Superorganisms and Holobionts

Looking for a term for the functional entity formed by a macrobe and its associated symbiotic microbes and viruses? The term is “holobiont”

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The term “superorganism” was coined in 1928 by the great myrmecologist William Morton Wheeler to describe a colony of eusocial insects, such as ants. The “super” in superorganism denotes a higher level of organization, an association composed of multiple organisms of the same species. Individual members perform specific tasks, much like the cells in different tissues of an organism. Reproduction may be relegated to a specialized few. This division of labor is tightly integrated through a network of communications, the medium for the message being chemical in the case of insects. By virtue of the conspicuous analogies to human culture, the term has also wended its way into social and economic theory.

Of late, the superorganism appellation has been applied by some to symbioses between dissimilar species. Indeed, there is a need for a term. Throughout the biosphere, different species associate, transiently or permanently, to do things of ecological and evolutionary import. The labels initially applied to these relationships were rooted in economics and reflected the perceived benefit or harm, thus terms such as commensalism, mutualism, and parasitism. The actualities define a spectrum; the complex and sometimes subtle give-and-take defies such simple categorization. To better reflect this reality, Lynn Margulis proposed that any physical association between individuals of different species for significant portions of their life history constitutes a “symbiosis,” that all participants are bionts, that the resulting assemblage is a holobiont.

We find the term holobiont particularly useful. Every macrobe examined (and some microbes, as well) has been found to be associated with diverse microbes and viruses. Thus, although the macrobe typically contributes the name for the whole, each macrobe is but one biont among many that together constitute a functional holobiont. A holobiont occupies an ecological niche, adapts, and may be the organizational level at which natural selection acts. When challenged by environmental perturbations, a holobiont can employ strategies unavailable to any one species alone. Adaptation can occur rapidly by swapping microbial constituents or by reshuffling the relative proportions of current bionts. Natural selection will then favor the holobionts with constituents that confer increased fitness under the new conditions. Recognition of the holobiont inherently embodies the systems biology perspective; remove one biont to study it reductionist style and you learn not what that part does but how the now changed holobiont adapts.

Studying the complexity of a holobiont with all its diversity does not require the impossible. One can extract and sequence the DNA from the entire association—macrobios, microbes, and viruses. Analysis of the resulting metagenome can provide both a roster of the present membership and a survey of their combined metabolic functionalities. The genome of a holobiont, termed the hologenome, is the sum of the genomes of all constituents, all of which can evolve within that context.

Holobionts abound; every macrobe and its associates qualifies for this term. One of the first to receive the holobiont label was the coral-zooxanthella-microbe symbiosis. Here, the algal bionts living within the coral, known as zooxanthellae, represent several clades with different temperature and light requirements. The particular zooxanthellae in residence correlate with the holobiont’s position in the water column, thus with a particular light intensity and temperature. When subjected to temperatures above their thermal tolerance, corals lose their zooxanthellae, i.e., bleach. The adaptive bleaching hypothesis posits
that this bleaching can enable the holobiont to adapt by replacing less tolerant zooxanthellae with more tolerant ones. Reef-building corals exhibit exceptional productivity despite being located in nutrient-poor waters thanks to other microbial bionts. A complex web involving all three domains of life frugally recycles nitrogen within the holobiont. The abundant viruses that potentially infect all of the other bionts remain mostly unexplored.

Studies of insect holobionts have yielded attention-grabbing stories of the adaptive strategies of their microbial bionts. Bacteriophages infecting bacterial bionts within the pea aphid defend the holobiont against attacks by parasitoid wasps. Mealybugs host two bacterial endosymbionts, one nested within the other; the pathways for synthesis of some essential amino acids require genes from both. Similarly, looking to the plants, panic grass thrives in geothermal zones where soil temperatures can exceed 50°C thanks to a viral biont hosted within an endophytic fungal biont. Among the fungi, viral bionts within yeasts turn their hosts into killers armed with toxins.

Returning full circle to the eusocial insects, an ant colony remains a superorganism, but now seen as one composed of many individual ant holobionts. What better-known example of an ant holobiont than the fungus-growing ants? This holobiont includes attine ant macrobes, the monocultured fungal bionts in their “farm,” and various antibiotic-producing Bacteria, some of which protect the farm from invading fungal pathogens.

With the flourishing studies of our own microbiome has come the need for an accurate term for this combined macrobe-microbe-viral functional unit. It has long been realized that our metabolism is the product of many genomes not commonly regarded as our own. More recent studies continue to reveal more complex and essential interactions with our microbial bionts. Re-evaluating our anthropocentric view, we can now declare, with humility and with deep appreciation, that we are but one biont within the human holobiont.

Note: “Supraorganism” (meaning above the organism) has also been used as a synonym for holobiont. However, it is often confused with superorganism and is superseded by the introduction of holobiont.

**Suggested Reading**


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