Received: 10 April 2018 | Accepted: 16 April 2018
DOI: 10.1111/mec.14706

SPECIAL ISSUE

WILEY MOLECULAR ECOLOGY

Introduction: The host-associated microbiome: Pattern, process and function

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KEYWORDS
community assembly, experiments, high-throughput sequencing, microbiota, symbiosis

1 | INTRODUCTION

An explosion of studies in recent years has established the ubiquity of host-associated microbes and their centrality to host biology (McFall-Ngai et al., 2013; Russell, Dubilier, & Rudgers, 2014). Microbes aid in digestion, modulate development, contribute to host immunity, mediate abiotic stress and more. While relationships with host-associated microbes are ubiquitous and important, they are certainly not monolithic. Characterizing the microbial diversity associated with an ever-broadening array of hosts (diverse animals, plants, algae and protists) has shown that essential functions can be performed by microbes that are integrated with the host to varying degrees, ranging from embedded endosymbionts to a variable cast of transient microbes acquired from the environment. The maturing host–microbiome field is now developing a mechanistic understanding of host/microbe relationships across this spectrum and the cross-talk mediating these interactions. Similarly, studies across systems are illuminating the ecological and evolutionary factors that shape host–microbe interactions today and providing hints into the origins of specific relationships.

The field of host-associated biology is often motivated by a desire to understand the impact of the microbiome on host organisms (Bordenstein & Theis, 2015; McFall-Ngai et al., 2013) and manipulate the microbiome to improve host health or performance (Busby et al., 2017; McKenzie, Kueneman, & Harris, 2018; Petrosino, 2018). Following from this, a consistent aim is determining which microbial symbionts are likely to most impact the host and should therefore occupy the bulk of our attention. Identifying key microbes and their interactions with the host requires different approaches across systems owing to the vast differences in microbiome diversity. Key microbes are readily apparent in some cases, exemplified by endosymbionts of animals that provide their host with nutritional subsidies (Wernegreen, 2012), such as those harboured by aphids and many other insects (Moran, McCutcheon, & Nakabachi, 2008). For hosts and tissues colonized by diverse microbial consortia—such as animal skin or plant rhizosphere—the observed community is a mix of transient microbes, variably present symbionts and core symbionts. Here, surveys across populations can often be an informative first step in differentiating transients from variable components of the microbiota, and identifying key players as the consistent presence of particular microbes (i.e., the core microbiome) can serve as a proxy for those most likely to contribute key functions (Busby et al., 2017; Shade & Handelsman, 2012). But even this approach may face challenges, as the core microbiome (if it exists) may often fail to encompass the full range of influential microbes. One complicating factor stems from the prevalence of functional redundancy across symbionts: core functions are often performed by substitutable sets of microbes (Burke, Steinberg, Rusch, Kjelleberg, & Thomas, 2011; Doolittle & Booth, 2017; Louca et al., 2018). Further, symbionts that are variably present may still have large impacts on host biology, as is the case with heritable, facultative symbionts that alter host ecology (Oliver, Degnan, Burke, & Moran, 2010).

While much focus is on the host, it is important to remain mindful of the microbial perspective. Microbes do not colonize eukaryotic hosts for the benefit of the host but rather out of self-interest, for example to take advantage of available food or habitat resources (Doolittle & Booth, 2017; Moran & Sloan, 2015). For hosts with diverse and variable microbiomes, the microbial perspective becomes an essential viewpoint for understanding community assembly and succession. For example, when host-associated microbiota are acquired from the environment (such as on seaweed surfaces), the microbes present are likely those that (i) are present in the water column, (ii) use some aspect of the seaweed (e.g., exuded sugars) as a resource, (iii) are resistant to host defences and (iv) can outcompete other microbes with these traits. While some environmentally acquired microbes engage in highly specialized, and selective symbioses (Nyholm & McFall-Ngai, 2004; Yang, Tang, Gao, Krishnan, & Zhu, 2010), others are more generalized, such that numerous microbial taxa can successfully colonize, utilize host resources and compete. In these cases, the structure of the host-associated microbiota varies as the environmental pool of potential colonizers changes across differing abiotic conditions, space or time (Lemay et al., 2018; Naylor, DeGraaf, Purdom, & Coleman-Derr, 2017).

Also key to the structuring of such communities are ways in which microbes impact one another. For instance, research in free-living systems has enumerated how early colonization of a resource may select for certain traits (e.g., motility, the ability to use the primary resource), while the successional process may unfold due to microbes' capacities to use by-products of colonizing microbes' metabolism (Datta, Sliwerska, Gore, Polz, & Cordero, 2016). Indeed, such dynamics may explain shifts in host-colonizing microbiota across development (Bengtsson, Sjotun, Lanzen, & Ovreas, 2012). Distinguishing between this possibility and a changing abiotic environment (i.e., habitat filtering due to factors such as changing host diet (Koenig et al., 2011)) requires careful investigation (Levy & Borenstein, 2013). Furthermore, additional types of biotic interactions may play out among members of the microbiota, including interference competition (Scheuring & Yu, 2012), exploitation competition, cooperation (Faust et al., 2012) or predation by phage (Koskella, Hall, & Metcalf, 2017; Manrique, Dills, & Young, 2017). The lesson here is that the within-host ecology of symbiotic microbes must be accounted for to fully make sense of the microbiome (Moran & Sloan, 2015).

In this special issue of Molecular Ecology on "The Host-associated Microbiome: Pattern, Process and Function," we present 29 articles that use rigorous surveys and experiments to probe host–microbe relationships in diverse eukaryotic hosts, using tools ranging from amplicon sequencing to genomics to genetic engineering. Although articles touch on multiple topics, we have organized them into four primary sections: (i) mechanisms behind influential symbioses, (ii) structure of the microbiome, (iii) the evolution of symbioses and their role in host adaptation and (iv) the stability of symbiosis in a changing world. At the end of our introduction, we also highlight a review article. This article concludes our issue setting out new terminology borrowed from ecological theory as a way to better explain and conceptualize the widespread phenomenon of symbiosis.

The symbioses discussed in each section span the continuum from tightly integrated and vertically transmitted endosymbionts to loose associations of microbes that are acquired from the environment at every generation. These studies offer novel insights into model systems and extend our understanding of host–microbiome relationships to a broad array of hosts. Our hope is that juxtaposing these systems and highlighting the unique lessons learned from each will lead to broader understanding of the host–microbiota relationships that are central to the diversity and functioning of our planet.

1.1 | A note on definitions

We use the term "microbiota" to discuss an assemblage of microbes, such as the catalogue of bacterial taxa identified by 16S rRNA gene sequencing. We use the term "microbiome" to refer to the collection of microbes, genes and their environment (Marchesi & Ravel, 2015). We note that the microbiome is often studied using techniques such as metagenomics or metatranscriptomics, and in these cases "meta" refers to bulk analysis of DNA or RNA from the whole community, sampled directly from the environment (i.e., without in vitro cultivation). The term "microbe" is used as a general, nonphylogenetic term of convenience for microscopic organisms. In most cases, the microbes studied here are bacteria, but also included are fungi, viruses and archaea. Finally, while sometimes used to imply beneficial, host-associated microbes, we use term "symbiont" in a more agnostic fashion, focusing on intimate, host-associated microbes whose relationships with hosts span a continuum from beneficial, to commensal, to detrimental (Leung & Poulin, 2008; Perez-Brocal, Latorre, & Moya, 2013). This broad definition recognizes the difficulty in categorizing the outcomes of host–microbe relationships and the fact that the host-level fitness consequences can vary according to ecological context (Leung & Poulin, 2008; Lukeš, Stensvold, Jirků-Pomajbíková, & Parfrey, 2015; Perez-Brocal et al., 2013). Moreover, relationships can and do evolve, with changes playing out over short to ancient timescales (Leung & Poulin, 2008). For example, *Wolbachia* transitioned from parasite to mutualist within ~20 years in a naïve *Drosophila simulans* population (Weeks, Turelli, Harcombe, Reynolds, & Hoffmann, 2007), while the normally commensal *E. coli* has repeatedly transitioned to a pathogen (Stephens & Murray, 2001). This flexibility and the hard-to-pin-down nature of interaction outcomes emphasize the value of a broad-tent approach in the symbiosis field, if the goal is indeed to understand the ultimate and proximate causes of symbiosis and the consequences, not just for the involved parties, but for the communities around them (Hopkins, Wojdak, & Belden, 2017).

2 | THE MECHANISMS BEHIND INFLUENTIAL SYMBIOSES

The realization that symbionts provide key functions to many hosts leads to many questions about the mechanistic underpinnings of these relationships. For example, how do host and symbionts communicate? What products are exchanged? How are host functions regulated by the symbiont and vice versa? How are these associations established in systems where microbial partners are acquired from the environment? We are gaining answers to these questions in both model systems of symbiosis and diverse nonmodel systems. As more host/microbe systems are studied in detail, we learn about unique pathways, but also common themes. For example, many of the best known tightly integrated endosymbioses involve nutritional codependence between partners. This includes the mutual reliance between aphids and *Buchnera* for a supply of amino acids (Shigenobu, Watanabe, Hattori, Sakaki, & Ishikawa, 2000) and the tri-partite reliance among hosts and co-infecting endosymbionts, in systems such as the mealybug–*Tremblaya*–*Moranella* symbiosis (McCutcheon & von Dohlen, 2011). These and other symbioses (Dubilier, Bergin, & Lott, 2008; Engl et al., 2018) remind us of the great diversity of metabolic functions found within bacteria and archaea, and their relative paucity in eukaryotes.

On the other end of the spectrum of symbiont integration, loosely associated microbes influence aspects of host biology such as defence, growth and development, and tolerance to abiotic stress (Bourne, Morrow, & Webster, 2016; Busby et al., 2017; Egan et al., 2013). The diverse and highly variable nature of the symbiotic systems makes mechanistic study a challenge, but model systems for the plant rhizosphere, seaweed surface microbiota and others are illuminating common themes underlying these host–microbe interactions as well. Both hosts and microbes frequently induce transcriptional responses in the other partner that lead to observed changes in both host biology (e.g., defence, growth and development) and symbiont biology (e.g., nutrient biosynthesis). We are also learning that many loose associations are mediated by general signals, such as salicylic acid in plants (Lebeis et al., 2015), bacterially produced lipids (Woznica et al., 2016) and organosulphur compounds such as DMSP (Kessler, 2018).

2.1 | The regulation and function of obligate symbioses

For several obligate endosymbioses of insects, current hypotheses on the regulation of symbiosis lean towards a notion of host control, due to extremely reduced endosymbiont genomes that are often lacking transcription factors and other regulatory elements. Indeed, a number of studies have shown transcriptional responsiveness to varying environmental pressures is muted in such endosymbionts (reviewed in Hansen & Moran, 2014). Changes to mRNA populations are, however, just one path towards plasticity, with studies of other avenues having previously been hindered by technological limits.

In this issue, two studies use the model aphid—*Buchnera* symbiosis to address the mechanisms of host- vs. symbiont-controlled symbiont plasticity, with Thairu and colleagues examining the latter (Thairu, Cheng, & Hansen, 2018), and Feng and colleagues investigating the former (Feng, Wang, Wuchty, & Wilson, 2018).

Prior efforts, using mass spectrometry and small RNA (sRNA) sequencing, had uncovered a likely driver of symbiont-controlled plasticity—a dynamic *Buchnera* proteome, and a suite of conserved *Buchnera*-encoded sRNAs proposed as drivers of this dynamism (Hansen & Degnan, 2014). Thairu and colleagues follow up on this work, using RNAseq to quantify *Buchnera* sRNA titre across two developmental stages of the pea aphid (Thairu et al., 2018). Dozens of sRNAs showed significant changes in relative abundance, primarily during the embryonic stage. Intriguingly, 18 of the upregulated sRNAs paralleled upregulation of proteins previously examined across these same stages. To test the capacity for sRNAs to mediate post-transcriptional regulation, and hence to cement the link between these RNA regulators and the proteome, the authors selected one sRNA predicted to regulate the protein-coding *carB* gene. Using recombinant DNA technology to develop a green fluorescent protein (GFP) reporter assay, the authors transformed *E. coli* cells with one or two recombinant plasmids containing the sRNA and, separately, its target sequence from the *carB* gene fused to a GFP reporter. Importantly, cells transformed with both constructs exhibited heightened fluorescence, compared to those with just the *carB* fragment–GFP fusion construct, demonstrating that the expression of this sRNA can favour increased protein production of its targeted gene (Thairu et al., 2018). This work exhibits the growing ability of symbiosis research to generate hypotheses using high-throughput omics technologies and to then test hypotheses through manipulative experiments in tractable model systems (e.g., Nguyen, Liu, & Thomas, 2014).

Intriguingly, Thairu and colleagues have shown that a good number sRNAs are conserved, spanning ~65 million years of *Buchnera* evolution, while others appear specific to particular *Buchnera* lineages. Thus, the authors propose that changes to these gene regulatory mechanisms across the history of this symbiosis could underlie *Buchnera*-mediated adaptation to the evolving ecology and physiology of their aphid hosts. Perhaps this ancient, seemingly handicapped relationship (Bennett & Moran, 2015) still has a few tricks up its sleeve after all.

On the other side of this symbiosis, Feng and colleagues isolated and sequenced host-encoded small RNAs in two aphid species to investigate the potential mechanisms used by hosts to regulate their symbionts (Feng et al., 2018). Using bioinformatics, they identified aphid-encoded micro-RNAs (miRNA), which are typically 17–35 bp in length. Of the 113 identified across the two host species, 69 were shared. Many were homologous to miRNAs in other insect species, with conserved arrangement in genomic clusters. Genes targeted by conserved miRNAs and expressed in the bacteriocytes that house

Buchnera symbionts were enriched for functions including signal transduction as well as the transport/metabolism amino acids. Interestingly, 10 of these 14 conserved, bacteriocyte-expressed miRNAs have been previously implicated in host–microbe interactions. In a proposed model, the authors suggest a mechanism by which one of their identified miRNAs could regulate glutamate transport to *Buchnera* symbionts, thus regulating the primary role of this endosymbiont—biosynthesis of essential amino acids (Feng et al., 2018). In summary, this study highlights a role for miRNAs in regulating host/symbiont interactions more broadly and lays out hypotheses for a central role of signal transduction in mediating metabolic integration. Between the Feng and Thairu studies, it is evident that sequencing efforts going beyond the traditional targets of DNA and mRNA are expanding our abilities to understand symbiosis.

While we often think of large, multicellular eukaryotes as the hosts of symbiotic microbiota, intimate symbioses are also common for single-celled eukaryotes (Nowack & Melkonian, 2010). This is particularly true in anoxic environments where bacterial symbionts can be integral to eukaryotic metabolism (Buck & Bernhard, 2002). In this issue, Beinart and colleagues use metagenomics and metatranscriptomics to characterize the metabolic association between intracellular bacteria and a karyorelictid ciliate from the sulphidic, anoxic deep sea of the Santa Barbara Basin, CA (Beinart, Beaudoin, Bernhard, & Edgcomb, 2018). They document a highly integrated host–symbiont relationship with two Deltaproteobacteria symbionts. The bacteria take up sulphate, nitrate and fermentative end products from host metabolism and use them for autotrophic growth via sulphate and potentially nitrate reduction. Genomes of the symbionts encode the capacity to synthesize and transport essential amino acids to the host. Beinart et al. also infer metabolic integration between the two endosymbionts via hydrogen exchange, based on their metagenome and metatranscriptome data. This study also highlights the utility of genomic techniques for nonmodel organisms, including those from difficult-to-access environments: this divergent ciliate resides 500+ m deep in the Santa Barbara basin in sulphidic and anoxic conditions and cannot be cultured. Beinart and colleagues worked from isolated single cells and gain novel insight into the genomic underpinnings of symbioses that extend the range of environments in which eukaryotes can thrive.

2.2 | Mechanisms of host–microbe interactions among loose symbiotic associations

By and large, seaweeds form loose associations with marine microbes. As we see reinforced in this issue, the taxonomic composition of the seaweed microbiome is incredibly variable, while function is more consistent (Roth-Schulze et al., 2018). Despite this variability, microbes play critical roles in seaweed biology (Egan et al., 2013). In a striking example, the seaweed *Ulva* requires bacterial associates that produce morphogenetic compounds to develop normally; in the absence of bacteria, *Ulva* is not an upright blade but a blob of cells (Marshall, Joint, Callow, & Callow, 2006; Tapia, Gonzalez, Goulitquer, Potin, & Correa, 2016; Wichard et al., 2015). Exploring the mechansims behind host–microbe communications in this system, Kessler combine analytical chemistry with detailed experiments to demonstrate that the organosulphur compound, dimethylsulphoniopropionate (DMSP), forms the currency of these interactions (Kessler, Weiss, Kuegler, Hermes, & Wichard, 2018). DMSP is a common osmolyte produced by seaweeds, phytoplankton and microalgae that also functions as a cryoprotectant, deterrent against herbivores and a chemical attractant for organisms ranging from fish to bacteria (Yoch, 2002). In this system, *Ulva* produces DMSP, which attracts their chemotactic study micobe—*Roseovarius* sp. MS2— *Roseovarius* take up and metabolize DMSP, but cannot grow on DMSP alone. However, DMSP appears to be a reliable signal of glycerol, which does support bacterial growth (Kessler et al., 2018). As the authors point out, this interaction is not a product of intricate co-evolution between this pair of species. Previous work from this group (Grueneberg, Engelen, Costa, & Wichard, 2016) demonstrated that many different bacteria can substitute to produce the morphogenetic compounds required for normal *Ulva* development, and likely are also responding to the DMSP cue produced by *Ulva*, and by many other species of marine algae (Kessler et al., 2018). Bacteria likely respond to DMSP because it is a reliable signal of their polysaccharide food source—in this case *Ulva*-produced glycerol. This represents an example of a more general ecological phenomenon, in which bacteria are attracted to general signals and, once recruited, co-opted in various ways by the host (Amin et al., 2015; Kessler et al., 2018; Woznica, Gerdt, Hulett, Clardy, & King, 2017).

Work from Hudson and colleagues (this issue) on the red seaweed *Delisea pulchra* and the opportunistic pathogen *Nautella italica* R11 also highlights the importance of widespread pathways in regulating seaweed/microbe interactions. The authors demonstrate that an *raiR* gene knockout mutation eliminates *N. italica* virulence. This gene encodes a key component of LuxR quorum-sensing mechanisms, helping to illustrate that virulence—in this instance—is dependent upon bacteria detecting, and responding, to conspecific population sizes. Using transcriptome sequencing, they also demonstrate a strong response of *N. italica* to the seaweed, with expression of ~10% of the genome changing in response to *Delisea* presence. Upregulated genes include those involved in carbohydrate and central metabolism (response to a food source) and oxidative stress responses (to overcome host defences). Their study also uncovers a connection between virulence of the bacterium and repression of prophages. Induction of bacteriophage by plants is one means of plant defence against bacterial pathogens (Gill & Abedon, 2003). These results suggest *Delisea* may protect itself in the same way and that *N. italica* subverts this defence by repressing prophage, through a quorum-sensing-dependent mechanism (Hudson, Gardiner, Deshpande, & Egan, 2018).

Working in the genetically tractable *Arabidopsis*/*Pseudomonas* model for rhizosphere interactions, Haney and colleagues investigate the role bacteria play in mediating the hormonal signalling that induces systemic defence in plants. Root-associated *Pseudomonas* strains can induce systemic resistance to herbivores but this exposes the plant to greater susceptibility to bacterial pathogens (Haney et al., 2018). Yet, different *Pseudomonas* strains induce different responses by altering plant transcriptional pathways towards jasmonic acid or salicylic acid signalling. Jasmonic acid signalling promotes resistance to chewing herbivores (e.g., the cabbage looper *Trichoplusia ni*), while salicylic acid signals resistance to piercing herbivores (aphids) and bacterial pathogens. Haney et al. show that microbially induced phenotypes that appear detrimental actually promote resistance to chewing herbivores: there is a trade-off. Further, they use *Arabidopsis* genetic knockouts, transcriptomics and careful experimentation to uncover the mechanistic basis by which some strains appear to protect against both types of herbivory. They show that *Pseudomonas* strain CH267 promotes JA signalling MYC2-dependent gene expression in the presence of chewing herbivory (*T. ni*), while *Pseudomonas* strain WSC417 favours expression through the ORA59/ERF1 pathway, which simultaneously induces both jasmonic acid and salicylic acid pathways and thus protection from both types of herbivory. This work highlights the functional diversity within bacterial genera in the plant rhizosphere, and the authors stress that strain-level variation may be an important contributor to host plant fitness.

Bost and colleagues address mechanistic questions in a transcriptome-based study in this issue, working to understand whether different gut symbiont communities elicit different transcriptional responses in the guts of *Drosophila melanogaster*. Work in this system has shown that gut microbiota can be highly variable (Chandler, Morgan Lang, Bhatnagar, Eisen, & Kopp, 2011), having also illustrated that specific genes are expressed in response to the presence of bacteria in the fruit fly gut (Dobson, Chaston, & Douglas, 2016). It is also known that varying bacterial communities can alter nutritional phenotypes of their fly hosts (Newell & Douglas, 2014). So might natural variability in microbiome composition drive consistent alterations to host physiology, detectable at the transcriptional level? And what might this tell us about the significance of symbiotic variability in nature? Using both wild and laboratory-reared fly stocks in their study, the authors first confirm that the presence of gut bacteria alters gut transcription in laboratory-reared flies (Bost et al., 2018). They next utilize wild-caught flies with variable gut microbiota, testing the hypothesis that varying symbiont composition will drive differential patterns of gut tissue transcription. Varying gene expression did not, however, correlate with particular bacteria detected in wild flies. Transcriptional profiles were, instead, seemingly influenced by the abiotic environment, specifically through fly exposure to metallic insecticides (e.g., copper) (Bost et al., 2018). These results identify challenges for understanding the natural relevance of symbiosis, even in well-studied systems. Microbes are clearly impactful, and they clearly vary. But knowing how impacts change with this variation and how host responses may mediate such changes are topics that await further study.

Despite the prevalence of host-associated microbial communities comprised of diverse, interacting partners, much of our understanding of host/microbe integration comes from studies of a host and a single symbiont. In other words, experimental approaches—for the sake of simplicity—often exclude other common symbionts to examine a focal symbiont. Thus, the response of hosts to multiple mutualists is largely unknown. Using the model legume host *Medicago truncatula*, Palakurty and colleagues take on this more complex topic, examining transcriptional responses from plant roots after inoculation with rhizobial symbionts, mycorrhizal symbionts, neither or both (Palakurty, Stinchcombe, & Afkhami, 2018). Using previously generated transcriptomic data (Afkhami & Stinchcombe, 2016), the authors here identify coexpression modules: networks of genes showing consistent changes in expression across various treatments. They detect 18 such modules, which collectively contained over two-thirds of the genes in the plant's genome. Many modules showed strong contingency according to whether one vs. both mutualistic symbionts were present. In particular, relative to the no symbiont treatment, gene expression in five modules changed in the presence of both symbionts but not in treatments with single symbionts. Expression changes in five other modules were driven by a single symbiont, but disappeared in the co-inoculation treatment. Among the plastic genes assigned to such modules, the authors found functions including energy metabolism, ammonium transport, photosynthesis, oxidative stress and terpenoid metabolism to be overrepresented, hinting at the mechanisms behind plant responses. Finally, the authors show that individual genes that responded in nonadditive ways to the presence of multiple symbionts hold central positions within their gene networks, or modules (Palakurty et al., 2018). In other words, these genes had expression patterns showing disproportionately tight correlations with expression for other genes in their network. This finding raises the possibility that just a few dozen genes may be key to how hosts respond to a multispecies microbiome. It also raises questions about whether plasticity, rather than segregating genetic variation, may be more relevant to how plants manage such interactions.

3 | STRUCTURE OF THE MICROBIOME

Understanding the processes that structure host-associated microbial communities is a central goal in the microbiome field. This is often boiled down to determining the relative importance of the host, the pool of available microbes and within-host microbial dynamics. Documenting the overall composition and structure of the community is a first step towards disentangling the relative influence of evolutionary and ecological processes shaping the host-associated microbiome. Particularly in diverse and variable systems—for example seaweeds and the mammalian gut—rigorous surveys of the microbiome across many individuals, populations and time points are needed, in conjunction with surveys of the surrounding free-living microbiome. Through joint analysis of such data sets, researchers can identify microbes that are consistently present in or on hosts (core), which vary according to ecology (e.g., diet), and which exist as transients, temporarily acquired from the environment. Such surveys, together with experimental manipulation, enable researchers to narrow the range of possible drivers of microbiota community assembly, acquisition and turnover. This knowledge can then be used to test hypotheses about the host and ecological factors that structure the microbiome.

3.1 | Host phylogeny or ecology?

Comparative studies across related hosts often target taxa with contrasting ecologies to ascertain the relative role of ecology vs. host phylogeny in determining microbiome structure. A correlation with host phylogeny suggests that phylogenetically constrained host traits (such as immune defence) select for microbiota composition. Such a pattern may indicate a shared, faithful history between hosts and their microbes (Brooks, Kohl, Brucker, van Opstal, & Bordenstein, 2016), but may very well be driven by physiological, morphological, ecological or behavioural similarities in closely related hosts that lead to environmental filtering (Moran & Sloan, 2015). Previous studies have documented a strong signal of host identity and phylogeny in primates (Ochman et al., 2010), insects (Colman, Toolson, & Takacs-Vesbach, 2012; Sanders et al., 2014) and plant root endophytes (Fitzpatrick et al., 2018). However, in systems ranging from sponges (Thomas et al., 2016), trees (Kembel et al., 2014), amphibians (Bletz et al., 2017) and kelp (Lemay et al., 2018), host identity is a strong predictor of communities, but the signal disappears at broader phylogenetic levels (e.g., genus and above). Contributions in this issue test the importance of host phylogeny vs. ecology as predictors of microbiome composition by sampling closely related host taxa in controlled environments (Kohl, Dearing, & Bordenstein, 2018) (Erlandson, Savage, Wei, Cavender-Bares, & Peay, 2018), related species with contrasting ecologies in uncontrolled, natural environments (Ivens, Gadau, Kiers, & Kronauer, 2018) and through broad phylogenetic sampling of animals with both divergent and convergent feeding ecologies (Nishida & Ochman, 2018; Schuelke, Pereira, Hardy, & Bik, 2018).

Diet and environment play a strong role in determining the composition of the gut microbiota, but their effects are often confounded by host phylogeny. Kohl and colleagues control for these confounding factors by rearing seven species of mice in a common environment with common food in their test of the degree to which microbiota composition and diversity correlate with phylogeny. They sampled the bacterial communities at distinct regions across the digestive tract in these seven species to further ask whether signals of host specificity vary across gut chambers. Through analysis of 16S rRNA amplicon sequence data, and the distributions of sequence groups ≥99% sequence similarity (99% OTUs), the authors find a strong and consistent effect of host phylogeny, with *Mus musculus* and *Peromyscus eremicus* harbouring particularly distinctive microbiota. Overall, microbiota become more distinctive between host species as one moves in a posterior direction, from foregut to faeces (Kohl et al., 2018). Many of the same bacterial genera are common across host species, though variable in relative abundance, raising questions about whether these genera diversify along with rodent hosts or whether the same strains can colonize many host species.

While Kohl and colleagues confirm prior findings on the importance of phylogeny as a microbiome correlate in mammals, microbiota from mammalian guts are also well known to vary according to host ecology (Groussin et al., 2017; Ley et al., 2008; Ochman et al., 2010). Ecological effects may not be realized across short timescales, with microbiomes showing inertia in groups such as pandas in spite of fairly drastic dietary shifts (Ley et al., 2008). Addressing this point, novel research on the relative importance of diet and phylogeny, and the timing of microbiome divergence across the host phylogeny, is presented in this issue. Specifically, Nishida and Ochman gather previously generated 16S rRNA amplicon sequencing data of faecal bacteria from dozens of mammals, combining these with previously published estimates of the host phylogeny and the absolute timing of their evolutionary divergence (Nishida & Ochman, 2018). Unlike some prior studies, which had assessed community membership after binning sequences to higher order bacterial taxa (e.g., phyla), the authors assess microbiome similarity through 97% OTU composition. And after controlling for host habitat and diet, they find that community composition measured at this scale indeed shows a strong phylogenetic signal, supporting results from a recent study on this same system (Groussin et al., 2017). Intriguingly, the authors document steady trends of microbiota divergence over time, estimating that ~1–2% of shared OTUs are lost for every 10 million years of host divergence. Transitions between lifestyles (terrestrial to marine for Cetartiodactyla and the evolution of flight in bats) were associated with the largest wholesale changes to the gut microbiota. Somewhat surprisingly, microbiota divergence rates were not greatly accelerated in groups with higher numbers of dietary shifts. This work reinforces the importance of the environment in structuring the microbiota in humans (Rothschild et al., 2018) and other mammals (McKenzie et al., 2017), although it is unclear just how, and how fast, major lifestyle transitions drove natural shifts in whale and bat microbiomes. This work also highlights the nuanced insights that can be gained by probing individual lineages, showing that lineages at a detailed taxonomic scale (OTU or genus level) strongly reflect host phylogenetic signal, while broad taxonomic categories are associated with lifestyle or dietary transitions (Groussin et al., 2017; Nishida & Ochman, 2018).

Working with tending ants (*Lasius* and *Brachymyrmex*) and their “trophobiont” hemipteran partners (aphids and mealybugs), Ivens et al. also interrogate the role of host phylogeny vs. ecology. These researchers studied ants that tend both aphids and mealybugs in the same nest, presenting a potential opportunity for symbiont transfer across trophobionts or from trophobionts to ants. Tendencies towards host specialization could, however, serve as a formidable barrier to such transfer and establishment, a concept that would be supported should symbionts show little overlap among unrelated hosts. To address this, the authors use a rigorous study design with many individuals across different colonies to survey each insect’s microbiome (Ivens et al., 2018). Their efforts across both groups revealed remarkably low-diversity microbiomes, in keeping with prior findings (e.g., Jing et al., 2014; Moreau & Rubin, 2017). With the exception of a few likely pathogens, aphids and mealybugs harboured only known endosymbionts. The phylogenies for several of their symbionts (*Buchnera*, *Tremblaya* and *Sodalis*) mirrored the host phylogeny, consistent with their strict vertical transmission (Ivens et al., 2018). Such cospeciating symbionts of aphids and mealybugs were rarely found in ants; when they were detected, it was argued to represent “dietary DNA”—that is remnants of symbionts from consumed trophobionts. Ivens and colleagues hence conclude that strong adaptation to disparate hosts presents a very strong barrier to horizontal transfer for endosymbionts. Among the bacteria dominant in their studied ants, Acetobacteraceae were among the most common, with occasional *Wolbachia* and *Oxalobacter* (Ivens et al., 2018). Examinations of correlates across this host group revealed ecology to be a key predictor of the microbiota; that is, Acetobacteraceae are also found in other ants with sugary diets (Russell, Sanders, & Moreau, 2017) and are predicted to ferment dietary sugars in the gut. In addition, *Lasius* species that farm the same mealybugs appear to share the same strains of Acetobacteraceae (Ivens et al., 2018). While this result awaits further confirmation, it implies that changing ecological conditions (i.e., identities of tended insects) can promote relatively quick changes in the composition of transferrable, extracellular gut symbionts.

Variation in the immune system is often cited as an underlying cause of host specificity for vertebrate microbiota. Previous work has linked variation in major histocompatibility complex proteins (i.e., MHC)—key components of the adaptive immune response—to gut bacterial composition in stickleback fish (Bolnick et al., 2014) and mice (Kubinak et al., 2015). Building off of this in this issue, Hernández-Gómez and colleagues study skin microbiota and MHC variation in two subspecies of the endangered hellbender salamander. They use both amplicon sequencing of 16S ribosomal RNA and amplicon sequencing of MHC IIb alleles from salamander blood. The plausible expression of the encoded MHCIIb proteins on salamander skin is argued to enable direct interactions between these molecules and the microbiota. The authors show that the salamander subspecies are distinct in microbiota and MHC profiles (Hernández-Gómez, Briggler, & Williams, 2018). Most importantly, they find that divergence in MHC at the amino acid level, and differential presence/absence of specific MHC alleles, significantly predict a portion of interindividual microbiome variability within populations (Hernández-Gómez et al., 2018). In mice, MHC-induced changes in bacterial composition alter disease susceptibility (Kubinak et al., 2015), suggesting the importance for this discovery in the disease ecology of endangered amphibian species. It is also of relevance given the known capacities of skin-associated microbes to inhibit the growth of the chytrid fungal pathogen (*Batrachochytrium dendrobatidis*) (Becker, Brucker, Schwantes, Harris, & Minbiole, 2009), which has devastated many amphibians worldwide.

Schuelke and colleagues compile an impressive data set of marine nematodes with convergent feeding ecology across three ocean basins to assess the role of phylogeny vs. ecology. In doing so, they provide a striking example in which there is no clear taxonomic structure to host-associated communities. Schuelke et al. sampled the bacterial and eukaryotic microbiota of nearly 300 individual nematodes—largely from the deep sea—spanning 33 morphologically identified genera that differ in feeding ecology. They find no patterns in the bacterial or eukaryotic microbiota, or even in particular lineages, that correlate with host identity, geography or ecology (Schuelke et al., 2018). Instead, they paint a picture of animals that likely associate with a wide array of microbes in their environment—a point reinforced by finding many generalist bacteria that show up again and again on hosts, such as *Alteromonas* and *Thalassomonas*, among the common taxa. They do find hints of parasitic interactions and occasionally detect bacteria and archaea likely involved in nitrogen cycling, such as ammonia-oxidizing bacteria. The impacts of such functions on host biology and their breadth of relevance across individuals, populations and species should be tested in future studies, as well as the possibility that the marine nematode microbiome shows structure at the functional level, even if not at the level of taxonomy.

An example where functional, but not taxonomic, microbiome structure exists has been reported for seaweed species from the genus *Ulva*. Microbiomes of these hosts vary tremendously in populations 10 km apart, but the functions they encode—sugar metabolism and osmotic stress—appear consistent and likely enable diverse microbes to utilize polysaccharides exuded by *Ulva*, while withstanding the periodic drying faced in its intertidal habitat (Burke et al., 2011). This finding necessitated a change in our understanding of host/microbe relationships and the factors that determine microbiome assembly. It has also been replicated across systems (Louca et al., 2018), again pointing towards next steps for systems like the aforementioned marine nematodes. In this issue, Roth-Schulze and colleagues expand on this body of work in *Ulva*, targeting closely related species from Spain and Australia with metagenomics (Roth-Schulze et al., 2018). They find that the functional core extends across the globe, further confirming that there is no taxonomic core community. By comparing functional profiles within and between populations, they show that functional similarity also declines across large distances or across host species, suggesting local factors may be selecting for different functions.

3.2 | Structuring the surrounding microbiome

In systems where symbionts are environmentally acquired—such as *Vibrio* and squid or rhizobia and legumes—one question of relevance is how, or whether, the presence of hosts alters the microbiota of the surrounding environment by either seeding it with symbiotic bacteria or secreting resources or antimicrobials that favour certain host-orbiting microbes. Such manipulation of the environmental pool of microbes can alter transmission dynamics and potentially enrich for host-specific microbiota or may alter ecosystem processes such as carbon cycling. Seaweeds present one example of environment-engineering eukaryotes, by secreting abundant polysaccharides and antimicrobial inhibitors that alter nearby microbial communities in the water column (Lam & Harder, 2007) and on nearby hosts (e.g., corals Zaneveld et al., 2016).

In this issue, Chen and Parfrey use manipulative experiments to ask whether seaweeds alter the environmental microbiota or the surface microbiota of their neighbours by sampling bacteria on seaweeds and in the surrounding water after incubation with kelp, a red alga or both. Their data indeed show that kelp and red algae modify microbiome structure in the surrounding water column, but in unique ways. These macroalgae also shaped each others' surface microbiota, though in a more subtle fashion. But by and large, the two focal species retained fairly distinct microbiota in the laboratory, and in the case of *Nereocystis* (the kelp species), across 100s of kilometres (Chen & Parfrey, 2018). This argues that these hosts exert strong selectivity over their microbiota (Chen & Parfrey, 2018) and that not all seaweeds have microbiota as taxonomically variable as those of *Ulva*. Finally, proliferation of waterborne microbes that were exceedingly rare without hosts suggests the capacity for host-introduced metabolites (e.g., organic carbon, antimicrobial compounds) to promote the rapid growth of weedy bacterial taxa that would otherwise persist at low levels. These impacts resemble the effects that plants have on their rhizosphere, and suggest a need for further study on the interplay between hosts, their abiotic environment and the encompassed microbiomes.

Along related lines, Shukla and colleagues (this issue) investigate the role of behaviour and the environment in shaping the microbiota of burying beetles, which feed on and develop within the carcasses of small vertebrates (Shukla, Vogel, Heckel, Vilcinskas, & Kaltenpoth, 2018). Burying beetles have a core microbial community that is transmitted from parent to offspring through the carcass. Many of these bacteria appear specialized and have persisted within this group for millions of years (Kaltenpoth & Steiger, 2014). A decaying carcass is a nutrient-rich resource, but also comes with some significant drawbacks including a potentially toxic food source due to bacteria that are responsible for the breakdown of the tissues. Burying beetles exclusively use this substrate to rear their young and have overcome this obstacle through the regulation of the carcass microbiota. Carcasses "prepared" by beetles with oral and anal secretions have much different microbial communities and do not go through normal stages of bloat and decay. By sampling across developmental stages and the nearby environment, the authors demonstrate that the beetles transmit a core microbial community of bacteria and fungi to the prepared carcass through these aforementioned oral and anal secretions. This community is in turn transmitted to the beetle larvae through contact with the carcass surface. In addition, the core microbial community transmitted by the adult beetles suppresses the growth of competing microbes, facilitating efficient "vertical" transmission of a pure inoculum of symbiotic core microbiota from adult to larvae. In several ways, these findings resemble those from the *Steinernema/Heterohabditis* nematode *Photorhabdus/Xenorhabdus* (Gammaproteobacterium) system. In this latter case, bacterial symbionts create a suitable environment in parasitized arthropods for their nematode hosts, helping to establish competitive dominance while uniquely, in this case, subverting host arthropod defences (Burnell & Stock, 2000).

3.3 | Microbiome structure changes across development

The microbiota can change dramatically over the course of development in many animals (McFall-Ngai et al., 2013; Yatsunenko et al., 2012), and amphibians provide a case study (Kueneman et al., 2016). Tracking both the microbiota on boreal toads over the course of development as well as environmental bacteria, Prest et al. document dramatic changes in the toad microbiota. They demonstrate a complete reorganization of the microbial community during this time, with major shifts corresponding to hatching of eggs and tadpole metamorphosis. At each stage of development, there is also general succession of microbiota from copiotrophic (organisms that thrive in high nutrient conditions) to oligotrophic (those common in low nutrient conditions) taxa, which, they argue, supports a scenario of initial colonization by opportunistic taxa followed by replacement with competitive dominants (Prest, Kimball, Kueneman, & McKenzie, 2018). By comparing amphibian communities to those in the environment, they also show that colonizing microbes are predominately coming from pond water throughout development (Prest et al., 2018). That different communities are assembled over time from the same environmental pool demonstrates how changes in the host impose a varying habitat filter, favouring different colonizers as they acquire their microbiota anew each life cycle stage.

3.4 | Manipulative experiments elucidate factors structuring the microbiome

Manipulation studies are another way to separate the core components of the host-associated microbiome from the variable components. They can also powerfully assess the relative roles of host vs. environment in structuring the microbiome by controlling for each and illuminate systems with highly static symbionts that are impervious to manipulation (Hu, Lukasik, Moreau, & Russell, 2014). Such studies are often particularly informative in the many cases where microbes are predominately acquired from the environment, as in seaweed surface microbiota (Chen & Parfrey, 2018), the plant rhizosphere (Deveautour, Donn, Power, Bennett, & Powell, 2018; Erlandson et al., 2018) and gut microbiota of some animals (Newell & Douglas, 2014).

In this issue, Erlandson et al. (2018) manipulated host environment, taking advantage of a multiyear, ecological study on young willow and poplar trees. A total of 13 willow species and one species of poplar were planted in common gardens. These species varied in their tendencies to thrive in wet vs. dry habitats, with some trees being generalized for both types of habitat. Also manipulated for the experiment was the nature of the soil habitat. Specifically, of the 20 plots utilized, half were dry, upland habitats, while the other were wetter, lowland habitats. And by covering the ground with landscaping cloth, the influence of other plant species on soil microbes was limited for the duration of the experiment. Through use of two different of amplicon sequencing strategies (i.e., bacterial 16S rRNA, fungal ITS), the authors found that abiotic factors most strongly shape the soil rhizosphere communities surrounding willow roots. Through abiotic measurements from soil, the authors were able to identify strong abiotic correlates of microbiome structure and alpha diversity, including ammonium and soil water content for fungi, and ammonium, nitrate and pH for Eubacteria and Archaea. Interestingly, genetically encoded features of host trees had subtle, but significant effects, on microbiomes. This was manifested by different microbiomes residing beneath habitat generalist vs. specialist trees and, in some cases, beneath different willow species. To conclude, the controlled nature of this study gave the authors unique abilities to assess the importance of environmental vs. host effects on the surrounding soil microbiome. Abiotic factors were clearly the most influential factors in this study. But the detection of host effects among a group of mostly congeneric (i.e., highly related) trees raises the prospects of common and, perhaps, even strong impacts of plant genotype in driving the natural patterns of soil microbe alpha and beta diversity.

Morella and colleagues use manipulation to gain insight into a hard-to-study fraction of earth's microbiome, bacteriophage and their effects on host-associated bacterial communities. Phage is hypothesized to underlie bacterial community dynamics, particularly in systems with high functional redundancy (Louca et al., 2018). Such effects can, in turn, impact the eukaryotic hosts of these bacteria (Manrique et al., 2017). To address phage impacts here, the authors isolated bacteria and phage from tomato plants. They used these fractions to inoculate tomato seedlings, performing follow-up studies to measure bacterial density (via droplet digital PCR), diversity and community composition (via 16S rRNA amplicon sequencing) (Morella, Gomez, Wang, Leung, & Koskella, 2018). At 24 hr postinoculation, bacteriophage reduced densities of bacteria co-inoculated onto tomato plants; at this time, their presence also altered bacterial community composition, suggesting that variable abundance of lytic phage could drive community divergence. Bacterial titres evened out across treatments by day 7, and interestingly, communities of phage-treated plants showed convergence by this time point, hinting at a possible homogenizing effect of phage on meta-communities. Their findings support the "kill the winner hypothesis," as dominant pseudomonads were knocked back early. They also point forward to a pressing need to incorporate phage studies into other symbiotic systems to gain insight into their impact on bacterial community dynamics and, more broadly, to assess the potential for phage therapy to improve human health and, potentially, that of natural ecosystems.

3.5 | Hallmarks of influential microbe interactions in a well-studied laboratory model for symbiosis

Sharing goals with Morella et al. is a study by Rock et al. (2018). This work has characterized microbiome structure in alfalfa-feeding pea aphids, along with its likely causes—namely within-host symbiont interactions governing the stability of particular communities. Using standard diagnostic PCR, their study explored the distributions of seven maternally transferred, nonessential endosymbionts. Aside from the obligate, ubiquitous *Buchnera*, these bacteria are thought to comprise the entirety of the heritable, endosymbiotic microbiome for the sampled populations. In addition, their functions and lifestyles resemble those of other "facultative" endosymbionts, found commonly across insects and playing roles in defence or in mediating of heat stress (Oliver, Smith, Russell, & Clay, 2014). Given their vertical inheritance (maternal transmission efficiency in the laboratory is often 100%), they would seem to be models of stability in symbiosis. Yet, each facultative endosymbiont is variably present in the field, infecting just a fraction of the surveyed pea aphids. Inefficient transmission under natural conditions could help to explain this finding, and perhaps, this unfolds when particular symbionts co-infect, as hinted at anecdotally by prior work (Sandström, Russell, White, & Moran, 2001). Should this be the case, one would expect certain microbes to live together often (i.e., those improving each others' transmission) and others to co-infect more rarely. Through a widespread North American screen for the seven known facultative symbionts, the authors first demonstrate that multiple endosymbionts often inhabit the same host, but that their tendencies to co-infect are indeed nonrandom (Rock et al., 2018). For example *Serratia symbiotica* and *Rickettsiella viridis* frequently co-infect together across. *Spiroplasma* generally infects aphids without other facultative symbionts, living alongside only the obligate *Buchnera* endosymbiont. In the second part of their study, the authors performed field trials examining transmission of natural symbiont combinations, across a wide range of host genetic backgrounds and field conditions. They found that vertical transmission patterns mirrored the structure of the microbiome. Most notably, *Serratia* and *Rickettsiella* improved each others' transmission, while *Spiroplasma* suppressed transmission of these and, likely, other co-infecting symbionts. While the authors have not ruled out a role for host-level natural selection (i.e., an influence of host ecology) or host genotype (i.e., a type of habitat filtration) in shaping community composition (Rock et al., 2018), this work adds to Morella et al.'s (2018) finding to show how microbial interactions, and within-host symbiont ecology, may often be influential in structuring the microbiome.

3.6 | Defining communities through strain-level examinations

In the last 5 years, amplicon sequencing of single genes has become the most common method for sampling microbial communities. And with this takeover has come a large focus on slowly evolving genes, including 16S ribosomal RNA of bacteria and archaea. For various reasons, analyses of microbiome composition, and alpha and beta diversity, have relied on binning sequences into groups with ≥97% identity (i.e., 97% OTUs). As 16S rRNA will approximately diverge at a rate of 1% per 50 million years (Ochman & Wilson, 1987), and as these rates may be faster in certain symbiotic bacteria (Ochman, Elwyn, & Moran, 1999), such a focus will be insufficient to address questions relating to dispersal and colonization dynamics, as the low variability will mask neutral and functional strain-level variability (Cordero & Polz, 2014). New methods for parsing unique sequences, amidst sequence-introduced noise (Di Segni et al., 2018), can extract additional information from the 16S rRNA gene, leading, for example, to deeper insights into bacterial distribution (Thompson et al., 2017). But even with such resolution, a 16S rRNA focus may miss significant cryptic strain variation and biologically relevant patterns of strain distributions (Łukasik et al., 2017). Researchers are now turning amplicon sequencing towards protein-coding genes to address specific questions (e.g., MHC divergence by Hernández-Gómez and colleagues, discussed above) or gain strain-level resolution (Raymann, Bobay, & Moran, 2018a), or are turning to whole-genome sequencing of symbionts (Dhami, Hartwig, Letten, Banf, & Fukami, 2018; Vanderpool, Bracewell, & McCutcheon, 2018), with its wealth of provided data on both neutral diversity and function.

The first study in this issue to focus intensively on such method comes from the honeybee gut microbiome system. Commonly used in apiculture (i.e., bee husbandry), antibiotics are used to kill or reduce pathogen infection across a number of hosts, but also more broadly alter the composition and diversity of the resident microbiota (Francino, 2015). Honeybees are of concern as they are in decline in many places and are impacted by antibiotics (Raymann, Shaffer, & Moran, 2018b). The honeybee gut microbiota consists of a handful of core bacteria, including *Snodgrassella alvi* and *Gilliamella apicola*, which themselves consist of multiple, functionally diverse strains (Engel & Moran, 2013). Previous studies documented a decrease in bacterial diversity in response to antibiotics with 16S rRNA amplicon sequencing (Raymann et al., 2018b). Yet, even bacteria with identical 16S rRNA barcodes may differ greatly in function. Here, Raymann and colleagues (this issue) use amplicon sequencing of two protein-coding genes and population genetic metrics of diversity to address the impact of antibiotics on genetic diversity in these two key symbiont species from the honeybee gut (Raymann et al., 2018a). They demonstrate that strain diversity within *S. alvi* is mostly unaffected, despite a precipitous decline in abundance for this species when exposed to antibiotics. In contrast, genetic diversity within *Gilliamella apicola* drops significantly, although the abundance of *G. apicola* remains high (Raymann et al., 2018a). Using population genetic metrics at multiple loci, they open a window into the genome dynamics of these bacteria and provide evidence that declining strain-level diversity—which is likely correlated with functional diversity—may be just as important a contributor to bee declines, in the face of antibiotic usage, as species loss.

Also in this issue, Dhami and colleagues leverage the fact that flowers are effectively ephemeral island habitats for nectar yeast. In doing so, they test the roles of environmental sorting and dispersal limitation on the genetic variation in the nectar yeast *Metschnikowia reukaufii*. The authors take a population genomics approach by sequencing whole genomes of over 100 strains of *M. reukaufii* from the shrub *Mimulus aurantiacus*, deriving these isolates from a span of over 200 km along the California coastline (Dhami et al., 2018). These strains clustered into three genetically distinct groups that were correlated with metabolic activity and interspecific competitiveness, but the authors find no signal of geographic distance structuring the genetic and phenotypic variation of the yeast. Indeed, the full range of genetic diversity was encapsulated in as small as a scale as 200 m. The ecological functional traits measured including colony morphology, growth rate, metabolic ability and interspecific competitiveness also fail to explain *M. reukaufii* strain distribution; notably, the least competitive strain with the narrowest metabolic capacity is the most common in the field. The authors acknowledge other ecological factors, such as tolerance to drought or biotic interactions, likely explain intraspecific diversity.

4 | EVOLUTION OF SYMBIOSES AND THEIR ROLES IN HOST ADAPTATION

Intricate host/symbiont relationships and the repeated finding that hosts rely on their microbial partners for key functions beg the question: When did symbiotic relationships originate, and are the evolutionary histories of partners entwined? Phylogenetic analysis of host and symbiont, often combined with fossils and molecular clock analyses to assign dates, is used to answer these questions. As discussed above, comparative studies of the whole microbiota (i.e., correlating community divergence with phylogenetic divergence) across related species are commonly used to assess the influence of host phylogeny on symbionts. Such studies can serve as jumping off points for evolutionary analysis by identifying key microbial taxa or functions whose evolutionary history might be tightly entwined with that of the host.

Vertically inherited symbionts and their hosts are hypothesized to share a long evolutionary history, particularly when the symbiosis is obligate and hosts and symbionts are dependent upon one another for survival and/or reproduction. These intimate associations enable symbiont-encoded phenotypic variation to respond to selection acting at the host level. Hence, symbionts can directly shape host adaptation and diversification through conferring novel or improved capabilities. The fidelity of such interactions over ancient timescales is often a focus of symbiosis research, as even vertically transmitted microbes may jump between hosts given sufficient timescales. Similarly, hosts that depend on symbionts may occasionally exchange partners, creating a complicated history and opportunities to relate such shifts in symbiosis to historical events that may have shaped, or been shaped by such changing partnerships. Studies in this issue have addressed this question, and explore, the mechanisms by which faithfully transmitted, sometimes domesticated, symbionts have facilitated adaptive host evolution.

Vanderpool et al. (2018) study the history of ancient associations between ambrosia fungi and ambrosia beetles (specialized weevils)—the world's oldest insect farmers (Vanderpool et al., 2018). The origins of fungal farming in weevils are fairly complex in the subfamily Scolytinae, with over a dozen relatively recent transitions towards this habit, and comparatively simple in the subfamily Platypodinae, which evolved the lifestyle just once (Hulcr & Stelinski, 2017). On the fungal side, there have also been multiple transitions towards symbioses with weevils, but fungal relationships are poorly resolved. Using a combination of PacBio and Illumina technologies, the authors sequence the genomes of 12 cultured fungal isolates from the order Ophiostomatales. Combining their robust phylogenomic tree with molecular clock dating, the authors approximate that the oldest lineage of farmed fungi dates back at least 86 million years ago (Ma), congruent with the proposed age for farming in the Platypodinae of 96 Ma (Vanderpool et al., 2018). The history of domestication is complex: this robust phylogeny confirms the polyphyly of the *Raffaela* farmed "ambrosia" fungi and points to multiple domestication events. The authors propose that these fungal lineages were then repeatedly co-opted in by sympatric Scolytinae weevils during their repeated transitions to a farming lifestyle. Ambrosia beetles and ambrosia fungi require each other, but fungi promiscuously associate with different beetles, thus providing an easy path to host switching over time. The use of genome sequencing to resolve microbial phylogenies is indicative of how far the field of microbial phylogenetics has come. When combined with molecular clock calibrations, this study shows how we can learn a great deal about the order and timing of historical events surrounding important symbioses.

Engl and colleagues use 16S rRNA sequencing, microscopy and experimental manipulation to investigate the identity of bacterial endosymbionts of grain beetles—major stored grain pests worldwide—further assessing the adaptive significance of these faithfully transmitted, bacteriocyte-dwelling microbes (Engl et al., 2018). They first find that the endosymbionts are from the Bacteroidetes phylum and related to well-known insect symbionts *Sulcia* (cicadas) and *Blattabacterium* (cockroaches), which are both obligate nutritional symbionts (Moran et al., 2008). These endosymbionts were seemingly acquired by Silvanidae and Bostrichidae beetles, independently, more than 100 million years ago, painting a picture of ancient and somewhat specialized symbioses. Interestingly, although these Bacteroidetes symbionts are prevalent, they are not ubiquitous or obligate in grain beetles. As shown here, the host beetles exhibit a history of multiple acquisitions and symbiont exchanges, punctuated by occasional loss. Several species even have two Bacteroidetes symbionts that occupy different compartments in the bacteriome. To address just why and how these microbes may be useful to hosts, the authors remove symbionts from the grain pest *Oryzaephilus surinamensis* and show that the beetles are much more susceptible to dry conditions in this aposymbiotic state. The Bacteroidetes endosymbionts promote cuticle synthesis and, as a result, resistance to desiccation. This appears to be a common function that has convergently evolved among endosymbionts of insects, and similar functions have been documented for the Gammaproteobacteria symbiont (*Sodalis pierantonius*) of grain weevils, which occupy a similar niche (Heddi, Grenier, Khatchadourian, Charles, & Nardon, 1999). Overall, the authors suggest that this symbiotic relationship may have been a preadaptation that enabled grain beetles to so successfully colonize human grain stores and become major pests.

Gauthier and colleagues (this issue) address a similar question on the role of symbionts in host adaptation, focusing on a distinct, yet ancient symbiosis—that between bracovirus symbionts and *Cotesia* parasitoid wasps (Gauthier, 2018). Bracovirus are domesticated virulence weapons used by *Cotesia* during infection of stem-boring caterpillar hosts. The genomes of these viruses are normally fragmented and integrated into the *Cotesia* genome. Yet during infection, this genetic material is injected alongside *Cotesia* eggs into caterpillars. Here, active bracovirus suppress the caterpillar immune system, allowing wasp larvae to develop. To characterize their molecular evolution, the authors sequence bracovirus genomes across multiple populations of *C. sesamiae* and a related species, *C. typhae*, enriching for bracovirus genes via custom-designed target enrichment probes, and subjecting the captured fragments to Illumina HiSeq sequencing. They show that bracovirus evolution tracks population structure of *C. sesamiae* and *C. typhae* (Gauthier, 2018). Genome alignments revealed common trends of gene loss and pseudogenization. The authors also detect high levels of nonsynonymous substitutions in coding regions of six bracovirus genes, which represent signatures of positive selection. They argue that increasing divergence in bracovirus genomes correlates with different patterns of host caterpillar use and preference, and their discovery of genes with adaptive substitutions and inactivation histories suggests candidate mechanisms underlying such changes. In short, the authors propose that viral symbiont evolution may play a central role in adaptation to new lepidopteran hosts and that it may go some way towards explaining the staggering diversity of parasitoid wasp species.

5 | THE STABILITY OF SYMBIOSIS IN A CHANGING WORLD

With the ushering in of the Anthropocene, many of the world's ecosystems have come to exhibit remarkable fragility. The near ubiquity of symbiosis for the world's eukaryotes raises the question of how symbionts might facilitate or impede their hosts' responses to this changing world. For example, how will host-associated microbiota shift in response to changing climate, and will microbial changes promote resilience in the host or accelerate declines? Elevated temperatures stress the obligate *Buchnera* symbiont of aphids and decrease fitness, but function can be rescued by facultative symbionts (Montllor, Maxmen, & Purcell, 2002). Rising temperatures also threaten corals by disrupting symbioses with photosynthetic *Symbiodinium*, although shuffling of symbiont genotypes buffer the coral host against stress (Cunning, Silverstein, & Baker, 2015). More generally, acquisition of symbionts from the environment has arisen as one mechanism that might increase resilience of corals to changing conditions (Webster & Reusch, 2017) and of hosts more broadly (e.g., Fitzpatrick et al., 2018).

In this issue, Ramsby and colleagues ask how heat stress impacts the microbiota of the sponge *Cliona orientalis*, which lives on coral reefs and erodes the calcium carbonate reef matrix (Ramsby, Hoogenboom, Whalan, & Webster, 2018). The eroding capacity of *Cliona* is expected to increase as reefs warm. Like corals, *Cliona* harbour symbiotic *Symbiodinium*, although sponges more typically have cyanobacterial symbionts, and bleach at high temperatures. Bleaching and microbial dysbiosis at high temperature might disrupt or alter their eroding capacity. Ramsby et al. find that the microbiota is stable up to 27°C and then shifts gradually until 32°C, at which point *C. orientalis* bleaches (i.e., loses *Symbiodinium*) and the microbiota is irreversibly altered; the sponge did not recover. Most of the sponge-associated microbes are highly variable across individuals and treatments, but a core community that is consistently present throughout warming was composed of *Rhodothalassium* (Alphaproteobacteria), *Nitrosopumilus* (Thaumarcheota) and a number of Planctomycetes that may play a role in nitrogen cycling. These persistent core microbes may enable *Cliona* to persist in a warming world up until the bleaching threshold is reached.

Focusing on another symbiosis with societal relevance—in this case due to its biological control implications—Doremus and colleagues assess the abilities of defensive, facultative symbionts in the pea aphid to protect against a parasitoid wasp, historically used as a biocontrol agent (Doremus et al., 2018). The defensive phenotype was studied across a range of temperatures, using multiple symbiont strains, and several clonal aphid backgrounds. Results showed that both aphid and symbiont genotype can govern the efficacy of defence across temperatures. Most consistent, however, was the failure of symbiont defence at moderately warm temperatures frequently encountered in the field (Doremus et al., 2018). Consistent with these experimental findings, the protective symbionts (*Hamiltonella defensa*) were less common in warm locales across North America. As aphid-encoded, nonsymbiont-based defences remained robust across the laboratory-explored climactic conditions the authors argue that parasitoids may be selected to overcome a very different set of defensive modalities (i.e., endogenous vs. symbiont-conferred) across climactic gradients, enabling a geographic mosaic for host–enemy co-evolution.

Increased drought and altered precipitation regimes will become more common with climate change and are key factors in understanding how plant communities—and food crops—will respond. In this issue, Deveautour et al. (this issue) take advantage of an experimental rainfall manipulation experiment. Focusing on four grassland plants, they assess the effect of drought on arbuscular mycorrhizal fungal communities and plant traits related to resource acquisition and symbiosis. They find host species-specific fungal communities that are responsive to drought, and in contrast to Erlandson et al. (this issue), host species identity is the strongest predictor of microbiota composition, rather than abiotic factors. The difference may result from the phylogenetic scale considered: the plants here are distant relatives compared to the congeneric willows. Deveautour et al. find that functional traits, such as root phosphorous and calcium levels, are correlated with host species and their fungal communities, but as these functional traits did not respond to drought regime, it is not possible to say whether fungal communities respond to these traits per se or other host-specific factors (Deveautour et al., 2018). Overall, these results suggest that arbuscular mycorrhizal fungal communities will change in response to future abiotic conditions, but find no evidence of indirect effect mediated by shifts in host physiology.

6 | THEORETICAL AND CONCEPTUAL FRAMEWORK FOR SYMBIOSIS

In this review, McKenney and colleagues take an explicitly host centric perspective and argue that the role the microbiome plays for the host—especially in the mammalian gut—can be productively viewed within the categories of the ecosystems services framework (McKenney, Koelle, Dunn, & Yoder, 2018). They use the terminology of ecosystem services to categorize functions necessary to build the host/microbiome ecosystem or benefit the host. In this framework, initial colonization of a host and biofilm formation are supporting services, while production of short chain fatty acids is a provisioning service, and immunomodulation a regulating service. This review provides a framework test whether certain services and conditions as likely to increase host fitness in a reliable manner in mammals and beyond.

7 | CONCLUSION

The studies presented in this issue advance our understanding of the ecology and evolution of symbioses between hosts and their associated microorganisms, as well as the mechanisms behind these associations. This body of research investigates a broad array of hosts and microbes using an equally broad array of molecular biology tools and experiments that test hypotheses and generate many more. These works are united by incorporation of high-throughput sequencing of DNA, RNA or proteins, variously used to gain insight into the microbial partners present, what they are doing and their evolutionary history—in some ways fulfilling a promise of accessible sequencing to illuminate biodiversity patterns and the mechanisms that underlie them. This collection highlights the diversity of host–microbiome relationships and their functional consequences, but also points to commonalities behind the mechanisms of integration, patterns in the assembly of the microbiome and response to environmental stress.

Future work should build upon the foundational knowledge gathered by studying symbioses across diverse systems to further fundamental and applied research goals, such as the examples below. Studies in this issue, and in the field at large, raise numerous hypotheses for the mechanistic underpinnings of symbioses that should be tested in future research. The results of such tests can illuminate new modes of host/symbiont crosstalk, as seen here in Thairu et al. (2017). Second, biotic interactions are widely viewed as important in structuring the host-associated microbiome (e.g., Koskella et al., 2017; Louca et al., 2018), but these assumptions have been tested in just a few systems, including a few here (Morella et al., 2018; Rock et al., 2018). Investigating the impact of microbial competition and predation is an important direction for the field.

Another promising direction is delving further into the evolutionary history of symbioses with the current understanding that while very few symbionts have a long history of exclusive vertical inheritance long-term associations between clades of symbionts and clades of hosts are common, suggesting a strong role for habitat filtering, highly specific partner choice mechanisms, or limits to microbial host range. These trends of phylogenetic tracking also raise questions on the potential for diffuse co-evolution and for contributions by reliable, microbial partners towards host adaptation and the colonization of new ecological niches.

Finally, the deeper understanding of the ecology, evolution and function of the microbiome—gained by studying a multitude of hosts and symbionts—promises tangible benefits to the welfare of humans and the ecosystems surrounding us. Microbiome manipulations, for instance, may help us to achieve societal goals such as improved crop yield and resilience, to combat devastating hospital-borne infections or insect-vectored pathogens and to restore the vigour of amphibian populations threatened by a global pandemic. Basic research on symbiosis has been catapulted by technological innovations and growing interest in recent decades, which have placed microbes firmly near the centre of host eukaryote biology. As the tools for manipulation become further honed, we are finally realizing the translational potential of innovative, multifaceted microbiome science.

ACKNOWLEDGEMENTS

We thank Armando Geraldes and Karen Chambers for their guidance and patience throughout the process of assembling this issue, David Crespo for assembling the cover images and Loren Rieseberg for providing this opportunity. We also thank the many authors and reviewers for assembling excellent contributions.

AUTHOR CONTRIBUTION

L.W.P., C.S.M. and J.A.R. all conceived of and wrote this introduction.

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How to cite this article: Parfrey LW, Moreau CS, Russell JA. Introduction: The host-associated microbiome: Pattern, process and function. *Mol Ecol*. 2018;27:1749–1765. https://doi.org/10.1111/mec.14706