

REVIEW ARTICLE



## Co-niche construction between hosts and symbionts: ideas and evidence

RENEE M. BORGES\*

Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560 012, India

\*E-mail: renee@ces.iisc.ernet.in.

Received 22 November 2016; revised 17 December 2016; accepted 27 December 2016; published online 5 July 2017

**Abstract.** Symbiosis is a process that can generate evolutionary novelties and can extend the phenotypic niche space of organisms. Symbionts can act together with their hosts to co-construct host organs, within which symbionts are housed. Once established within hosts, symbionts can also influence various aspects of host phenotype, such as resource acquisition, protection from predation by acquisition of toxicity, as well as behaviour. Once symbiosis is established, its fidelity between generations must be ensured. Hosts evolve various mechanisms to screen unwanted symbionts and to facilitate faithful transmission of mutualistic partners between generations. Microbes are the most important symbionts that have influenced plant and animal phenotypes; multicellular organisms engage in developmental symbioses with microbes at many stages in ontogeny. The co-construction of niches may result in composite organisms that are physically nested within each other. While it has been advocated that these composite organisms need new evolutionary theories and perspectives to describe their properties and evolutionary trajectories, it appears that standard evolutionary theories are adequate to explore selection pressures on their composite or individual traits. Recent advances in our understanding of composite organisms open up many important questions regarding the stability and transmission of these units.

**Keywords.** co-niche construction; holobiont; hologenome; microbes; microbiome; niche construction; symbiosis.

### Introduction

As early as 1878, Anton de Bary stressed that symbiosis was an important source of evolutionary novelty, even resulting in ‘new’ organisms such as lichens; therefore, it was proposed that the study of symbiosis as a generator of innovative phenotypes would open up a new field of research (Sapp 1994). The idea of symbiogenesis or symbiosis as a mechanism facilitating evolutionary novelties (Margulis 1991) and allowing new environments to be utilized was advanced in the early 20th century by Russian botanists well before Lynn Margulis (Khakhina *et al.* 1992). Whatever the process of generating ‘organisms’, that organismal features and their environments are in a dynamic feedback process has long been acknowledged (Van Valen 1973). Ideas regarding organism–environment feedbacks, their influence on an organism’s niche, and niche construction have been ably stated by Lewontin (1983):

*[g]enes, organisms, and environments are in reciprocal interaction with each other in such a way that each is both cause and effect in a quite*

*complex although perfectly analysable way . . . More paradoxical is the necessity of defining environments without organisms. To make the metaphor of adaptation work, environments or ecological niches must exist before the organisms that fill them . . . The history of life is then the history of the coming into being of new forms that fit more and more closely into these pre-existent niches. But what laws of the physical universe can be used to pick out the possible environments waiting to be filled? In fact, we only recognize an ‘environment’ when we see the organism whose environment it is. Yet so long as we persist in thinking of evolution as adaptation, we are trapped into an insistence on the autonomous existence of environments independent of living creatures . . . Organisms do not adapt to their environments: they construct them out of the bits and pieces of the external world.*

The idea that organisms can engineer and also influence their external environments is, therefore, an old one, as is the notion that organisms and external environment

can exert feedbacks on each other. Classical and oft-cited examples of niche construction and ecosystem engineering include those of termites constructing nests that house their colonies and millions of symbionts including cultivated fungi, of coral with their photosynthetic symbionts constructing reefs, and of beavers constructing dams that modify their own ecosystems (Laland and Sterelny 2006). In recent times, however, many interesting discoveries emphasise the view that the internal environments of organisms can also serve as ecosystems and can consist of coevolving niches that are constructed by symbionts such as microbes. The symbiont community involved in constructing these internal niches can in turn affect the development and phenotype of the organism within which these niches occur (Moczek 2015). This phenomenon of co-niche construction which can also extend into the phenomenon of developmental symbiosis, wherein the development of an organism is a joint endeavour between host and symbionts, is an exciting frontier (Gilbert *et al.* 2015). In the current paper, the term co-niche construction is being used for those developmental activities where the interests of the host and symbiont are aligned, and also for those in which parasites take over the host for their own purposes, as occurs in gall-inducing insects for example. Whereas parasitism and its impact on host development have received ample attention, co-niche construction that achieves the 'normal' phenotype of an organism in the absence of obvious pathology is worthy of much more research. This paper will focus on the latter.

This paper draws from most recent and a few classic examples to demonstrate that research into co-niche construction is rich in questions that have bearing on how organisms or individuals are defined and how the components of their mutually constructed niches may be inherited.

### Co-construction of an organism and its physical and behavioural niche

The evidence for co-construction of organisms across the tree of life is mounting (McFall-Ngai 2002,2013; Fraune and Bosch 2010). Microbial communities with impressive features, both in terms of diversity and biomass, are contained within organisms, leading to the view that plants and animals should be considered as host–microbe ecosystems. The phenotype of the host organism, and of its symbionts, is extended as a result of these interactions. Such phenotype extensions could include organ development, multicellularity, new foraging substrates, and modifications to host behaviour.

The developmental symbiosis between the squid, *Euprymna scolopes*, and its bioluminescent bacteria is probably the best documented example of co-construction of an animal organ through partner choice by the host animal. The establishment of the symbiosis between the squid and its symbiotic *Vibrio* which ultimately leads to

the development of the light organ in the squid is a multi-step process (Montgomery and McFall-Ngai 1994; Doino and McFall-Ngai 1995; Schwartzman and Ruby 2016). In brief, the process begins at squid larval hatching, when peptidoglycan fragments of bacterial cell walls in the marine bacterial plankton community induce copious mucous production by the larvae; a winnowing process occurs within this mucous net such that only gram-negative bacteria and particularly *Vibrio fischeri* cells are selected; the bacteria are drawn into the larval mantle cavity by cilia, and are later responsible for inducing light organ morphogenesis, in which crypts are created, within which the bioluminescent *Vibrio* reside. Once a mature light organ has been developed and has been occupied by a carefully chosen symbiont population, a diel rhythm is established in which 95% of symbionts are expelled from the organ at dawn, while the remaining symbionts build up symbiont populations until dusk when the bioluminescence is triggered. This diel cycle is also accompanied by regression of the villi of the crypt epithelium before dawn when the symbionts are expelled, and a recrudescence of the villi when symbiont populations are re-establishing. There is thus an ontogenetic and a diel remodelling of the light organ in this system. Chemical conversations between host and symbionts dominated by glycans appear to be largely responsible for these phenomena (Schwartzman *et al.* 2015).

Molecules of bacterial origin have also played an important role in the evolution of multicellularity and eukaryotic morphogenesis. For example, colony formation leading to the rosette phenotype in the choanoflagellate *Salpingoeca rosetta* is induced by a sulphonolipid produced by a prey bacterium (Alegado *et al.* 2012). The aggregation response of the choanoflagellates occurs in a dose-dependent manner to sulphonolipid concentration to effect greater prey capture; high concentrations of sulphonolipid elicit no aggregation response presumably signalling to *Salpingoeca* that there is sufficient prey in the immediate environment such that a phenotypic shift is not necessary to capture prey effectively.

The classical symbiosis in which symbiotic nitrogen-fixing endosymbiotic rhizobia co-construct root nodules that harbour these bacteria has been well characterized for the specificity and signalling between plants and microbes (Wang *et al.* 2012). In vertebrates such as mice and zebrafish, gut microbiota are responsible for gut angiogenesis and gut development (Stappenbeck *et al.* 2002; Rawls *et al.* 2004). Mosquitoes also require gut microbiota for gut development during larval stages, and gnotobiotic larvae do not develop (Coon *et al.* 2014). The rickettsial bacterium *Wolbachia*, which is maternally inherited through the egg in insects, is usually considered an insect parasite since it, among other effects, feminises individuals and engages in killing males (Werren *et al.* 2008). However, in bedbugs, *Wolbachia* is housed within a special symbiotic organ called a bacteriome, and functions as

a nutritional mutualist of its host, supplying it with B vitamins that it synthesises (Hosokawa *et al.* 2010). On the other hand, the parasitic wasp *Asobara* is dependent on the presence of *Wolbachia* to complete egg maturation (Dedeine *et al.* 2001); this dependency is the possible outcome of parasitism by *Wolbachia*, and is unlikely to be indicative of a mutualism (Werren *et al.* 2008). Clearly there is a parasitism–mutualism continuum within these host–microbial symbioses. In all mutualistic symbioses, host sanctions likely control host exploitation by cheater symbionts (Frederickson 2013). These mutualism stabilizing mechanisms have been documented in some co-construction systems such as within plant–rhizobium and fig–fig wasp interactions (Oono *et al.* 2011; Borges 2015a).

Symbionts can extend the diet and niche space of their hosts. For example, genes have been transferred from the marine bacterium *Zobellia galactanivorans*, that feeds on the marine red alga *Porphyra*, to the bacterium *Bacteroides plebeius* residing in the gut of Japanese humans; this enables digestion of complex carbohydrates contained within seaweed (Hehemann *et al.* 2010), facilitating a seaweed-rich diet as is characteristic of Japanese sushi. The highly poisonous phenotype of pufferfish is likely due to symbiotic bacteria that produce tetrodotoxin (Chau *et al.* 2011); this symbiosis necessitates reciprocal adaptation in the fish to acquire toxin resistant genes, failing which the host would suffer the ill effects of symbiont toxicity (Jost *et al.* 2008). The presence of the toxin likely confers protection against predators, and thus the evolution of a predator-free niche for the host fish.

Besides the examples of niche expansions provided above, there is now ample evidence that microbes can contribute to behavioural changes, thus affecting the niche that the organism can exploit (Wong *et al.* 2015). Interchanging gut microbiota between two laboratory mouse strains (one known to be nervous and hesitant, and the other to be social and exploratory) interchanged the behavioural phenotype, suggesting that gut bacteria can influence behaviour (Bercik *et al.* 2011). These phenotypic changes can potentially affect the extent of environment exploration by the mice, influencing the expansion of the space, food, microhabitat and other niche axes. Microbiota play an important role in humans and not only in digestion and nutrient acquisition. Humans harbour a huge microbial community; that within a single human weighs 1–2 kg (Forsythe and Kunze 2013). There is now increasing evidence that gut microbiota influences the behavioural phenotype of humans by affecting the CNS through production of neurotransmitters and other neurotropic factors, and that this interaction may have implications for behavioural disorders (Cryan and Dinan 2012; Dinan *et al.* 2015). While microbial influences on human behaviour represent effects on organisms with higher levels of nervous system evolution, microbes are also implicated in the early evolution of neurons and nervous systems. During the evolution of early invertebrates, interactions with

microbes at epithelial surfaces may have resulted in the internalization of neurons and nervous systems; owing to the similarity of signalling molecules between these three classes of cells, this internalization would ensure that signalling between epithelial cells and microbes no longer interfered with signalling between neurons (Eisthen and Theis 2015). This suggests that microbes have always been an important factor in the evolution of cell–cell signalling and continue to impact neurons even in higher organisms, affecting behaviour.

Signalling to mates is an important aspect of behaviour with profound implications for reproductive success. The discovery that many pheromones in animals are of microbial origin (Ezenwa and Williams 2014) makes signalling during reproduction in animals and plants a combined effort between organisms and microbes. Indeed, the scent glands of many mammals such as the Indian mongoose *Herpestes auropunctatus* are colonized by specific bacteria that contribute significantly to species-specific and individual-specific odours (Gorman *et al.* 1974; Eisthen and Theis 2015). That flower petals are often colonized by microbes (Junker *et al.* 2011; Junker and Tholl 2013) and that removal of floral microbes reduces terpene emissions from flowers (Peñuelas *et al.* 2014), suggest that floral scents in plants also have a microbial component. Therefore, symbionts appear to play an important role in generating the reproductive phenotype of plants and animals.

Is there evidence of symbionts other than microbes being involved in co-niche construction? There are some examples, but perhaps many more await discovery. Plants are associated in mutualistic relationships with symbiotic ants that offer protection to plants from herbivory; in order to facilitate interactions with ants, plants provide rewards to ants to increase attractiveness and to promote their fidelity to plants (Mayer *et al.* 2014; Borges 2015a). These rewards are in the form of food for ants such as extrafloral nectar or nesting spaces called domatia that are specially developed by plants for ants. Such domatia are colonized by founding queen ants and are used as brood development sites. Ant-plants express the domatia trait constitutively; i.e. domatia are produced even before the colonization of the plants by ants. There is only one exception, i.e. *Vochysia vismiaefolia* (Vochysiaceae), in which the ants induce domatia after colonizing the plant (Blüthgen and Wesenberg 2001); the mechanism for this is completely unknown but may be the only known example wherein a mutualistic invertebrate symbiont may be co-constructing a niche. There are, of course, many examples in which galling invertebrates (insects and nematodes) infect plants and produce galls within which their offspring develop by hijacking plant development pathways (Ferreira *et al.* 2016; Oliveira *et al.* 2016). This is, of course, co-construction, but here, the host is hostage to the symbiont. In brood-site pollination mutualisms, the brood of mutualistic pollinators develops within the pollinated

inflorescence (Borges 2016). The fig system is an iconic example of a brood-site pollination mutualism in which pollinating fig wasps enter enclosed inflorescences and gall some flowers within which their offspring develop while simultaneously pollinating others to form seeds; thus the fig inflorescence (fig or syconium) is transformed into a nursery to produce both seeds and wasps, and may also include other parasitic wasps that develop within this co-product of mutualism (Ghara *et al.* 2014; Krishnan and Borges 2014; Borges 2015b). Other brood-site pollination mutualisms also include co-constructed niches for brood development such as those made by galling flies that pollinate globe-flowers (Hembry and Althoff 2016).

### Developmental transmission and transgenerational inheritance of symbionts

If symbionts are beneficial to the host organism, which is now dependent on them for morphogenesis and other aspects of the host phenotype, there should be reliable mechanisms that ensure transmission of symbionts between generations and even between developmental stages, especially in those organisms undergoing metamorphoses, such that the fidelity of the symbiont consortium is maintained. In the nonmicrobial symbioses that are involved in co-niche construction between plants and insects, there is no possibility of vertical transmission between generations, and the mutualistic symbioses have to be reconstituted by horizontal transmission and partner choice each time.

The various mechanisms by which mutualistic bacteria are transmitted to offspring in insects have been ably reviewed by Salem *et al.* (2015). A few examples will illustrate some of these mechanisms. In a classical nutritional symbiosis exemplified by the aphid–*Buchnera* association, *Buchnera* is contained within specific bacteriocytes in the adult aphid, within which it synthesises important nutrients such as essential amino acids and vitamins, and is transmitted to the offspring through the egg (Bennett and Moran 2015). In the association between sap-sucking stinkbugs and the beneficial gut microbe *Burkholderia*, females excrete bacteria-laden capsules while laying eggs; these capsules are consumed by the hatchlings; alternatively the eggs are contaminated by excreted gut symbionts (Hosokawa *et al.* 2013). It is possible that the microbiota comprise a core indispensable fauna besides facultative symbionts which may respond to local variations in environments, thus contributing to local niche adaptations (Shapira 2016).

In holometabolous Lepidoptera, metamorphosis from larval to pupal stages can lead to severe reduction of gut microbiota (Ebert 2013); consequently mechanisms should be in place to ensure that the gut microbiome does not change significantly during metamorphosis. For example, in the lepidopteran *Galleria melonella*, the combination of a specific lysozyme produced by the lepidopteran

host and an antimicrobial peptide produced by the beneficial microbial symbiont *Enterococcus mundtii* controls the proliferation of pathogenic gut microbiota in the pupa, which, if unchecked, would result in adult mortality (Johnston and Rolff 2015). In *Hydra*, maternal antimicrobial peptides produced during oogenesis regulate the colonization of the embryo by bacteria (Fraune *et al.* 2010), allowing this basal metazoan to create a suitable symbiont-laced environment for its developing offspring.

Partner fidelity between *Cephalotes* ants and gut microbiota in an ant colony is maintained by a specific gut structure called the proventriculus, whose anatomy serves as a bacterial filter so that only specific microbial fauna are acquired by callow ants just after eclosion during oral–rectal trophallaxis from adult ants (Lanan *et al.* 2016). Similarly, a specialized intestinal organ to house gut symbionts has been found in stinkbugs; this organ effectively allows the passage of only flagellated *Burkholderia* symbionts into its lumen (Ohbayashi *et al.* 2015). In beewolf wasps, only mutualistic *Streptomyces* bacteria that protect against pathogenic fungi are applied from antennal gland reservoirs onto brood cells, facilitating vertical transmission of the mutualists, while application of nonmutualistic bacteria is blocked by an unknown mechanism thus serving as a filter to effect partner choice (Kaltenpoth *et al.* 2014).

Honeybee and bumble bee gut symbionts appear to have coevolved with their hosts and show evidence for nutritional co-dependencies as well as horizontal gene transfer within their respective gut environments (Kwong *et al.* 2014); the benefits to their host are unknown but this system demonstrates that the internal environment of the host can provide environments for microbial ecosystems to be established (Kwong and Moran 2015). These bacterial symbionts have also extremely reduced genomes as expected from residents of specialized host environments. Most specialized symbionts, especially those that are reliably transmitted and that have helped to establish a novel ecosystem within their host, usually show genome reduction as also evidenced in the *Buchnera* that are closely associated with aphids and that exhibit vertical transmission between generations (Salem *et al.* 2015). Co-occurring bacteria within host ecosystems may influence their own evolution by the presence of bacteria within these consortia that produce beneficial products that ‘leak’ out into the environment; those bacteria that do not produce these products actually benefit from these ‘public goods’ that are freely available in the local environment. This can set up a race between co-occurring bacteria to lose genes producing these benefits such that those bacteria within the local environment that do not lose genes fast enough are left with having to produce the public benefit and losing this evolutionary race. Bacteria that evolve reduced genomes as a result of this process are then dependent on the so-called ‘leaky’ helpers that are left

with intact unreduced genomes. This is the Black Queen theory of reductive evolution (Morris *et al.* 2012; Fullmer *et al.* 2015; Morris 2015) which can explain the evolution of dependencies among co-occurring bacteria within a niche. The first laboratory demonstration of the evolution of an obligate endosymbiosis by reductive gene evolution involved *Amoeba proteus* and gram-negative bacteria (*Legionella*-like bacteria called X-bacteria) (Jeon 1983; Jeon and Jeon 2003); here the host amoeba no longer produces its own S-adenosylmethionine synthetase, and relies on its endosymbiont for this important enzyme. Such results suggest a complex ongoing evolutionary process between host and symbiont and between the symbionts themselves.

Are some organisms more predisposed to co-construct niches or form symbioses? This question is an important one and has not been adequately addressed. Lichens intrigued the early students of symbiosis (Sapp 1994); however, that algae and fungi may have a latent capacity for a mutualism which could give rise to a beneficial symbiosis was only recently shown. By co-culturing the yeast *Saccharomyces cerevisiae* and the alga *Chlamydomonas reinhardtii* in a CO<sub>2</sub>-free atmosphere, the yeast produced CO<sub>2</sub> from glucose; the CO<sub>2</sub> was fixed through photosynthesis by the alga and it reduced NO<sub>2</sub> into NH<sub>3</sub> which could then be used by the yeast as a nitrogen source. This co-culturing environment resulted in close physical association between fungus and alga and the emergence of a mutualism (Hom and Murray 2014). Such co-dependencies can result in selection for a more permanent and reliable physical association between organisms that can result in ‘new’ organisms.

The finding that organisms are nested within each other has resulted in an expansion of the lexicon of symbiosis to include terms such as hologenome and holobiont (Gilbert *et al.* 2012; Chiu and Gilbert 2015; Gilbert and Tauber 2016) and to encourage a new view of selection and speciation to include the holobiont (Zilber-Rosenberg and Rosenberg 2008; Doolittle and Booth 2016; Shropshire and Bordenstein 2016). Since most organisms harbour a hugely diverse microbiota, there must be processes whereby the immune system of the organismal ‘genetic self’ avoids cross-reactivity with that of the ‘microbial self’; therefore, it has been proposed that holobiont immunity or holoimmunity must unify this composite entity to prevent holoautoimmunity (Root-Bernstein 2016). Such processes are evident in the legume–rhizobial mutualism (Wang *et al.* 2012). Incompatibilities between microbiomes held within organisms can result in reproductive isolation between hosts. This has been seen recently in *Nasonia* wasps, in which mutualistic gut microbiota form host species-specific communities that can cause hybrid lethality in interspecific wasp hybrids (Brucker and Bordenstein 2013). Administration of antibiotics to such hybrids increased hybrid wasp survival while feeding bacteria to microbe-free hybrids caused lethality. Here the

gut microbiome appears to have coevolved or to be coadapted to particular host-species gut environments, and may thus be responsible for maintaining reproductive isolation between the *Nasonia* species. Brucker and Bordenstein (2013) interpret this phenomenon as a co-adapted hologenome which fractures during hybridization and thus contributes to speciation. However, it has been pointed out that it is sufficient to use conventional ecological and evolutionary theory and natural selection perspectives to describe and investigate the rich tapestry of such interspecies interactions (Wray *et al.* 2014; Moran and Sloan 2015; Mushegian and Ebert 2015; Douglas and Werren 2016). In cases where there is reliable, heritable transmission of symbionts, it is possible to consider selection on the symbiotic community or the hologenome (Moran and Sloan 2015). However, since there are so many microbiota associated with hosts, many of whose interests are not perfectly aligned, and many of which show a range of interactions ranging from enslavement through parasitism to mutualism, it is difficult to conceive of host–microbe symbioses as holobionts (Douglas and Werren 2016).

The discovery of complex, codependent, co-constructed organismal niches and consortia present many challenges to unravelling and understanding the composite phenotypes that are the result of selection pressures acting at a multiplicity of levels. It is true then that: *Life is sustained by symbioses between nitrogen-fixing rhizobial bacteria and legumes, sulphide-oxidizing bacteria and clams in tidal seagrass communities, algae and reef-building corals, and protective mycorrhizal or endophytic fungi and plants. In addition to these grand symbioses are the nodes of symbioses called organisms* (Gilbert *et al.* 2015).

## References

- Alegado R. A., Brown L. W., Cao S., Dermenjian R. K., Zuzow R. and Fairclough S. R. 2012 A bacterial sulfonolipid triggers multicellular development in the closest living relatives of animals. *eLife* **1**, e00013.
- Bennett G. M. and Moran N. A. 2015 Heritable symbiosis: The advantages and perils of an evolutionary rabbit hole. *Proc. Natl. Acad. Sci. USA* **112**, 10169–10176.
- Bercik P., Denou E., Collins J., Jackson W., Lu J., Jury J. *et al.* 2011 The intestinal microbiota affect central levels of brain-derived neurotrophic factor and behavior in mice. *Gastroenterology* **141**, 599–609.
- Blüthgen N. and Wesenberg J. 2001 Ants induce domatia in a rain forest tree (*Vochysia vismiae* folia). *Biotropica* **33**, 637–642.
- Borges R. M. 2015a How mutualisms between plants and insects are stabilized. *Curr. Sci.* **108**, 1862–1868.
- Borges R. M. 2015b How to be a fig wasp parasite on the fig–fig wasp mutualism. *Curr. Opin. Insect Sci.* **8**, 34–40.
- Borges R. M. 2016 On the air: broadcasting and reception of volatile messages in brood-site pollination mutualisms. In *Deciphering chemical language of plant communication* (ed. J. D. Blande and R. Glinwood), pp. 227–255. Springer International Publishing, Switzerland.

- Brucker R. M. and Bordenstein S. R. 2013 The hologenomic basis of speciation: gut bacteria cause hybrid lethality in the genus *Nasonia*. *Science* **341**, 667–669.
- Chau R., Kalaitzis J. A. and Neilan B. A. 2011 On the origins and biosynthesis of tetrodotoxin. *Aquat. Toxicol.* **104**, 61–72.
- Chiu L. and Gilbert S. F. 2015 The birth of the holobiont: multi-species birthing through mutual scaffolding and niche construction. *Biosemiotics* **8**, 191–210.
- Coon K. L., Vogel K. J., Brown M. R. and Strand M. R. 2014 Mosquitoes rely on their gut microbiota for development. *Mol. Ecol.* **23**, 2727–2739.
- Cryan J. F. and Dinan T. G. 2012 Mind-altering microorganisms: the impact of the gut microbiota on brain and behaviour. *Nat. Rev. Neurosci.* **13**, 701–712.
- Dedeine F., Vavre F., Fleury F., Loppin B., Hochberg M. E. and Boulétreau M. 2001 Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. *Proc. Natl. Acad. Sci. USA* **98**, 6247–6252.
- Dinan T. G., Stilling R. M., Stanton C. and Cryan J. F. 2015 Collective unconscious: how gut microbes shape human behavior. *J. Psychiatr. Res.* **63**, 1–9.
- Doino J. A. and McFall-Ngai M. J. 1995 A transient exposure to symbiosis-competent bacteria induces light organ morphogenesis in the host squid. *Biol. Bull.* **189**, 347–355.
- Doolittle W. F. and Booth A. 2016 It's the song, not the singer: an exploration of holobiosis and evolutionary theory. *Biol. Philos.* **32**, 5–24.
- Douglas A. E. and Werren J. H. 2016 Holes in the hologenome: why host-microbe symbioses are not holobionts. *mBio* **7**, e02099-15.
- Ebert D. 2013 The epidemiology and evolution of symbionts with mixed-mode transmission. *Annu. Rev. Ecol. Syst.* **44**, 623–643.
- Eisthen H. L. and Theis K. R. 2015 Animal – microbe interactions and the evolution of nervous systems. *Phil. Trans. R. Soc. B* **371**, 20150052.
- Ezenwa V. O. and Williams A. E. 2014 Microbes and animal olfactory communication: Where do we go from here? *BioEssays* **36**, 847–854.
- Ferreira B. G., Álvarez R., Avritzer S. C. and Isaias R. M. S. 2016 Revisiting the histological patterns of storage tissues: beyond the limits of gall-inducing taxa. *Botany* **95**, 173–184.
- Forsythe P. and Kunze W. A. 2013 Voices from within: gut microbes and the CNS. *Cell. Mol. Life Sci.* **70**, 55–69.
- Fraune S. and Bosch T. C. G. 2010 Why bacteria matter in animal development and evolution. *BioEssays* **32**, 571–580.
- Fraune S., Augustin R., Anton-Erxleben F., Wittlieb J., Gelhaus C. and Klimovich V. B. 2010 In an early branching metazoan, bacterial colonization of the embryo is controlled by maternal antimicrobial peptides. *Proc. Natl. Acad. Sci. USA* **107**, 18067–18072.
- Frederickson M. E. 2013 Rethinking mutualism stability: cheaters and the evolution of sanctions. *Q. Rev. Biol.* **88**, 269–295.
- Fullmer M. S., Soucy S. M. and Gogarten J. P. 2015 The pan-genome as a shared genomic resource: mutual cheating, cooperation and the black queen hypothesis. *Front. Microbiol.* **6**, 728.
- Gilbert S. F. and Tauber A. I. 2016 Rethinking individuality: the dialectics of the holobiont. *Biol. Philos.* **31**, 839–853.
- Gilbert S. F., Sapp J. and Tauber A. I. 2012 A symbiotic view of life: we have never been individuals. *Q. Rev. Biol.* **87**, 325–341.
- Gilbert S. F., Bosch T. C. G. and Ledón-Rettig C. 2015 Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents. *Nat. Rev. Genet.* **16**, 611–622.
- Ghara M., Ranganathan Y., Krishnan A., Gowda V. and Borges R. M. 2014 Divvying up an incubator: how parasitic and mutualistic fig wasps use space within their nursery microcosm. *Arthropod-Plant Interac.* **8**, 191–203.
- Gorman M. L., Nedwell D. B. and Smith R. M. 1974 An analysis of the contents of the anal scent pockets of *Herpestes auro-unctatus* (Carnivora: Viverridae). *J. Zool.* **172**, 389–399.
- Hehemann J.-H., Correc G., Barbeyron T., Helbert W., Czekaj M. and Michel G. 2010 Transfer of carbohydrate-active enzymes from marine bacteria to Japanese gut microbiota. *Nature* **464**, 908–912.
- Hembry D. H. and Althoff D. M. 2016 Diversification and coevolution in brood pollination mutualisms: Windows into the role of biotic interactions in generating biological diversity. *Am. J. Bot.* **103**, 1783–1792.
- Hom E. F. Y. and Murray A. W. 2014 Niche engineering demonstrates a latent capacity for fungal-algal mutualism. *Science* **345**, 94–98.
- Hosokawa T., Hironaka M., Inadomi K., Mukai H., Nikoh N. and Fukatsu T. 2013 Diverse strategies for vertical symbiont transmission among subsocial stinkbugs. *PLoS One* **8**, e65081.
- Jeon K. W. 1983 Integration of bacterial endosymbionts in amoebae. *Int. Rev. Cytol. Suppl.* **14**, 29–47.
- Jeon T. J. and Jeon K. W. 2003 Characterization of *sams* genes of *Amoeba proteus* and the endosymbiotic X-bacteria. *J. Eukaryot. Microbiol.* **50**, 61–69.
- Johnston P. R. and Rolff J. 2015 Host and symbiont jointly control gut microbiota during complete metamorphosis. *PLoS Pathog.* **11**, e1005246.
- Jost M. C., Hillis D. M., Lu Y., Kyle J. W., Fozzard H. A. and Zakon H. H. 2008 Toxin-resistant sodium channels: parallel adaptive evolution across a complete gene family. *Mol. Biol. Evol.* **25**, 1016–1024.
- Junker R. R. and Tholl D. 2013 Volatile organic compound mediated interactions at the plant-microbe interface. *J. Chem. Ecol.* **39**, 810–825.
- Junker R. R., Loewel C., Gross R., Dötterl S., Keller A. and Blüthgen N. 2011 Composition of epiphytic bacterial communities differs on petals and leaves. *Plant Biol.* **13**, 918–924.
- Kaltenpoth M., Roeser-Mueller K., Koehler S., Peterson A., Nechitaylo T. Y., Stubblefield J. W. et al. 2014 Partner choice and fidelity stabilize coevolution in a Cretaceous-age defensive symbiosis. *Proc. Natl. Acad. Sci. USA* **111**, 6359–6364.
- Khakhina L. N., Margulis L. and McMenamin M. A. 1992 *Concepts of symbiogenesis: a historical and critical study of the research of Russian botanists*. Yale University Press, New Haven, USA.
- Krishnan A. and Borges R. M. 2014 Parasites exert conflicting selection pressures to affect reproductive asynchrony of their host plant in an obligate pollination mutualism. *J. Ecol.* **102**, 1329–1340.
- Kwong W. K. and Moran N. A. 2015 Evolution of host specialization in gut microbes: the bee gut as a model. *Gut Microbes* **6**, 214–220.
- Kwong W. K., Engel P., Koch H. and Moran N. A. 2014 Genomics and host specialization of honey bee and bumble bee gut symbionts. *Proc. Natl. Acad. Sci. USA* **111**, 11509–11514.
- Lanan M. C., Rodrigues P. A. P., Agellon A., Jansma P. and Wheeler D. E. 2016 A bacterial filter protects and structures the gut microbiome of an insect. *ISME J.* **10**, 1866–1876.
- Laland K. N. and Sterelny K. 2006 Perspective: seven reasons (not) to neglect niche construction. *Evolution* **60**, 1751–1762.
- Lewontin R. C. 1983 Genes, organisms and environment. In *Evolution from molecules to men* (ed. D. S. Bendall), pp. 273–285. Cambridge University Press, Cambridge, UK.

- Margulis L. 1991 Symbiogenesis and symbiogenesis. In *Symbiosis as a source of evolutionary innovation: speciation and morphogenesis* (ed. L. Margulis and R. Fester), pp. 1–14. MIT Press, Cambridge, Massachusetts, USA.
- Mayer V. E., Frederickson M. E., McKey D. and Blatrix R. 2014 Current issues in the evolutionary ecology of ant–plant symbioses. *New Phytol.* **202**, 749–764.
- McFall-Ngai M. J. 2002 Unseen forces: the influence of bacteria on animal development. *Dev. Biol.* **242**, 1–14.
- McFall-Ngai M., Hadfield M. G., Bosch T. C., Carey H. V., Domazet-Lošo T., Douglas A. E. *et al.* 2013 Animals in a bacterial world, a new imperative for the life sciences. *Proc. Natl. Acad. Sci. USA* **110**, 3229–3236.
- Moczek, A. P. 2015 Re-evaluating the environment in developmental evolution. *Front. Ecol. Evol.* **3**, 7.
- Montgomery M. K. and McFall-Ngai M. 1994 Bacterial symbionts induce host organ morphogenesis during early postembryonic development of the squid *Euprymna scolopes*. *Development* **120**, 1719–1729.
- Moran N. A. and Sloan D. B. 2015 The hologenome concept: helpful or hollow? *PLoS Biol.* **13**, e1002311.
- Morris J. J. 2015 Black Queen evolution: the role of leakiness in structuring microbial communities. *Trends Genet.* **31**, 475–482.
- Morris J. J., Lenski R. E. and Zinser E. R. 2012 The Black Queen Hypothesis: evolution of dependencies through adaptive gene loss. *mBio* **3**, e00036-12.
- Mushegian A. A. and Ebert D. 2015 Rethinking “mutualism” in diverse host-symbiont communities. *BioEssays* **38**, 100–108.
- Ohbayashi T. *et al.* 2015 Insect’s intestinal organ for symbiont sorting. *Proc. Natl. Acad. Sci. USA* **112**, E5179–E5188.
- Oliveira D. C., Isaias R. M. S., Fernandes G. W., Ferreira B. G., Carneiro R. G. S. and Fuzaro L. 2016 Manipulation of host plant cells and tissues by gall-inducing insects and adaptive strategies used by different feeding guilds. *J. Insect Physiol.* **84**, 103–113.
- Oono R., Anderson C. G. and Denison R. F. 2011 Failure to fix nitrogen by non-reproductive symbiotic rhizobia triggers host sanctions that reduce fitness of their reproductive clonemates. *Proc. R. Soc. London, Ser. B* **278**, 2698–2703.
- Peñuelas J., Farré-Armengol G., Llusia J., Gargallo-Garriga A., Rico L., Sardans J., Terradas J. and Filella I. 2014 Removal of floral microbiota reduces floral terpene emissions. *Sci. Rep.* **4**, 6727.
- Rawls J. F., Samuel B. S. and Gordon J. I. 2004 Gnotobiotic zebrafish reveal evolutionarily conserved responses to the gut microbiota. *Proc. Natl. Acad. Sci. USA* **101**, 4596–4601.
- Root-Bernstein R. 2016 Autoimmunity and the microbiome: T-cell receptor mimicry of “self” and microbial antigens mediates self tolerance in holobionts. *BioEssays* **38**, 1068–1083.
- Salem H., Florez L., Gerardo N. and Kaltenpoth M. 2015 An out-of-body experience: the extracellular dimension for the transmission of mutualistic bacteria in insects. *Proc. R. Soc. London, Ser. B* **282**, 20142957.
- Sapp J. 1994 *Evolution by association: a history of symbiosis*. Oxford University Press, New York, USA.
- Schwartzman J. A. and Ruby E. G. 2016 A conserved chemical dialog of mutualism: lessons from squid and vibrio. *Microbes Infect.* **18**, 1–10.
- Schwartzman J. A., Koch E., Heath-Heckman E. A. C., Zhou L., Kremer N., McFall-Ngai M. J. and Ruby E. G. 2015 The chemistry of negotiation: Rhythmic, glycan-driven acidification in a symbiotic conversation. *Proc. Natl. Acad. Sci. USA* **112**, 566–571.
- Shapira M. 2016 Gut microbiotas and host evolution: scaling up symbiosis. *Trends Ecol. Evol.* **31**, 539–549.
- Shropshire J. D. and Bordenstein S. R. 2016 Speciation by symbiosis: the microbiome and behavior. *mBio* **7**, e01785-15.
- Stappenbeck T. S., Hooper L. V. and Gordon J. I. 2002 Developmental regulation of intestinal angiogenesis by indigenous microbes via Paneth cells. *Proc. Natl. Acad. Sci. USA* **99**, 15451–15455.
- Van Valen L. 1973 A new evolutionary law. *Evol. Theory* **1**, 1–30.
- Wang D., Yang S., Tang F., and Zhu H. 2012 Symbiosis specificity in the legume–rhizobial mutualism. *Cell. Microbiol.* **14**, 334–342.
- Werren J. H., Baldo L. and Clark M. E. 2008 *Wolbachia*: master manipulators of invertebrate biology. *Nat. Rev. Microbiol.* **6**, 741–751.
- Wong A. C. N., Holmes A., Ponton F., Lihoreau M., Wilson K., Raubenheimer D. and Simpson S. J. 2015 Behavioral microbiomics: a multi-dimensional approach to microbial influence on behavior. *Front. Microbiol.* **6**, 1359.
- Wray G. A., Hoekstra H. E., Futuyma D. J., Lenski R. E., Mackay F. C., Schuller D. and Strassmann J. E. 2014 Does evolutionary theory need a rethink? No, all is well. *Nature* **514**, 161–164.
- Zilber-Rosenberg I. and Rosenberg. 2008 Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. *FEMS Microbiol. Rev.* **32**, 723–735.

Corresponding editor: T. N. C. VIDYA