

Holobionts as evolving units

by [Javier Suárez](#)

Microorganisms, including viruses, bacteria, Archaea, and some fungi, are ubiquitous, occupying diverse niches and ecosystems. They associate stably or transiently with all macrobes on Earth, and this interplay sometimes gives rise to very close and intimate connections. In fact, some microorganisms carry the genes that encode very important phenotypic traits within their hosts (animals and plants), some of which are required for activities as important as nutrition, development, protection against parasitoids, thermal tolerance, among others.

In light of these findings, a group of biologists and philosophers has recently coined the concepts of “holobiont” and “hologenome”. Holobiont refers to the ecological entity of a macrobial host plus the set of associated microorganisms that compose its microbiome. Hologenome refers to the collection of genes of this ecological unit (host genome plus genes of the microbiome). The goal of this essay is to explain the biological implications of the hologenome perspective. I will show why, if biologists want to have a complete picture of the evolutionary process, they should pay more attention to the evolutionary effects of the microbiome on animal and plant evolution.

The hologenome concept reconceptualizes hosts as communities or ecosystems of genetically diverse organisms. Resultantly, variation in the holobiont compositions (either at the level of the host, at the level of the microbiome, or at both levels) can lead to neutral or selective changes in hologenome composition over multiple generations. A key point of the hologenome concept is that response to selection may not just occur at the host genomic level, but at the microbial or host-microbial levels, thus claiming that the holobiont is a level (or unit) of selection in evolution.

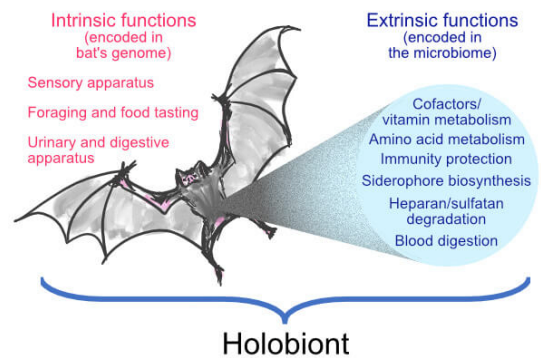
Proponents of the hologenome concept assume a multilevel, hierarchical view of the evolutionary process (selection occurs at multiple levels, including the holobiont unit). They accept that the hologenome can be shaped both by selection and neutrality forces (selection is not the only process that determines evolutionary trajectories); thus, the hologenome concept does not necessarily require the cospeciation of the host and its microbes. Their point is that the wide variety of specializations (dietary, behavioural, ecological, etc.) that we see in macrobes may be the result of a selection or a drift process on the host genome and/or on the genetic components of the microbiome, and consequently both levels must be studied.

In [my research](#), I introduced the concepts of “trait-recurrence” or “stability of traits”, to describe this perspective. This terminology puts the emphasis on the genes of the microbiome that transgenerationally give rise to the phenomenon of phenotypic trait-recurrence in the holobiont. The peculiarity of the stability of traits perspective is that it does not require that the bacterial taxa (or genomes) containing the genes with phenotypic effects on the holobiont are transgenerationally preserved: only the relevant genes need to be consistently preserved. This means that what is ultimately important is the preservation of the phenotypic effects, irrespective of the taxa bearing them.

For the stability of traits perspective, thus, the microbiome should not be taken merely as part of the host environment, it must be integrated with it as an “extended genome” or hologenome.

Let me use an example that highlights the importance of the hologenome perspective to properly characterize animal evolution. In a recent [research paper](#) about the evolutionary origin of blood-dietary specialization in common vampire bats (order Chiroptera), Dr. Mendoza and her colleagues demonstrated that genes in the host genome as well as genes in the microbiome had been shaped in specific ways to cope with the dietary challenges posed by hematophagy (obligatory blood-sucking diet). Their research was conducted in three stages:

- First, they observed that the genes in the vampire bat genome were insufficient to explain some of their adaptations to hematophagy, including the capacity to deal with blood-borne pathogens, or the adaptation to a protein-based diet.
- Second, they observed that the vampire bat microbiome was functionally very different from the microbiomes of frugivorous, insectivorous, and carnivorous bats, indicating the specificity of the microbiome to hematophagy.
- Third, they proved that part of the diverging functional genes in the vampire microbiome were directly related to hematophagy. Concretely, they played a substantial role in dealing with some of the dietary challenges associated with the blood-sucking lifestyle.



Dr. Mendoza and her collaborators concluded that the microbiome had played a substantial evolutionary role in the evolution of vampire bats. This led them to conclude that some of the genes of the microbiome, despite not being physically integrated into the bat genome, evolved as a part of an “extended bat genome”.

The main lesson that we can draw from this research is that animal and plant genomes have the capacity to “externalize” part of their genetic resources, rather than incorporating them within their molecular structure. By “externalizing” these resources, an emergent entity—the hologenome—results from the sum of the animal or plant genome, plus the genes coded in its microbiome. This emergent entity can experience selection (and mutation, neutrality, drift, etc.).

Through this process of externalization, complex adaptations in hosts become feasible without the necessity of substantial genomic changes, relying in some cases just on changes in the genetic makeup of their microbiomes. As changes in the genetic compositions of the microbiome can occur (and spread) more rapidly than changes in the host genome, the possibility of hologenomic evolution opens up a completely new avenue for animal and plant evolution, including new ways to cope with sudden environmental challenges like climate change.

The momentum for the hologenome perspective is coming, and it is thus time for biologists to realize that the best way of properly thinking about animal and plant evolution requires one to take into account the important and selectable effects of the microbiome on animal and plant genome evolution.



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