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Cultural group selection and holobiont evolution – a comparison of structures of evolution

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Abstract

The notion of *structure of evolution* is proposed to capture what it means to say that two situations exhibit the same or similar constellations of factors affecting evolution. The key features of holobiont evolution and the hologenome theory are used to define a *holobiont structure of evolution*. Finally, Cultural Group Selection, a set of hypotheses regarding the evolution of human cognition, is shown to match the holobiont structure closely though not perfectly.

Introduction

Holobionts are entities consisting of a host and its persistent symbiotic microorganisms, making up an integrated biological entity (see Gilbert et al., this volume). The paradigmatic example being reef building corals, in which algal symbionts produce carbon compounds for the backbone and the host provides the symbionts with nutrients and a hospitable habitat. Proponents of the hologenome theory (to which and to related views I will refer as the holobiont perspective) argue that holobionts are units of selection. In other words, that there is selection on the holobiont, not only on the partners. There are ongoing debates on whether this is the case and on exactly what the claim amounts to (see Gilbert et al. this volume, Lloyd, this volume). Here I am going to mostly side-step these debates and suggest focusing on the evolutionary consequences of the holobiont model more generally. The holobiont notion refers to several features that distinguish holobionts, among them symbiosis with microorganisms and specific variation mechanisms. These features support predictions that are specific to holobionts, most notably about the evolvability of holobionts and about coevolution among the partners.

The discussion about whether holobionts are units of selection is in part an attempt to generalize – to provide an account of a large multitude of concrete cases. To supplement the discussion of holobionts as units of selection, I will propose the notion of *structures of evolution* – constellations of evolutionary relevant factors, which include selection, but also other factors, such as properties of heredity. I will then specify a particular structure of evolution that I will refer to as the holobiont structure of evolution. I will go over the evolutionary consequences of the holobiont structure, and argue that the structure of evolution perspective helps identify what differentiates holobiont evolution from other evolutionary scenarios. The key features I discuss are how the evolvability of the holobiont relies on the evolvability of the constituents and the coevolutionary opportunities differentiating holobionts from other collectives. To further test the utility of the holobtiont structure, I will consider whether the cultural group selection model of human evolution, concerned as it is with radically different phenomena, matches the holobiont structure and what can be gained by pursuing the analogy. This discussion shows that human groups have remarkable similarities with holobionts.

The holobiont perspective as a generalization

Nancy Moran and Daniel Sloan argue against the holobiont perspective: “The central claim of the hologenome concept, that a host and its microbiome together form the primary unit of selection, is sometimes true, and sometimes false; its validity will depend on the particular case." And they further state that, "insofar as there is a primary unit of selection common to diverse biological systems, it is unlikely to be at the level of the holobiont" (Moran and Sloan 2015). Thus, Moran and Sloan take the debate about whether holobionts are units of selection to be concerned with the generalization that the holobiont *is often* the most relevant unit of selection. If true, this claim will support the further claim that holobionts are of general evolutionary significance. This generalization can serve as a heuristic advice: look for selection at the holobiont level, since this is often the unit targeted by natural selection. It is also sometimes suggested that holobionts played a crucial role in significant evolutionary junctures; this claim is distinct from the generalization identified by Moran and Sloan.

To support the general claim, it is useful to enumerate many potential cases – as the proponents of the holobiont perspective do. It is also important to show that the factors that are together needed to make a given holobiont a unit of selection co-occur frequently or typically. Marshalling many examples of holobionts combined with an account of holobionts as units of selection may be intended as instantiating an inference to the best explanation: the holobiont unit of selection being the best explanation for the existence of many diverse holobionts; hence their existence supports the claim that holobionts are the important unit of selection.

The general role of holobiont selection is attributed to the ubiquity of symbiosis with microorganisms. In support its proponents marshal large swaths of evidence from a wide variety of species. They also highlight the fact that microorganisms predate eukaryotes, had evolved important adaptations before eukaroytes came along, and were already present as potential partners. These considerations all point to the holobiont generalization being grounded in contingent empirical facts about the living world, not in nomological or logical necessity. It is not the claim that the holobiont notion logically entails sufficient conditions for something to be a unit of selection, nor that it is possible for a holobiont to be one.

Granting holobionts may be units of selection (see Lloyd, this volume), and putting to one side the empirical support for the general importance of selection on holobionts, it is clear that holobionts have features that differentiate them from other systems. The holobiont notion is a claim about a whole class of systems that share properties that differentiate them from other systems. The holobiont notion can thus be seen as an abstraction, capturing the commonalities of these symbiotic partnerships and ignoring their other particulars. If it is a unit of selection, the holobiont is a specific type of unit of selection. For the rest of this chapter I will be concerned with the evolutionary features shared by holobionts that differentiate them from other units of selection.

Scientific generalizations may be used for a variety of purposes, including summarizing information, making predictions, and explaining diverse phenomena. The questions to ask about a scientific generalization include its scope (e.g., is the claim about all animals or all eukaryotes?), its purported realism (is it intended to be true or is it merely presented as a phenomenological model?), and, when the generalization is truth-directed, what makes it true, whether it is a sharp or just an approximate claim (of the kind, most animals move around but not necessarily all of them), and the implications of the truth of the generalization (e.g., does it allow predictions?).

Focusing on whether holobionts are units of selection may cause two kinds of difficulty. It may lead us to ignore the reason for the general significance of holobionts, i.e. the ubiquity of partnerships with microorganisms, and it draws attention away from the evolutionary features shared by holobionts that differentiate them from other units of selection. The focus on units of selection may thus obscure both the grounds and scope of the generalization and lead us to miss its real significance.

Structures of evolution

Both philosophers and evolutionary theorists have discussed and elucidated the notions of levels and units of selection for several decades, discussions that typically hark back to Lewontin's criteria (Lewontin 1970). Elisabeth Lloyd has, over the years, clarified and organized this complex terrain and in her contribution to this volume she applies her perspective to the holobiont case.

To supplement the various rich and enlightening analyses of the unit of selection notion, I want to consider here a related but fundamentally different question, namely what it means to say that two situations exhibit the same or similar constellations of factors affecting evolution, a notion I call *structure of evolution*. As an illustration, consider discussions about the evolution of altruism that focus on whether a group is, or can be, a level or unit of selection. A key part of the evolutionary explanation, in this case, is that group-level (or between-group) selection favors altruistic behavior while individual-selection (or within group) selection opposes it. The two levels and their opposition is an example of what I mean by structure of evolution. Articulating structures may involve identifying levels and their interaction, identifying the role of specific forms of transmission, drift versus selection, coevolutionary dynamics etc.

In a classic discussion from the heyday of the group selection debate, John Maynard Smith noted that the conditions sufficient for something to undergo selection may not suffice for adaptation and so introduced the alternative notion *unit of evolution* (Maynard Smith 1987). Units of evolution require appropriate heredity, otherwise adaptations will not evolve:

> To qualify as a unit of evolution, it is not sufficient that an entity be selected for or against: it must have heredity. In contrasting units of evolution with units of selection, I am making a distinction different from that drawn by Dawkins (1976) between a "replicator" (i.e., an entity whose structure and information content is copied more or less precisely in the process of reproduction) and a "vehicle," whose structure is not replicated, but that is the object upon which selection typically acts. Thus organisms are units of evolution, but they are not replicators. What makes organisms into units of evoluion is that
>
> i. they have heredity, in the sense in which Darwin would have used the word — that is, offspring resemble their parents — and
>
> ii. the replicators, or genes, that are responsible for heredity behave in a way that, typically, does not permit within-individual, between-replicator selection; thus in typical cell division one copy of each gene present in the mother cell is transmitted to each daughter cell, and in meiosis each member of a pair of genes is equally likely to be transmitted.

Using this distinction Maynard Smith concluded that "whether an entity qualifies as a unit of evolution *depends on the relationship between that entity and the replicators that* *are ultimately responsible for heredity*. In this sense, the distinction between units of evolution and selection is less fundamental than that between replicators and vehicles. Nevertheless, it is important to distinguish between objects we can expect to evolve adaptations and those we cannot. In particular, selection may act between groups of organisms, but it does not follow that group adaptations will evolve" (my italics).

The different interpretations of the notion of unit of selection that Lloyd provides (see her contribution in this volume) help clarify the issue that bothered Maynard Smith. The important point for my purposes here is different. The unit of evolution notion was introduced to identify one specific constellation of evolutionary factors and their relations. I refer to a specification of a *constellation of evolutionary factors and their relations* as a structure of evolution. The constellations of factors that make up structures of evolution may include factors that go beyond selection. I have mentioned three examples of structures of evolution: the altruism scenario, as described earlier, Maynard Smith's definition of a unit of evolution, and the holobiont structure, which will be precisely defined in the following section.[1]

Any evolutionary scenario may be understood as a structure of evolution, but some structures encompass more systems of interest than others and produce richer predictions or deeper understanding. A structure of evolution is intended to be a tool: the aim of identifying and specifying a structure of evolution is to provide scientists with a common framework and terminology and to elicit research questions and hypotheses that apply to many systems of interest.

Rather than being a set of necessary and sufficient conditions, a structure is a characterization of various factors and their possible interactions; it need not refer to all factors that affect the evolution of the biological system. Moreover, the evolutionarily significant factors for understanding a specific system may change over time.

The holobiont structure of evolution

As a working definition, I define the holobiont structure of evolution to consist of the following:

1. A host.
2. Symbiotic partners.
3. Genomes, of both the symbionts and the host.
4. Vertical or quasi-vertical transmission of symbionts in holobiont reproduction.

A few clarifications are in order. (3) refers to the fact that in holobionts the host and the symbionts all have their own genomes. Indeed, the hologenome notion refers to their combined genomes. Since there are many symbionts (i.e., many bacteria), the hologenome is of the form {multi-cellular host genome, {set of genomes of individual symbionts}}. The symbionts may be of multiple species. As the holobiont changes, both in ontogeny and phylogenetically, this collection changes; in particular the set of microorganisms fluctuates much more readily than evolutionary changes in the host genome. The hologenome is thus a statistical abstraction. The separate genomes of host and symbionts can coevolve. In contrast, paradigmatic groups and collectives do not have genomes that are independent and separate from the genomes of the individuals comprising them.

As to (4), transmission, the holobiont as unit of selection discussion emphasizes the role of vertical transmission of symbionts; however microbiota can be acquired from the environment and the acquisition of the microbiome may be regulated (perhaps the best studied case is the *Vibrio*-squid system discussed below). The important factor is reliable parent-offpsring similarity, leading to a lineage of holobiont individuals, regardless of the details of the transmission process.

Cultural Group Selection and holobionts: the parallel

Cultural Group Selection (CGS) is a hypothesis about the evolution of human collectives. The key element of CGS is competition between groups, driven by cultural rather than genetic differences between them. This leads to group selection on cultural variation, which explains the functionality, purportedly at the group-level, of culture and of social institutions. The CGS model is committed to the idea that culture is an inheritance system, though we should be careful to distinguish between inheritance of the culture of a group, say when a group splits in two, and inheritance of cultural replicators (i.e., memes) among group members. According to CGS, human cognitive adaptations for social learning and pro-social behavior are the result of culture-led gene-culture coevolution. The debate whether this is the correct explanation is ongoing, and there are many nuances that I have elided. My purpose here is not to assess the CGS model but rather to note parallels between the evolutionary scenario it draws and the evolutionary scenario raised by holobionts. My primary aim in doing this is to assess the fertility of the holobiont structure of evolution as a device for thinking about diverse biological systems, and through this to assess the notion of structures of evolution more generally. With several important caveats that I will point out, I think the exercise highlights interesting aspects of both the CGS model and the hologenome theory.

Human groups are in important ways more similar to holobionts than they are to mere collections of individuals. This is because they are characterized by group-level properties that are possibly best attributed to the group *qua* container rather than to the individuals within it. One reason to think this may be the case is the role of social institutions that shape and organize the group and that, in some sense, transcend individuals. Other reasons to explore this possibility include the idea that individuals in human groups operate in We-mode rather than I-mode (Tomasello 2014) and the suggestion that in early human society individuals and groups were more tightly integrated than they are today (Bader this volume, Jablonka this volume). I use the CGS model in developing the analogy with holobionts since it is a rich and well-developed set of ideas that can be directly related to the holobiont structure and because debates surrounding it resemble debates about holobionts. The following six sections examine these parallels.

Holobionts as individuals and as groups

Holobionts consist of multiple organisms comprising microorganisms of different kinds and a multi-cellular host. However, holobionts are not typical groups. First, they consist of multiple species. Gilbert et al. (this volume) refer to them as “multilineage biological entities.” Second, and more significantly, the holobiont host has its own genome. In other words, holobionts are not simply collections of individuals; the “container” (i.e., the host), as it were, is its own biological entity. I take this to be a defining characteristic of holobionts, distinguishing them from, on the one hand, collectives that consist of multiple individuals and nothing else, and, on the other hand, run of the mill symbiotic relationships in which several individuals are involved but the structure need not be that of a host and a population of multiple encompassed symbionts.

The holobiont structure of evolution specifies the existence of separate genomes for the host and the symbiotic partners. In the CGS case the role of the host genome is played by culture and social institutions. Cultural groups have cultural traits that are, at least on a first approximation, separate from the traits of their constituent individuals and that exhibit descent with modification (Richerson et al. 2016). This fulfills the minimal demands of the structure, by having both a lineage forming container and lineage-forming individuals within it.

Gilbert et al. (this volume) stress the individuality of holobionts. Expounding on holobionts as a special kind of individual, rather than as a special kind of collective, puts a second, different, strain on the analogy between human cultural groups and holobionts, since we typically do not consider human groups to be as tightly integrated. Perhaps a notion of a "loosely" coupled holobiont is useful. This applies to the paradigmatic cases as well – anatomical, physiological and developmental integration, discussed by Gilbert et al., are all matters of degree.

Parallel vertical transmission

To match the holobiont evolutionary structure the host genome and the symbiont genomes must be tightly coupled evolutionarily, paradigmatically by being transmitted in tandem. Important support for the holobiont perspective is thus the mounting evidence for systems in which contained symbionts are transmitted vertically, alongside the host genome (Gilbert et al, this volume). This is used to support the claim that holobionts can be units of selection *qua* replicators (see Lloyd, this volume).

To have the same structure, the cultural evolution case also has to demonstrate that the cultural host genome and the genomes of group members are transmitted in tandem when groups reproduce. The vertical transmission of individual genomes (as well as traits) when daughter groups form from individuals of the parent group, say by fission, is straightforward. What is more challenging in the cultural group case is the transmission of the group traits, analogous to the transmission of the host genome.

The two cases thus raise different questions: in the holobiont case the transmission of the host is a given, while the vertical transmission of the symbionts needs to be demonstrated; in the cultural case the transmission of the group members is a given, while the transmission of the culture is what calls for further explanation. Since the discussion of symbiont transmission is covered by other chapters in this volume, I will concentrate on the transmission of the cultural group-traits to see how well CGS matches the holobiont structure of evolution.

One way to approach this issue is to consider the more general question of whether culture is best viewed as the collection of individual psychological states in the group and their relationships (the reductive view) or whether culture is best viewed, in some relevant sense to be determined, as going beyond that (the holist/emergentist view). Two cases that raise challenges to the individualist perspective are social power and social institutions. Consider the example of stealing sheep introduced by Geertz (1973; see discussion in Lewens 2015). The knowledge of how to steal sheep may be best understood at the level of individuals, who learn directly or through others how to get the job done. However, it is not as clear that this is the correct kind of description for understanding what is involved in a society with a notion of ownership, which is a necessary condition for stealing sheep to be intelligible. Personal property and ownership rights are social institutions that seem to involve more than a snapshot of individual traits and their relationships at a point in time. This is clearly the case in complex societies, in which legal statutes, court systems and police are all key parts of property rights, but even simple societies have social institutions that may resist simple reductive explanation.

Whether all cultural phenomena can be reduced to individual states and interactions raises many issues that I am not going to discuss. The issue ultimately leads back to the question of methodological individualism in the social sciences, implicitly or explicitly endorsed by prominent cultural evolution scholars. Instead, I want to illustrate how the holistic/emergetist view and the reductive view relate to the issue of heredity of the cultural host genome, and thus to the question of whether the cultural case matches the holobiont structure.

Consider the reductive view that institutions are group level equilibria that arise from individuals’ interactions and norms. When daughter groups are formed by splitting from the parent group, then if we assume that daughter groups contain a good enough sample of the original culture, the group level equilibria should presumably persist. So in this case the requirements of the holobiont structure are apparently met. More complex, internally organized social institutions, especially if they involve social division of labor and social hierarchy, may not be so directly reproduced in daughter groups and may thus be more fragile. To clarify, the issue is not whether reductive accounts can provide analyses of complex institutions like property or marriage, questions theoreticians have addressed (see Lewens 2015). Rather, the questions that the holobiont structure highlights are whether such cultural institutions are transmitted or reestablished with enough fidelity when groups reproduce, and, if they are, how is this achieved.

In some formal models of cultural evolution the analogy to the holobiont case is stronger than in the reductive approach, since groups have group level traits that are copied when groups propagate (see Bowles and Gintis 2011). These traits are analogous to the host's genome in paradigmatic holobionts, making the models structurally analogous to holobionts.

In addition to vertical transmission and natural selection, CGS discusses two other routes through which group traits can spread (Richerson et al. 2016). The first route is selective imitation of successful groups. This happens when individuals in one group copy behaviors of successful members of another group. The second route is selective migration, in which individuals migrate to more successful groups, thus leading inferior groups to collapse or reform. Both these processes are selective and reduce variation between groups; however they do not involve group reproduction.

The holobiont perspective highlights three processes affecting holobiont variation that go beyond holobiont reproduction and selection: microbial amplification, acquisition of symbionts from the environment, and horizontal gene transfer. Microbial amplification refers to changes in the relative abundance of microorganisms in the microbiome, reflecting their success in given conditions. Acquisition of symbionts from the environment depends on the abundance of different symbionts in the environment (possibly from, but not restricted to, other holobiont individuals) and may be highly regulated. Horizontal gene transfer involves transfer of alleles between genomes, a process most commonly encountered in bacteria. These three process affect variation at the holobiont level (i.e., between holobionts), as do the somewhat similar processes highlighted by CGS.

In both of these cases, CGS and holobionts, there are selective variational processes. In the CGS model these are selective imitation and selective migration, while in holobionts both amplification and acquisition may be selective processes. Amplification involves natural selection among the symbionts, which may be shaped by the environment constructed by the host. Acquisition from the environment may involve selective attraction of specific species of bacteria, selective retention, resistance to unwanted partners, immunity and so on. The well-studied *Vibrio*-squid system demonstrates just how intricate selective acquisition can be. In this symbiotic partnership, the bioluminescent bacteria populate the light organ of the bobtail squid, allowing it to not cast a shadow on moonlit nights and so avoid predators. The squid emits and acquires the bacteria daily and only *V. fischeri* can maintain stable association with the host (Lloyd this volume, Zilber-Rosenberg and Rosenberg (2008), Lamm and Kammar (2014)). Generally speaking, selective acquisition processes affect both between-holobiont similarity and parent-offspring similarity and tend to reduce variation.

The conceptual relations between selective processes and reproduction are the subject of philosophical debate. In her discussion of holobionts as reproducers, Lloyd (this volume) analyzes these processes and contrasts her view with that of Godfrey-Smith (2009), noting:

> Godfrey-Smith conflates and combines reproduction (the replicator/reproducer) and selection (the interactor, the entity which that possesses "variation in character," and which "leads to differences in reproductive output" when functioning as an interactor) into his single concept of a 'Darwinian Population.'

Lloyd argues that "the means and methods of reproduction" should be kept separate from the consideration of "selection processes involving interactors." Godfrey-Smith, in contrast, emphasizes the co-evolutionary opportunities afforded by the possibly independent heredity of the symbiotic partners, especially with the construction of symbiotic partnerships through the acquisition of symbionts from the environment, as happens in the development of the light organ in the squid. The emphasis on coevolution is also found in the arguments of biologists objecting to the unit of selection claim of the hologenome theory (Moran and Sloan 2015).

The two perspectives reveal valid points. It is necessary for holobionts to be lineage forming entities, with robust parent-offspring similarity, if selection is to operate. But, as Lloyd notes, this does not determine the allowed processes of reproduction. The selective processes affecting both cultural groups and holobionts operate ontogenetically and a developmental approach to heredity, as argued for in James Griesemer's reproducer concept, is more helpful than the traditional notion of replicator. In other words, parent-offspring resemblance need not depend on vertical transmission. On the other hand, Godfrey-Smith is correct in pointing out the coevolutionary possibilities that a focus on the unit of selection question may obscure. As the debates on both holobionts and CGS show, the main burden in these debates is evidential. It is not a trivial matter to interpret the empirical signature, either to determine the evolutionary or coevolutionary origin of a particular holobiont or in order to make a general claim about what is the typical case (Hester et al. 2015).

Processes that produce and maintain variation

Variation is required for natural selection. However, natural selection, coupled with selective processes like those discussed in the previous section tends to reduce variation. Evolution is thus an interplay between variation-producing and variation-reducing processes. Multiple, diverse, and complicated processes are involved in producing similarity and variation in both holobionts and cultural groups. This is reflected in the scientific literature, which emphasizes variation-producing and variation-reducing processes and empirical measurement of variation over discussions of replication. This can be seen in both the CGS literature (Richerson et al. 2016) and in the holobiont literature (Hester et al. 2015).

The holobiont perspective suggests acquisition of new symbionts from the environment and horizontal transfer as variation producing processes. Analogous ways of creating variation may not seem as relevant to the cultural group case as they are to paradigmatic holobionts. Immigrants can, of course, supply a population with new skills; and attraction and reception of immigrants involve social institutions. While selective migration from dysfunctional groups is one of the processes highlighted by CGS, it refers to individuals joining the successful group and accepting its culture, reducing variation between groups. One important mechanism that maintains inter-group variation is the marking of group members to distinguish between them and outsiders. This can be done through dress, dialect, religion and so on (Richerson et al. 2016). Such markings can be used to ensure that only group members receive the benefits of group membership. They also increase the cost of immigration into the group or even bar it altogether. These processes are analogous to selective acquisition of symbionts, which, as I noted in the previous section, can involve selective retention but also selective attraction of profitable symbiotic partners by the holobiont.

Summarizing, CGS mostly considers migration as reducing variation, and enforcing group boundaries as a mechanism for maintaining variation, whereas in the holobiont literature there is more emphasis on acquisition as increasing variation.

Evolvability

In cultural group selection, selection operating between culturally diverse groups can select for genetic predispositions to pro-social or group advantageous behavior. The result is gene-culture coevolution, in which social institutions play an important role. Natural selection between groups (i.e., at the holobiont as interactor level), however, is considered to be relatively slow (Soltis, Boyd, and Richerson 1995; Richerson et al. 2016). The two other processes CGS points to, namely selective imitation and selective migration, favor group beneficial institutions and norms. These processes are individual-level processes, possibly affected by social institutions, rather than group level processes. So even putting aside the interaction between genetic and cultural evolution, we find several cultural evolutionary processes that can affect the evolvability of the holobiont: those operating on individuals as well as selection on groups.

The hologenome theory also addresses evolvability. It claims that holobionts are able to respond more quickly to changing environmental challenges because microorganisms evolve more quickly than their multi-cellular host alone. Assuming vertical transmission, changes in the microbiome will then be transmitted when the holobiont reproduces (in effect establishing inheritance of acquired characteristics). How changes in the symbiont population produced by natural selection affect the holobiont population when symbionts are acquired from the environment requires more careful consideration than I can attempt here.

Coevolution

Since both the host and the symbionts have genomes, the evolutionary dynamics in the holobiont structure of evolution may involve coevolution between host and symbionts. One of the central debates about the evolution of holobionts is whether they evolved through coevolution of several parties with diverse interests or through selection on the holobiont, as the hologenome theory argues. Lloyd is correct that this debate is in danger of conflating the holobiont as interactor and the holobiont as reproducer. The holobiont as interactor may be the context in which microorganisms are selected.

Even if it is accepted that holobionts can be units of selection, the claim that a particular holobiont evolved through selection at that level rather than through the coevolution of the host and partners requires careful interpretation of evidence (Moran and Sloan 2015). It is, for example, possible that a trait that is helpful for the holobiont (e.g., bioluminescence), and is suggestive of design, in fact evolved for other purposes by the symbionts, prior to and independently of the holobiont, and was later co-opted, in which case there was neither coevolution nor selection at the holobiont level (Lamm and Kammar 2014). Parallel phylogenies of two species are evidence against preadaptation, but do not distinguish between coevolution and selection at the holobiont level. The stronger claim that *many* or *most* holobionts are the result of selection at the holobiont level rather than coevolution requires statistical interpretation of variation in multiple holobionts and evidence from multiple kinds of biological systems. This kind of data can alter our beliefs about which is more probable, coevolution or holobiont selection (Hester et al. 2015).

The debate concerning cultural group selection takes a very different form than does the debate about holobionts. The CGS model argues for culture led gene-culture co-evolution, in which cultural differences between groups lead to selection on genes for pro-sociality and group advantageous behavior. The “tribal social instincts hypothesis” suggests that, once cultural groups came to exist due to the transmission of simple social norms, these norms exerted selection pressure for pro-social genes by causing misbehaving individuals to be punished and by affecting mate choice and child neglect (Richerson et al. 2016). So, unlike the debate about holobionts, in the CGS model coevolution is a feature, not a bug: culture led gene-culture coevolution is not an alternative to CGS but what you expect CGS to produce; hence evidence for coevolution is evidence *for* CGS. In other words, the coevolutionary extension of the CGS model includes selection between cultural groups, but adds coevolution to the claim that groups can be units of selection.

The alternative to culture led gene-culture coevolution is the hypothesis that the necessary cognitive adaptations for full-fledged human culture evolved independently of concomitant evolutionary changes in culture, either predating them or as a reaction to changes in social organization or culture that happened for independent reasons. Such magic-moment or key innovation accounts posit that a single adaptive change, be it cooking (suggested by Richard Wrangham), cooperative reproduction (Sarah Hrdy), or language, which happened before or is independent of cultural and genetic changes that ensued, set the ball rolling on the evolution of human culture and cognition (Sterelny 2012; Lamm 2014). Coevolutionary accounts, on the other hand, are based on bidirectional influences (Lamm and Kammar 2014), and it is often suggested that coevolutionary spirals can lead to increasing complexity, which is otherwise hard to explain.

Evolutionary Psychology competes with the coevolutionary account, arguing that social cognition evolved in the Pleistocene without cultural changes playing a coevolutionary role (Tooby and Cosmides 1995; Richerson et al. 2016). Another suggestion is that the cognitive capacities underlying culture are pre-adaptations that evolved before cultural transmission (Ayala 2010). One kind of evidence that would support these hypotheses might be that cognitive changes, say docility, evolved early, probably before cultural transmission. Compare this with the bioluminescence *Vibrio*-squid case (Dunlap et al. 2007). If bioluminescence evolved prior to symbiosis, as evidence from non-symbiotic species supports, a coevolutionary origin of bioluminescence would be rejected. If, alternatively, we find evidence of parallel diversification of *Vibrio* and squid species we may suspect coevolution occurred. However, evidence of parallel diversification does not rule out the holobiont hypothesis that the symbiotic system was the unit of selection – both the coevolutionary and the unit of selection hypotheses remain viable.

If social institutions appeared late, only in the Holocene, then it is probable that the cognitive capacities for culture evolved beforehand and are preadaptations. However, the evidence according to Richerson et al. is that even in the simplest family-based and egalitarian hunter-gatherer societies, like the Ju/’hoansi (!Kung) and Shoshone, social institutions that differ from society to society structure social interaction to a significant degree. In addition, multi-family camps and regional networks are found. They conclude that “a reasonable assumption is that Late Pleistocene foragers exhibited a range of institutional complexity comparable to modern day foragers” (Richerson et al. 2016) and hence the coevolutionary CGS model is supported.

Cheaters

The central issue in understanding the evolution of sociality is the problem of free-riders or cheaters. Free-riders enjoy the benefits of the social behavior of others but do not contribute in return. If social behavior is altruistic in the sense of reducing the fitness of the individual and increasing the fitness of others, non-altruistic behavior, or free-riding, will drive out altruistic behavior. A significant literature deals with how biological altruism may nonetheless evolve, keeping free-riders at bay. Evolution of new levels of individuality is typically taken to imply a suppression or regulation of the independent evolutionary destiny of previously independent constituents, be they genes, independent cells, or non-social organisms, in favor of the new collective individual, be it a chromosome, a multi-cellular organism, or a social group (see Michod, this volume). A variety of biological mechanisms evolved to ensure this. Gilbert et al. (this volume) suggest:

> The immune system may have evolved for the suppression of potential “cheaters,” those lower-level parts of the group that would proclaim their own autonomy and that would multiply at the expense of the others (Tauber 2000, 2009; Ulvestad 2007; Eberl 2010; Pradeu 2010). The problem of “cheaters” then has to be solved

> in such a way that associates in a symbiotic relationship are under the social control of the whole, the holobiont (Stearns 2007).

Similarly, policing behaviors in human groups (punishment), norms, social institutions, and social emotions, may have evolved along similar lines. It is worth noting that some theorists suggest side stepping the issue of the evolution of altruism by locating the origin of social behavior in mutualistic interactions (Skyrms 2001; Sterelny 2012; Tomasello 2014). This matches the logic of the holobiont perspective, with its emphasis on mutually beneficial symbiosis and "team selection."

Concluding remarks

The analogy between cultural group selection and holobionts leaves me with mixed feelings and some tentative conclusions. The similarity is significant, even though human groups are not tightly-coupled holobionts, nor holobiontic individuals. Identifying a common structure of evolution in both the hologenome theory and cultural group selection helped hone in on common theoretical and evidential challenges that affect both notions, despite the fact that they are concerned with very different domains. The major questions I discussed are: the use of evidence to distinguish between pre-adaptations, coevolution, and selection at the holobiont level; the evolvability properties of holobionts of the two kinds; and the role of developmental processes in group reproduction.

The structure of evolution, as characterized at the beginning of this chapter, specifies the unique evolutionarily properties that differentiate holobionts from other evolutionary scenarios. It is thus the appropriate way to generalize from the discussion of particular holobionts. Some of the evolutionary properties of the holobiont structure depend on selection at the holobiont level, others are independent of it. A more rigorous model of the holobiont structure than I could provide here seems like a worthwhile goal.

I also indicated several aspects of current scientific debate that the focus by philosophers on the unit of selection discussion may obscure. The debate I have in mind is concerned with the evidence for selection at the holobiont level and with its prevalence, not with whether selection at the holobiont level is conceptually possible. The major alternative explanation of the phenomena is coevolution. The conceptual discussion of holobionts as units of selection cannot settle the empirical debate about the evolutionary significance of selection between holobionts as compared to coevolution. The holobiont structure account I presented also does not aim to settle this. On the contrary, both coevolution and selection at the holobiont level are features of the holobiont structure.

Finally, there is the question of the hologenome theory, which posits the combined hologenome consisting of the host and microbiome genomes as the unit of selection. Is this theory limited to symbiosis of multi-cellular hosts and microorganisms or can fundamental ideas from it be formulated in generic, structural, terms? Overall, the exercise here points in the direction of the former option. The hologenome theory comes from microbiology and highlights distinctive properties of symbiosis with microbiota, such as horizontal gene transfer and rapid evolution. And yet, the more general notion of a holobiont structure of evolution may guide thinking about other similarly structured collective phenomena, in particular the evolution of human cultural groups, and organize their analysis.

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Index terms: holobiont; Unit of selection; unit of evolution, replicator; reproducer; interactor; horizontal transmission; vertical transmission; holobiont; hologenome, hologenome theory, levels of selection; multilevel selection; microbial amplification; horizontal gene transfer; Cultural Group Selection, gene-culture coevolution, structure of evolution, coevolution, variational mechanisms, evolvability, social institutions; *Vibrio* squid; adaptation; pre-adaptation, methodological individualism, cultural evolution, scientific generalization, abstraction, inference to the best explanation (IBE) [also index under: abduction], I-mode, We-mode, Inheritance system; Holist, view of culture; Reductive, view of culture; Tim Lewens; selective imitation; selective migration; evidence; variation; policing; pro-social behavior; Kim Sterelny; Evolutionary Psychology; Cheating [also: cheaters]James Griesemer; group selection; Peter Godfrey-Smith; John Maynard Smith, Ilana Zilber-Rosenberg; Eugene Rosenberg; Scott Gilbert; Eva Jablonka, Oren Bader, Michael Tomasello, Peter Richerson, Robert Boyd, Elisabeth Lloyd, Nancy Moran, Daniel Sloan.

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[1] A unit of selection is also a structure of evolution, but it is typically taken to play a more fundamental role than the other structures I discuss.