Artificial economic life: a simple model of a stockmarket. Physica D 75:264–274

Pena R, Offermann C, Simon J, Maumann PS, Geßler A, Holst J, Dannenmann M, Mayer H, Kögel-Knabner I, Rennenberg H, Polle A (2010) Girdling affects ectomycorrhizal fungal (EMF) diversity and reveals functional differences in EMF community composition in a beech forest. Appl Environ Microbiol 76:1831–1841

Pepper JW, Herron MD (2008) Does biology need an organism concept? Biol Rev 83:621–627

Pozo MJ, Azcón-Aguilar C (2007) Unraveling mycorrhiza-induced resistance. Curr Opin Plant Biol 10:393–398

Prigogine I, Nicolis G, Babloyants A (1972) Thermodynamics of evolution. Phys Today. Part I 15:23–28, Part II 25:38–44

Rennenberg H, Dannenmann M, Gessler A, Kreuzwieser J, Simon J, Papen H (2009) Nitrogen balance in forest soils: nutritional limitation of plants under climate change stresses. Plant Biol 11(Suppl 1):4–23

Reynolds CW (1987) Flocks, herds, and schools: a distributed behavioral model. ACM SIGGRAPH Comp. Graphics 21(4):25–34

Richards EJ (2006) Inherited epigenetic variation—revisiting soft inheritance. Nat Rev Genet 7:395–401

Rook GAW, Brunet LR (2005) Microbes, immunoregulation, and the gut. Gut 54:317–320

Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I (2007) The role of microorganisms in coral health, disease and evolution. Nat Rev Microbiol 5:355–362

Rosenberg E, Sharon G, Zilber-Rosenberg I (2009) The hologenome theory of evolution contains Lamarckian aspects within a Darwinian framework. Environ Microbiol 11(12):959–2962

Rosenberg E, Sharon G, Atad I, Zilber-Rosenberg I (2010) The evolution of animals and plants via symbiosis with microorganisms. Environ Microbiol Rep 2(4):500–506

Rosselló-Mora R, Amann R (2001) The species concepts for prokaryotes. FEMS Microbiol Rev 25 (1):39–67

Ruse M (1989) Do organisms exist? Am Zool 29(3):1061–1066

Şahin E, Winfield A (2008) Special issue on swarm robotics. Swarm Intell 2:69–72

Sapp J (2011) Lamarckian leaps in the microbial world. In: Gissis SB, Jablonka E (eds) Transformations of Lamarckism. From subtle fluids to molecular biology. MIT Press, Cambridge, MA, pp 271–282

Schrödinger E (1944) What is life? Cambridge University Press, Cambridge

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16:284–307

Thellier M, Lüttge U (2013) Plant memory: a tentative model. Plant Biol 15:1–12

Turner MG, Rommer WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. Front Ecol Environ 1(7):351–358

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85(2):183–206

Weiss BL, Wang J, Aksoy S (2011) Tsetse immune system maturation requires the presence of obligate symbionts in larvae. PLoS Biol 9, e1000619

Wilson DS, Sober E (1989) Reviving the superorganism. J Theor Biol 136:337–356

Wilson DS, Sober E (1994) Reintroducing group selection to the human behavioral sciences. Behav Brain Sci 17(4):585–654

Wilson DS, Wilson EO (2008) Evolution 'for the good of the group'. Am Sci 96(5):380–389

Wooldridge M (2002) Introduction to multiagent systems. Wiley, Chichester

Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviors. Hafner Publishing, New York, NY

Wynne-Edwards VC (1986) Evolution through group selection. Blackwell, New York, NY

Zamioudis C, Pieterse CMJ (2012) Modulation of host immunity by beneficial microbes. Mol Plant Microbe Interact 25:139–150

Zenil H, Gershenson C, Marshall JAR, Rosenblueth DA (2012) Life as thermodynamic evidence of algorithmic structure in natural sciences. Entropy 14:2173–2191

Zilber-Rosenberg I, Rosenberg E (2008) Role of microorgnisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol 32:723–735