17

Niche construction and the transition to herbivory: Phenotype switching and the organization of new nutritional modes

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Introduction

Eukaryotic organisms are not autonomous individuals. Rather, we are holobionts. The term "holobiont" refers to the consortium of zygote-derived cells plus their numerous associated microorganisms, including protists, archaeans, bacteria, fungi, and viruses. In the past decades, advances in microbiome research have shown that microbiomes are often essential for animals to develop, function, or reproduce normally (Funkhouser and Bordenstein, 2013; Gilbert et al., 2012; McFall-Ngai et al., 2013). The diverse ways animals and microbes shape and form symbiotic relationships with each other have important implications for the nature and boundaries of holobionts as biological individuals. What kinds of relationships imply that an animal is a "part" of a developing, living, evolving holobiont "organism"

Much work has centered on mutually beneficial, obligatory relationships within the holobiont. The reasoning is that holobionts are multispecies individuals when microbes are essential for host development and physiological functioning. The classic example is reef-building coral that survive only through the photosynthesis of their algal symbiont, *Symbiodinium*, which enters into the ectoderm of its host (zoon) and transports over 90% of its photosynthetically derived carbon compounds to the host cells (Muscatine et al., 1984). In exchange, the coral gives

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those endosymbionts critical nutrients and a safe, sunlit habitat in an otherwise nutrient-poor habitat (Roth, 2014). Without these symbionts, the coral, a keystone species for reef ecosystems, loses its color (bleaches) and dies. In animals, bacteria critical to the construction of the vertebrate immune system as well as gut capillaries and epithelia (Bates et al., 2006; Camp et al., 2014; Crabtree et al., 2007; Lee and Mazmanian, 2010; Stappenbeck et al., 2002). They also appear to be critical for the normal development of the vertebrate enteric and cerebral nervous systems (Cussotto et al., 2018; De Vadder et al., 2018).

Other arguments for holobiont organismality go beyond the complementarity of animal and microbes. Holobionts are individuals when host and microbes co-instigate developmentally novel and evolutionarily selectable phenotypes (Gilbert, 2016; Gilbert et al., 2010; Sudakaran et al., 2017). A remarkable example is the development and regulation of the mammalian immune system. The microbial colonization of the animal is facilitated by both maternal physiology and the animal's own immature immune system (Round et al., 2011; Chu and Mazmanian, 2013; Chiu and Gilbert, 2015). The recruited microbes in turn help induce the necessary development and functioning of host immune tissue, and these lifelong immune activities are well-regulated only in the continuous presence of microbes, which in turn constantly regulate which microbes stay with the animal (Chiu et al., 2017; Eberl, 2010; Eberl and Pradeu, 2017; Pradeu, 2012; Tauber, 2017). The immune system is a continuously coconstructed property of the holobiont.

In this paper, we develop a new line of reasoning for holobiont individuality—that animal and microbes coconstruct the ecological niches of the holobiont ("reciprocal niche construction"). Mounting evidence suggests that microorganisms can affect the niches of their host animals by changing the latter's diets, supplying defense systems against host predators, or by altering how hosts behave, determining a variety of niche parameters such as habitat space, diet, and ecological relationships with other species (Borges, 2017). Symbiotic microbes have been critical in determining nutritive niches. For instance, the endosymbiont *Buchnera aphidocola* enables the pea aphid *Acyrthosiphon pisum* to sustain itself on plant sap (Bennett and Moran, 2015). This bacterial symbiont is inherited vertically as a cytoplasmic contribution of the mother. One of us (Gilbert, 2019) has recently argued that horizontally transmitted microbial communities have also facilitated evolutionary innovations into new nutritive modes, specifically, from nonherbivory to herbivory diets (see also Vermeij and Lindberg, 2000). Consider the cow. It is an herbivore that occupies a plant-eating ecological niche. Yet, the animal—the multicellular organism developed from a single zygote—is not an herbivore. The animal, in fact, has no gene in her genome that encodes enzymes that facilitate the degradation of the cellulose or hemicellulose of grasses. Without its community of cellulose-digesting enzymes within its specialized rumen stomach, the cow cannot digest plant material. Cows occupy a plant dietary niche only *as* holobionts. The ability to eat living plant material opened numerous new evolutionary trajectories, giving rise to adaptations in animal digestive systems, mandibles, and locomotor organs.

In this chapter, we will focus on ruminants and elaborate niche construction frameworks to explain how evolutionary phenotypic switching occurred between drastically different nutritive modes as a function of gut microorganisms. It may be tempting to think of symbiont microbiota as building blocks that supply the animal with extended phenotypes and expanded niches. On this view, microorganisms harbor specific, functional traits that are recruited and added to the host organism. However, the transition from carnivory to herbivory is not just the gradual addition and removal of adaptive traits. It is also a dramatic shift in the significance and relevancy of the environments the microorganisms and host organisms find themselves in, mediated by their plasticity and abilities to construct their environments. The transition to herbivory involves various forms of niche construction at different levels of organization that facilitate transitions in niche space and adaptations. A holobiont perspective is crucial to capture, within a single explanatory unit, the important niche construction processes occurring at these different levels and between multiple species. We propose an eco-evo-devo (ecological evolutionary developmental) approach that focuses on changes in the developmental capacities of the holobiont that direct the dynamic construction of environmental opportunities and challenges.

Let us start by telling a microbe-filled story of how the cow gets its rumen.

How the bovine got its stomach

Herbivores typically arise from carnivores, making herbivory a derived condition. This runs counter to the ecological condition of extant ecosystems, wherein herbivores eat the herbs, and the carnivores eat the herbivores. However, genomic and paleontological evidence both show that the basal state of both Ecdysozoa and Vertebrata is carnivory, and that herbivores are late additions to the tree of life (Román-Palacios et al., 2019). In the sea, “macrophagous primary consumers” were not found in early marine ecosystems. Instead, the ocean fauna was dominated by filter feeders, detritovores, and the carnivores that ate them (Vermeij and Lindberg, 2000, p. 200).

Ruminants are an extremely successful mammalian lineage, and they are characterized by a multichambered stomach (including the rumen, which can digest plant fiber), cranial headgear (that include horns and antlers), and specialized hypsodont dentition for grinding plants. Representative species include cattle, buffalo, deer, sheep, goats, and yaks. Crown group ruminants begin to appear in the late Oligocene, about 35 million years ago. The horned ruminants appear about twelve million years later (Chen et al., 2019).

One of the classic examples of developmental and nutritive symbioses concerns the relationship between the microbial symbionts and the four-chambered stomach characteristic of the ruminants. In the following, we examine three critically important symbioses between the gut microbes and the bovine organism. In each case, microorganisms are proactively involved in facilitating the transition of the holobiont and its constituents into an herbivory niche. The first set of symbioses involves the roles of microbes in constructing the rumen of the gut. This new region of the stomach, from which “ruminants” get their name, creates a suitable environment for further bacterial proliferation while initiating developmental processes that mature the previously nonfunctional rumen organ. The second set of symbioses involves the roles of these rumen bacteria in digesting the plant fibers, thereby enabling the calf survive by digesting grass and plant fibers. The third set of symbioses involves the microbe-dependent neutralization of plant defense chemicals, allowing the calf to continue to utilize plants as a food source.

As we will see, these symbioses scaffold two types of niche construction. The first is “perturbational niche construction” (Odling-Smee et al., 2003) by microbes and their by-products that alter the host rumen environment. Here, the bacteria build their residence from the host tissue of their environment, which in turn deeply alters the digestive organs of the host. The second is “mediational niche construction” (Chiu, 2019) of the ecological niche experienced by the holobiont. Here, through the microbe-induced developmental and physiological processes, the holobiont gradually enters and maintains an herbivorous ecological niche whereby plants have significance as nutritive sources. This developmental process suggests an evolutionary sequence of niche transition also mediated by microorganisms.

Developmental symbiosis: the microbial-dependent development of the ruminant stomach

In the newborn calf, the four chambers of the stomach are already evident. The largest chamber of this organ is the abomasum, the "true stomach" that is homologous to other mammalian stomachs. This comprises about 60 % of the gastric volume. Another 15% of the volume is found in the omasum and reticulum chambers, and the rumen of the newborn contains about 25% of the stomach volume (Tamate et al., 1962).

Newborn calves have sterile rumens, and the digestive tube becomes colonized by microbes as the calf pass through the birth canal. Within 2 days of birth, the area of the rumen is seen to have microbes within it. These microbes are capable of degrading cellulose plant fibers (Moraïs and Mizrahi, 2019). However, the baby calf does not receive grass or grain to eat until it is weaned. Before that time, it receives milk from the mother cow, and the rumen, although containing bacteria, is small and nonfunctional. The milk does not go into the rumen, but is shunted by an esophageal groove into the abomasum. Upon weaning, the esophageal groove flattens, and the masticated grain proceeds directly into the rumen (Baldwin and Connor, 2017; Daniels and Yohe, 2014). There, bacteria such as *Ruminociccus flavefaciens* produce "cellulosomes," plant wall-digesting enzyme complexes that are bound to the bacterial cell surface, which efficiently metabolize the complex polysaccharides.

The bacteria in the rumen multiply when given this plant food, and as they proliferate, they produce volatile fatty acids, including butyrate. Butyrate causes the dramatic growth of the rumen as well as the differentiation of the ruminal papillae and musculature. Indeed, butyrate will cause the premature growth and differentiation of the calf rumen when it experimentally infused directly into the immature rumen or when it is placed into the milk drunk by the calf (Baldwin and Connor, 2017; Sander et al., 1959). Numerous genes encoding transcription factors, especially those associated with cell proliferation, are induced by the infusion of butyric acid into the rumen (Baldwin et al., 2018; Chen et al., 2019), and butyrate produced by gut bacteria is known to regulate gene expression through its activity as a regulator of histone deacetylase (Wu et al., 2012;

Yuille et al., 2018). The regulation of rumen development is thought to be achieved through bacterially driven host genome transcription through DNA methylation changes and microRNA production (Li et al., 2019; Malmuthuge et al., 2019). By three months, the rumen comprises about 85% of the calf's stomach volume. It is thusly that the gut bacteria construct their own niche, the rumen.[1]

Nutritional symbiosis: the microbe-dependent digestion of plant fiber

The second symbiotic effect of the ruminal bacteria is the digestion of plant fiber. The bacteria have helped build the rumen, and the rumen will now serve as a place of residence for these microbes and the calf's body will be modified to supply them and the calf with food. Plant cell walls, rich in pectin and cellulose, are the largest reservoir of organic carbon on earth (Gilbert, 2010), and the architecture and physiology of the rumen have evolved for millions of years to obtain the solar energy stored in these plant fibers (Mackie et al., 2002). Over 70% of the cow's energy comes from this microbial digestion of plant fiber (Flint et al., 2008; La Reau and Suen, 2018), demonstrating the primacy of microbes in a cow's herbivorous feeding strategy. Most animals (with the exception of certain plant-eating beetles that acquired their genes for digesting plant fiber by lateral gene transfer from microbes) do not have genes encoding the enzymes that digest these plant polysaccharides (Calderón-Cortés et al., 2012; Kirsch et al., 2014). Bacteria, protists and fungi, however, evolving as plant pathogens or saprophytic detritovores, often have genomes that do synthesize and secrete such enzymes.

Most of these plant cell wall-digesting enzymes belong to various glycoside hydrolase families, constituting cellulases, hemicellulases, and pectinases (Moraïs and Mizrahi, 2019). The enzymes can be secreted by bacteria, protists, fungi, and archea. Bacteria comprise the dominant proportion of the ruminal

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[1] Butyrate can also function as a nutritional substrate, RNA splicing regulator, or as a G-protein activator, and microbiome-produced butyrate appears to be critical for normal human intestinal homeostasis (Dowhaniuk et al., 2019). Moreover, this short-chain fatty acid plays several roles in activating dormant development throughout the animal kingdom, including the reactivation of tick development through the smell of bovine butyrate (von Uexküll, 1934).

microbes (about 95% of the microbial population), with the archaea comprising 2%–5%. The eukaryotic component of the ruminal ecosystem is very small (Flint, 1997; Mizrahi, 2013). The microbial cellulose degraders (primarily bacteria and fungi) often produce several types of cellulases, including those that attack the ends of the fiber and those that cleave internally (Lombard et al., 2014). Hemicellulose has fewer carbohydrate units, and often contain xylose. Again, many different hemicellulose-digesting enzymes can come from a single microbe, and numerous species of microbes secrete such enzymes. Most of the cellulases and hemicellulases are secreted from bacteria, with some species producing both types of enzymes. Cellulose-degrading enzymes are produced by genera such as *Ruminococcus* and *Fibrobacter*. Many of the hemicellulases originate in those genera and in *Prevotella* (Dai et al., 2015). Interestingly, the giant panda (*Ailuropoda melanoleuca*), which only eats the new shoots of bamboo trees, comes from a carnivorous lineage and seems to be "learning" herbivory. It has a symbiont that can digest hemicellulose, and so its diet is fixed to the new shoots that have not yet made their cellulose and lignin-containing stalk. Giant pandas cannot eat mature branches (Zhang et al., 2018).

Within the rumen ecosystem, there are interactions at several levels. Synergy between the hemicellulases and cellulases is essential for plant fiber digestion, and different microorganisms contribute enzymes with overlapping functions for digesting these plant fibers (Artzi et al., 2017; Bayer et al., 2013). Moreover, the products of fiber digestion appear to regulate interactive networks that sustain the rumen ecosystem. The digestion of complex fibers into simple sugars supports the growth of a second set of microbes that can persist on the sugar monomers. The digestion of simple sugars, in turn, not only generates new metabolites for other microbes, but also generates hydrogen that can be used by methanogens. The presence of such methanogens accelerates the cellulose hydrolysis. Fungi and protists probably assist the bacteria in supporting this ring of symbiosis (Morvan et al., 1996; Newbold et al., 2015). Competitive interactions between bacteria, and between bacteria and protists, also contribute to the stability of the ruminal ecosystem (Allesina and Levine, 2011; Chen and Weimer, 2001; Moraïs and Mizrahi, 2019). The host genome also plays some role in determining which of the keystone cellulose-degrading and hemicellulose-degrading bacteria will thrive and proliferate in the rumen

(Sasson et al., 2017; Wallace et al., 2019). Thus, the symbiotic microbiome is stabilized through interactions between the microbes and between the microbes and the host environment.

Protective Symbiosis: the microbe-dependent detoxification of plant defense chemicals

Herbivory can be maintained only if the herbivore is capable of neutralizing those toxic secondary compounds that are made either by the plant or by the plant's symbionts. Each plant makes its own set of secondary compounds, and ingestion of these chemicals can lead to the death or severe impairment of the herbivore that eats them. Herbivory would not be possible unless animals had ways of degrading or excreting these poisons (Freeland and Janzen, 1974).

Dominguez-Bello (1996, p. 323) has characterized the rumen "as a detoxification chamber," where detoxification can be done by evolutionary changes in the animal's genome (Malenke et al., 2014) or by the acquisition of particular symbionts (Smith, 1992). For instance, ruminants need certain tryptophan-utilizing bacteria (such as *Clostridium sporogenes*) to degrade the alkaloid toxin ergovaline found in the seeds of tall fescue seeds (Harlow et al., 2017). The ergovaline, itself, is made by an endocytic fungus that lives between the cells of the plant. Indeed, there is a "the three-way interaction" between plants, herbivores, and microbes (Wielkopolan and Obrepalska-Steplowska, 2016), and Smith (1992, p. 25) notes that "it has been suggested that rumen microbial detoxification of poisonous plants might have been as important as rumen microbial degradation of cellulose for the evolutionary development and ecological expansion of ruminants as herbivores."

Thus, symbiotic microbes help construct the rumen, digest the fiber into short-chain fatty acids that can serve as nutrition for the organism, and detoxify the poisons that plants and their symbionts produce in the evolutionary defenses against such herbivory. In return, the microbes get room, board, and roommates—a residence, masticated plant material, lipids for their cell membranes, and other microbes that integrate them into a stable community. The bovine ruminant is completely dependent upon the symbionts after it has been weaned. Such vertebrates go from a set of maternal symbiotic relationships to the nutrition produced by the plant fiber-digesting ruminal ecosystem comprised of symbiotic microbes. As Moraïs and Mizrahi

(2019, p. 5) conclude, “Bacteria are obligate inhabitants of the rumen; without them, the host animal would not survive.”

Perturbational and mediational niche construction

It is tempting to think of these three types of symbiotic relationships as microbe-induced adaptive phenotypes of the animal and the microbes to a plant dietary niche. The ruminant animal and microbes have benefited from these coconstructed traits and were thus likely selected for their continued alliance. Yet there are several[2] explanatory problems with this approach. One main issue is that it assumes a process of adaptation that gradually matches traits to environments through natural selection. Microbes helped induce or provide selectable, adaptive traits better adapted to a previously unexplored part of the environment—an empty niche. This way of thinking assumes that an herbivory niche preexisted in the environment ready for the ruminant ancestor to adapt into (eventually, through microbes).

The notion of an empty niche existing independently from organisms, however, is explanatorily problematic (Lewontin, 1982, 1983, 2000). Organisms—through their physiology—define which aspects of the external world are relevant and how they are significant. They also actively construct and change the physical features of the environment surrounding them. Ecological niches do not preexist the organisms that “occupy” them. If the “empty niche” does not exist, then niches cannot be used as a prior cause to explain evolutionary outcomes.

We argue that the rumen symbionts helped *construct* a different niche from the same environment. The characteristic niche of a cow—being an herbivore—is in large part determined by its gut microbiota. The microbes did not modify the external niche of the host (the plants outside of the cow). Rather,

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[2] An issue with perceiving the holobiont as extended phenotype comes from *whose* phenotype is being extended. The default view is to privilege the multicellular eukaryote and describe microbes as its extensions. However, as Gould (1994) has noted, the prokaryotic microbes preceded eukaryotes by billions of years, and the eukaryote, itself, is derived from the symbiosis of archaean and bacterial prokaryotes. Richard Dawkins (1976) has claimed that “the individual organism is a survival machine for its genes.” The “extended phenotype” principle would insist that the eukaryotic organism is an extended phenotype of the microbes and a survival machine for the microbial genomes. Animal and plant reproduction and evolution would become the generation of more niches for the proliferation and diversification of microbes (see Gilbert, in press). Such a fusion of Dawkins and Gould is a precarious undertaking.

vegetation, which had always been in the environment of the carnivores, has now been transformed into a nutritive resource. This evolutionary innovation switched organisms from one type of niche to another, creating a fundamental change in the types of relationships between them and the environment. Vegetation that was once not edible becomes edible to the organism; plant parts that were not nutritious became nutritious.

Perturbational niche construction

In standard niche construction theory, two types of niche construction have been identified (Laland et al., 2017; Odling-Smee et al., 2003): (1) *perturbational niche construction*, whereby modifications organisms make to the environment results in a part of the environment acquiring a different property (e.g., built structures), (2) *relocational niche construction*, whereby the organism surrounds itself with a different environment, leaving its original environment. Both perturbational and relocational niche construction processes determine the intrinsic, physical properties of the environment surrounding an organism. In the first case, the properties in the environment are directly modified. In the second case, the organism enters an environment with a different set of properties.

In the switch to an herbivore niche, perturbational niche construction occurred within the cow. Microorganisms created host-internal niches that induce complex innovations in host development, morphology, and function. Here, niche construction and developmental plasticity meet as microbes engage in a "developmental niche construction[3]" that alters the development of the host (Gilbert, 2016; Laland et al., 2008; Stotz, 2017; Sudakaran et al., 2017). Hosts in turn engage in perturbational niche construction that determine and alter the niches of its microorganisms (Bevins and Salzman, 2011; Donaldson et al., 2015). The rumen codevelops and coevolved with the microbial communities that can flourish within.

Mediational niche construction

There is a third type of niche construction that occurs when the organism experiences a different environment despite no changes to the latter's intrinsic, physical properties. The organism instead alters which aspects of the environment are

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[3] See (Flynn et al., 2013; Stotz, 2017) for discussions on developmental niche construction and how it differs from selective niche construction.

relevant to it or change the significance of the environment to the organism. The environment *affords* a different opportunity for exploitation (Walsh, 2015).

This "experiential" type of niche construction was described by Richard Lewontin (1982, 1983, 2000), who noticed that organisms do not just alter their environments, but also determine which components of the environments are relevant and in what way. The organism's phenotype could determine how an environment is experienced. A fluctuating environment can be experienced as constant if the organism has ways of compensating for the changes through mechanisms such as fat storage or temperature regulation. Jakob von Uexküll (1934) and his notion of *Umwelt* also emphasized the interpretation of the environment by the organism. While most organisms would be unaffected or slightly irritated by the faint odor of butyrate coming from mammalian sweat, to the aforementioned tick, it is the pivotal signal that reactivates its dormant life cycle.

This third mode of niche construction has been coined "*mediational niche construction*," since the parts of the environment that are relevant (in what way) are mediated by the organism's makeup (Chiu, 2019). It has only recently been explicitly treated under the lens of phenotypic plasticity and organismal agency (Sultan, 2015; Walsh, 2015). Sonia Sultan (2015) has compiled a large collection of morphological, physiological, and behavioral changes in microbes, animals, and especially plants that alter whether an organism experiences its environment as plentiful, warm, fluctuating, threatening, or competitive. For instance, an environment that has more predators can be experienced as less "threatening" when plastic changes in the organism decreases the activities or impact of the predators.

To Sultan, the relevance of the environment is mediated through the perceptual and information transduction networks of the organism. These include experiences of the environment's temperature, threat levels, and the richness of its resources. When plastic responses to environmental cues occur in the organism, the phenotypic changes in these networks can alter the way the environment is experienced. Since the selective environment is determined by the experience of the environment, plastic, developmental responses to environmental cues can have evolutionary consequences mediational niche construction. Applying these perspectives to the ruminant holobiont, we can find an alternative interpretation of the three symbiotic relationships. The three symbiotic events between cows and microbes—microbe-dependent development, digestion, and toxin neutralization in and of the rumen—are features that determine the ecological niche of the cow holobiont. The cow, as a holobiont, can experience plants as edible and, furthermore, a safe, nontoxic source of nutrition, only because microorganisms helped *mediate* a plant-based nutritive niche (mediational niche construction). This niche was also possible only due to the microbe-induced development of the rumen, which was part of the microbiota's efforts to modify the rumen into its own ecological niche (perturbational niche construction). The transition into herbivory thus involved multiple types of niche construction.

Niche construction, plasticity, and developmental scaffolding

To better understand how developmental plasticity figures into the evolutionary transition between nutritive modes, we can make use of another conceptual framework that has been developed for holobiont systems—the idea that biological systems form "hybrid" life cycles of scaffolded development and reproduction (Chiu and Gilbert, 2015; Griesemer, 2014a,b). The basic idea is that each developmental stage or phase of a biological system is reached only by engaging with "scaffolds," catalytic entities and processes that allow novel processes to occur at lower difficulties and costs. Developmental scaffolds remove difficulties that would otherwise prevent some developmental process from occurring. The scaffold and scaffolded systems are temporary and distinct from each other, but when interacting is integrated into a larger, chimeric, hybrid system. This hybrid system acquires and realizes the developmental capacities to move on into the next stage only because of the interactions between the scaffold and the scaffolded. The hybrid then confers developmental capacities to the following phase, which may consist of a different scaffold-scaffolded hybrid.

In order to transform in and out of different hybrid states, the scaffold and scaffolded remain sensitive and responsive to each other. They are inherently plastic and readily engage in interactions that form hybrid systems. As in mammalian childbirth (Chiu and Gilbert, 2015), there is a mutual scaffolding between the animal and the microbial community. The microbial community scaffolds the development and procreation of the animal, while the animal scaffolds the organization and procreation of the microbes. The mammals create the environmental niches for the microbes; the microbes make the environmental niches for the mammals. In this coconstruction, they are each other's niches. This is reciprocal niche construction.

Indeed, in the ruminants, this is critical. Birth is a holobiont event, wherein symbionts are transferred from one generation to another, and this is when the calf receives the microbiome that will reside in its rumen. Then, there is an intermediate stage where the calf is fed only its mother's milk. This boosts its immunity, alters its microbiome, and nourishes the calf. Finally, there is weaning and the ingestion of grain that enables the production of the butyrate that induces ruminal growth and differentiation. The boundaries between the scaffolds, the scaffolded, and the perceived niche are a matter of perspective, and the same object or process can move between these categories.

Thus, we are able to provide a novel conceptual interpretation and explanation for the opening of herbivory as an evolutionary opportunity. We argue that microbes helped construct new physical niches by altering bodily development (developing the rumen) and generating a new mediational niche (plants as food) by altering the experience of the environment.

The coconstruction of niches in a symbiotic relationship is not a uniquely holobiont phenomenon. Coniche construction can be an instigator of mutualism between a microorganism and microorganisms when one party has an ecological niche (e.g., a nutritive source) that can only be constructed by another (or if both parties require a coconstructed niche) (Buser et al., 2014). For instance, unlike their evolutionarily cousins, bark beetles are unique in their abilities to live on nutrition-poor outer bark instead of the nutrition-rich phloem. This evolutionary shift in diet was made possible by symbiotic associations with fungi that transform the properties of wood (Six, 2019). These beetles kill the tree and transport these specific fungi to these trees, modifying the woody surface for the fungi. The fungi then digest the tree tissues, providing nutrients for the beetles. The fungi are obligate niche constructors for the beetles and vice versa. The beetles harbor highly selective mycangia that carry these specific fungi species and thus maintain their symbiotic relationship across generations.

However, unlike these cases where the modified niche is external to both symbionts, for the holobiont, microbes are modifying niches within the host, with consequences for niches experienced by the host and holobiont.

Implications for holobiont individuality

What kind of individual is a holobiont? Are they units of selection? In current debates, the answer hinges on whether the relationships between macro and micro actors and satisfy traditional criteria of evolutionary individuality. On the one hand, many have argued on the basis of functional integration, especially through obligatory symbiosis, that holobionts do satisfy criteria of anatomical, metabolic, developmental, immunological, and evolutionary units (Gilbert et al., 2012; Lloyd and Wade, 2019; McFall-Ngai et al., 2013; Rosenberg and Zilber-Rosenberg, 2016; Roughgarden et al., 2017; Zilber-Rosenberg and Rosenberg, 2008). Yet skeptics argue that such evidence is insufficient to establish the evolutionary individuality of holobionts as the organisms involved have conflicting evolutionary interests and their ecological relationships are similar to macroscale ecosystems (Bourrat and Griffiths, 2018; Christian et al., 2015; Costello et al., 2012; Douglas and Werren, 2016; Moran and Sloan, 2015; Skillings, 2016).

Neglected in these discussions is the importance of constructed environments and developmental plasticity for biological individuality. The examples we have described in this paper provide support for a different way of thinking about evolutionary units. The holobiont is an evolutionary unit or individual because evolutionary opportunities such as the plant dietary niche are made available for all constituents of the holobiont by the holobiont as a whole. The cow animal and its gut bacteria construct and solidify an herbivory ecological niche through perturbational (changes to the gut rumen) and mediational (changes to the significance of the plant environment) niche construction at a developmental time scale. This developmental process likely opened up evolutionary opportunities that placed the entire ensemble under the selective pressures specific to the plant-eating life.

Our proposal shifts attention from “what kinds of *individuals* are holobionts” to “what kinds of *processes* make holobionts.” We examined niche-constructing processes. Symbiosis is critical in producing the niche construction processes that bias selective environments, as well as the developmental scaffolding that biases developmental variations. An eco-evo-devo approach asks how these processes determine developmental and evolutionary trajectories. Following Sultan and Walsh, we propose to focus on how these hybrid systems create and alter experienced niches. Following Griesemer, we propose to look at the way host-microbiota hybrid systems dynamically alter through time as they come to acquire, realize, and pass on developmental capacities to reproduce.

Organisms and their environments (including other organisms) are commingled. Changes in organisms—their agency and plasticity—entail changes in their experienced environments, which alters the way they develop, are ecologically organized, and evolve. Host microbiota is involved in these types of changes. Developmental plasticity is a key element to the host-microbiota coconstruction of a plant-based niche that is relevant, accessible, and easier to live in. Animals are inherently plastic and symbiotic microbes are mediators of developmental plasticity, which enables the holobiont organism to develop in particular directions. Symbiosis-inducible plasticity can be adaptive, with the symbionts facilitating specific trajectories of development (Dunbar et al., 2007; Kikuchi et al., 2012; Oliver et al., 2009; Tsuchida et al., 2010).

Hypothetically, the original members of the ruminant fiber-eating ecosystem were detritovores that found residence in a vertebrate stomach. However, this community has evolved enormously. While it is not known whether there are "phylosymbiotic" associations of microbes and ruminants, such that those in hydra and primates, there appears to be a "core microbiome" in cow rumens. Sequencing the rumen microbiota of 1016 cows in four separated European countries. Wallace et al. (2019) found a core rumen microbiome of some 454 prokaryotes, 12 protists, and 46 fungi. A subset of 39 bacteria species was found to be linked physiologically to each other and to the host genomes. Differences within the core microbiomes correlated well with specific phenotypic traits such as methane production and milk quality, indicating the importance of the microbiome for holobiont phenotype (Wallace et al., 2019; Lima et al., 2019). It is also known that diet and housing regimen also contribute the diversity of the microbial populations of the rumen, and that genera between cows were more common than species (Hagey et al., 2019; Jami and Mizrahi, 2012). In this manner, the rumen appears to be similar to the conditions of gut microbes in humans (Bäckhed et al., 2012), suggesting that continuity of the species matters less than continuity of function.

Recently, some researchers (Doolittle and Booth, 2016; see also Suárez, 2018; Taxis et al., 2015) have proposed that the genes of the holobiont (the hologenome) constitutes a functional replicator, a network of genetic interactions that are instantiated across different generations of holobionts. In this view, it is the *functions* of the bacteria that matter, not the *species*, i.e., what

Doolittle and Booth (2016) call, “the song and not the singer.” This metabolic, physiological, view of organism reflects some of the basic ideas of inheritance that were popular before the field of heredity became limited to genetics. Indeed, in one of his prescient paragraphs, Wilson (1896, p. 431) writes, “In its physiological aspect, therefore, inheritance is the recurrence in successive generations, of like forms of metabolism…” The holobiont has similarly been seen in this regard. Suárez and Triviño (2019) note that holobionts are units of selection, even if they acquire their microbiota from the environment. What is critical for inheritance is transgenerational *trait-recurrence*. In this case, the trait is herbivory, and the host would die if the transfer of the plant fiber-digesting consortium of bacteria was not made.

The continuity of symbiotic species might not be critical in holobiont continuity, since (1) the same sets of functions can be contributed by different species of bacteria, and (2) horizontal gene transfer is probably common among symbionts (J. Suarez, personal communication).[4] Indeed, horizontal gene transfer, mediated through bacteriophages, overrides mutation as the source of variation for *Escherichia coli* colonizing the human gut (Frazão et al., 2019), and intra-species transfers of particular genes that provide the holobiont with a new source of nutrition have been identified (Hehemann et al., 2010). Certainly, vertical transmission is not the *sine qua non* for being a unit of evolution or natural selection. The cow receives its symbiotic communities horizontally, and these microbes are critical for the nutrition and the existence of the cow. There is probably a spectrum of phylosymbiotic compatibility. In some organisms, such as Hydra (Fraune and Bosch, 2007), different species may have vastly different symbionts than other species; while in others animals, any number of different species might fulfill a core metabolic function. In some cases, the song can be performed well by numerous singers, while in other cases, the singer may be critical to the quality of the song. After all, any rocker can belt out *Satisfaction*; but no one sings it like Mick Jagger. This is one of the many research projects that are opened by viewing organisms as holobiont functions.

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[4] Here we may be seeing the symbiotic equivalent of developmental systems drift, where the same trait may be accomplished by different genes in different species (Krol et al., 2011; True and Haag, 2001).

Conclusion

This essay has explored certain changes in our understanding of biological individuality that may have to be made if a holobiont view of organism means more than just a microbial extension of host phenotype. Using the cow as an example, we have presented a view of the holobiont that strengthens the claim that holobionts are developmental and evolutionary units.

Developmental plasticity and two modes of niche construction—perturbational and mediational niche construction—enable the host and microbial community to coconstruct an herbivory ecological niche experienced by the holobiont as a whole. Microbes are not just extended niche constructors of the *host*, but are coniche constructors of holobiont ecological and evolutionary niches. A cow is a holobiont, but is *Bos taurus* the holobiont or merely the animal component of it We would argue that it is the holobiont.

The exploration of the symbiotic origins of herbivory highlights the critical importance of developmental plasticity in making arguments in evolutionary developmental biology, for we are talking about holobiont evo-devo. To put it another way: If (1) evolution is brought about by inherited changes of development (a principle of evo-devo) and if (2) development is caused, in part, by symbiotic interactions with microbes; then changes in the interactions of host and microbial communities may cause changes in holobiont evolution.

In addition to the facilitation of developmental stages, this holobiont perspective also entails the transition between niches. The induced developmental capacities must be seen as capacities to exploit niches. Microbes can help secure certain selective ecological niches (maintaining access to niches and the ease and ability to properly utilize these niches) through scaffolding at the developmental level. Evolution and development are thus integrated not only in the production of new variants upon which natural selection can act; they are also integrated in the formation of new niches and the integration of the organism into the habitat it has helped to create.

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