Holobionts: An evo-devo perpsective

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1. *The challenge to individuality/organismality*

Holobiont *structure of evolution* (Lamm, 2018):

1. A host.
2. Microorganismic partners.
3. Genomes, of both the partners and the host.
4. Possible vertical transmission of partners in holobiont reproduction.

This is the appropriate generalization, rather than the debate about holobionts as u.o.s (see Lamm, 2018).

(3) is what opens up the co-evolutionary possibilities between host and microorganisms. It is what distinguishes holobionts from groups (who lack a group-level genome). It also differentiates between holobionts and both traditional organisms and Darwinian Individuals.

The combination of (3) and (4) is the basis of the analogy between the holobiont with its hologenome, and an individual (or organism) with its genome.

Holobiont "individuals" are semi-stable configurations, though the host is typically the more stable entity and the functional contributions distributed between bacteria in the microbiome are more fluid. The temporariness of associations produces a roughly hierarchical structure of degrees of stability.

Most of the purported challenges to notions of individuality are overblown (Lamm, forthcoming). The hologenome involves many of the same idealizations found in the notion of *a* genome of a multicellular organism. A key difference typically overlooked that I will explore today: holobionts can exchange symbionts. This and the role of goal directed acquisition, expulsion, and maintenance mechanisms are the focus of this talk.

I am going to mostly focus on holobionts as putative organisms, that is as entities having functional coherence.

2. *Overlapping individuals*

Acquisition of symbionts means that throughout their lives holobionts may overlap and exchange parts.

The term overlap may cause some confusion. I do not mean that the two (or more) individuals comprise shared parts at the same time, only that their constituent symbionts can transfer from one host to the other during the lifecycle (of either).

This makes counting the holobiont individuals problematic.

Godfrey-Smith proposed a multi-dimensional analysis of collective reproducers, consisting of three parameters: B (reproductive bottleneck), G (germline-soma specialization), and I (general degree of integration of the entity). In a nutshell, the higher an entity scores on these parameters the closer it is to the paradigm of Darwinian individuality. If one adopts such a picture, the degree of overlap, call it O, is an additional parameter.

In most traditionally analyzed cases it is essentially zero, and omitting it is reasonable. When we consider holobionts this parameter may be significant.
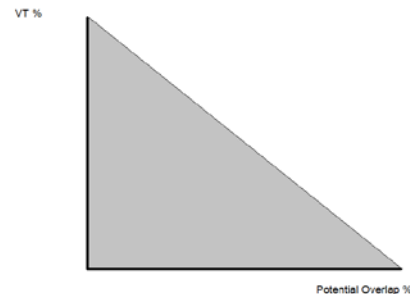
2.1 VT and *Overlapping individuals*

Overlapping is distinct notion from VT, and the two are not co-extensive:

Suppose an organism acquires all its microbiome from the environment, and recycles them daily by explusion and new acquisition (this is of course an extreme case, used for illustration). Also suppose many such individuals in a confined space, say an aquarium. It is probable that many if not all symbionts of a given host have previously belonged to other hosts in the population.

The degree of sharing or overlap is high. Now suppose the same biology, but in a sea environment with strong currents. Now, most of the symbionts acquired are new to the population of hosts, and the degree of overlap is smaller.

The mode of transmission is not enough to determine the degree of overlap of individuals. The ecological factors interact with the location and character of the symbiosis, as does the ability of the bacteria to survive outside the host.

2.2 HGT and *Overlapping individuals*

No exchange between holobionts in population		All non-vertically transmitted microbiome is exchanged
0		100

The following differences are significant:

The overlap or exchange in HGT is about type-identity, not the transfer of tokens.

Routine transfer may allow (adaptive) information to be passed between holobionts, reflecting current conditions.

3. *Peradaptations and goal-directed mechanisms*

The ability of hosts to make use of functional contribution by bacteria need not imply that the bacteria evolved these functions for that purpose.

It may very well be that at least initially the host takes advantage of previously evolved abilities. Examples: bioluminescence, heat

Specific acquisition/expulsion mechanisms: mechanisms that evolved for the particular species of symbionts and hosts

General purpose mechanisms: mechanisms that may be involved in relations with microorganisms in general, or in other functions of the host (including immunity).

Goal-directed mechanisms: mechanisms involved in acquisition, expulsion, and maintenance of the microbiome that are sensitive to functional contribution.

Goal-direct mechanisms may often be based on processes of selective

stabilization (Kirschner and Gerhardt 2005). Example:the lightening

squid's light organ has light detection capability.

- Specific acquisition/expulsion mechanisms may be goal-directed.

- General purpose mechanisms may be sensitive to particular functional contribution by microbes, and hence be goal-directed, but may be preadaptations keyed to conditions of the host that may change due to microbes, while not being adaptations for either acquisition, expulsion, or specifically the maintenance of the microbiome.

Specific mechanisms are the result of coevolution or of the holobiont being a unit of selection, while general purpose mechanisms may be the result of such processes but need not be.

Evolving specific mechanisms may be difficult since the symbiont providing the functional trait may change. Moreover, specific mechanisms, not tied to functional contribution of the symbiont, increases the chance of free riders.

Goal directed mechanisms may also be the most readily available way for the host to recognize the right partners, since identifying functional contribution may be easier than identifying where a horizontally transferred set of genes resides.

Arguably the higher the overlap O, the more probable are goal-directed, selective stabilization mechanisms:

1. Specific acquisition and expulsion, which are independent of the functional contribution, will be easier to exploit by free-riders. If the exchange is on-going and this exchange in ontogeny is functionally important (as may happen in high overlap cases), the fitness cost of free-riding will be higher, so we should expect acquisition, expulsion, maintenance mechanisms that are sensitive to functional contribution.

2. Exchange between individuals opens up the possibility of acquiring capabilities just-in-time they are needed, and more generally for information transfer via the symbionts.

3. High overlap implies higher rate of potential change in the microbiome, requiring more fine-tuned mechanisms than selective acquisition through evolved, static chemical attraction and non-differential expulsion.

While these factors are relevant in all cases involving acquisition from the environment, they may be particularly relevant when the degree of exchange is high, especially the acquisition of "memory" from other individuals.

4. *Conceptualizing holobiont evolution*

The holobiont structure, however, is richer than vanilla coevolution. A key element of holobionts is the existence of the host genome, a sort of group level genome that coevolves with the entities comprising the group (see Lamm, 2018).

Holobiont "individuals" are semi-stable configurations, though the host is typically the more stable entity and the functional contributions distributed between bacteria in the microbiome are more dynamic. The temporariness of associations produces a roughly hierarchical structure of degrees of stability, and hence fitness relations.

Keeping in mind the variety of temporal scales of the relations among the partners making up holobionts, perhaps the best model for understanding holobiont evolution would be of **holobiont singers coevolving with bacterial songs.**

This way of looking at things is distinct from other views in the field. It is different the notion of the holobiont as unit of selection, while also rejecting the attempt to view holobionts as vanilla cases of coevolution. At the same time, the view I argued for is distinct form the "song, not the singer" model, which considers the only thing of importance to be the song, or function, rather than the entities performing it.

Vanilla coevolution suggests that after long periods of time we should expect the partners to become coadapted, typically through the evolution of specific mechanisms (in the sense defined above). In contrast, the "holobiont singers coevolving with bacterial songs" model predicts holobiont mechanisms that are based on preadaptations for coexistence and on goal directed mechanisms, as found in the squid.

Overlapping individuals are not logically necessary to support the "holobiont host singers coevolving with bacterial songs" model, which is applicable to any cases involving acquisition from the environment playing a role in the functional coherence of the holobiont, and in which adaptations for acquisition, expulsion and maintenance of symbionts are observed. The more significant the overlap between holobionts, however, the more we should focus on selective stabilization mechanisms, beyond simple selective acquisition.

Overlapping individuality, at the end of the day, seems to me the conceptually challenging push by the holobiont perspective to other notions of individuality. This includes traditional notions of individuality, evolutionary individuality, as well as views that treat holobionts as organisms rather than as individuals. The focus here on functional coherence is closest the organismality view; but I highlighted that holobionts are weird, part exchanging, organisms.