Trends in Microbiology

CellPress

Review

Defining the Core Microbiome in Corals' Microbial Soup

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Corals are considered one of the most complex microbial biospheres studied to date, hosting thousands of bacterial phylotypes in species-specific associations. There are, however, substantial knowledge gaps and challenges in understanding the functional significance of bacterial communities and bacterial symbioses of corals. The ubiquitous nature of some bacterial interactions has only recently been investigated and an accurate differentiation between the healthy (symbiotic) and unhealthy (dysbiotic) microbial state has not yet been determined. Here we review the complexity of the coral holobiont, coral microbiome diversity, and recently proposed bacterial symbioses of corals. We provide insight into coupling the core microbiome framework with community ecology principals, and draw on the theoretical insights from other complex systems, to build a framework to aid in deciphering ecologically significant microbes within a corals' microbial soup.

Trends

Metagenomics and Illumina sequencing have permitted a wider exploration of coral-associated bacteria, including rare bacteria.

Understanding bacterial community patterns from the occurrence, rather than from the abundance, through the concepts of the core microbiome and abundance–ubiquity (AU) test allows identification of stable, potentially symbiotic interactions bypassing sequencing and sampling bias.

Identification of microbial niche and localisation of bacteria with coral habitats provides insight into the potential role of bacteria and the nutritional environment in which they reside.

Persistent bacteria in corals across spatial scales and depth gradient have been identified, despite the high variability reported in four decades of research in coral-associated bacterial communities.

The Coral Microbiome Symbioses and Functional Contributions of Coral-Associated Bacteria

Multiorganism partnerships are widespread in nature and can form the basis of organism and **ecosystem** (see Glossary) success in space and time [1–3]. Many of these symbioses have been studied in detail and the benefits provided by the **symbiont** to the **host** have been well documented [4,5]. However there are other systems in which **symbiosis**, particularly bacterial symbiosis, is hypothesized as an underlying mechanism of the host success but the exact nature of the symbiosis has not, or can not yet be, determined. Corals and coral reefs are one such ecosystem where specific bacteria, and bacterial communities, are hypothesized as crucially important in both organism function and ecosystem dynamics [6,7]. But the contributions made by specific bacterial symbionts have not yet been accurately deciphered.

The coral **microbiome** is one of the most complex microbial biospheres studied to date [6]. Corals host thousands of bacterial **phylotypes**, in species-specific associations across broad geographical and temporal scales that have been hypothesized as functionally significant [8–11]. The coral microbiome, its **composition**, spatial-temporal variability, and response to environmental change have been studied to date in over 25 coral species, from reef locations around the world, and from corals in both healthy and diseased states [9,12–23] (see Table S1 in the supplemental information online). As in other systems, advances in molecular technologies have unveiled the richness and composition of bacterial communities of the coral host, and high-throughput sequencing is now universally applied to evaluate bacterial diversity [24,25]. This methodology provides a representation of the bacterial **community**, identifies **rare** and less abundant species, and provides insight into the conservation of bacterial phylotypes within **microhabitats** and between individual hosts [26–28]. An average of 995 distinct bacterial **operational taxonomic units (OTUs)** and 22 520 sequences were identified from each coral species when sequencing technologies were first applied to the coral microbiome (Table S1,

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http://dx.doi.org/10.1016/j.tim.2016.11.003

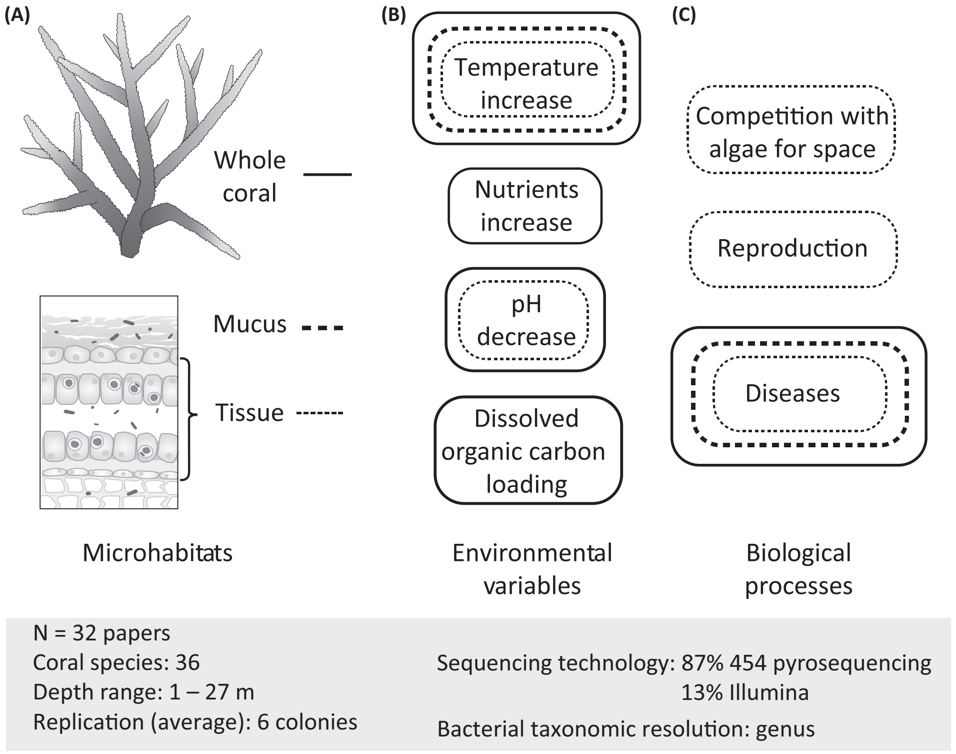

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Figure 1. Bacterial Community in Corals Is Responsive to Environmental Factors and Biological Events. Metanalysis results evidence that in shallow corals bacterial community composition and abundance within different microhabitats shifts in response to changes in environmental factors and in response to biological processes (see details in Table S1).

Figure 1). These estimates of microbiome complexity have recently increased substantially as higher sequencing coverage has been obtained. Now upwards of 100 000 bacterial OTUs and millions of reads are reported from each coral species [29–31]. In general, the dominant associations that have been identified in these studies are assumed as the healthy symbiotic state of the coral-associated bacterial communities [15,19,32,33].

γ- and α-proteobacteria dominate the bacterial communities of corals; other highly abundant bacteria include members of the phyla Bacteriodetes, Firmicutes, Actinobacteria and Cyanobacteria. *Endozoicomonas* is generally the highest **abundance** genus in the coral microbiome [6] (see citations in Table S1). The consistency of dominant associations between individuals, within and between coral species, across spatio-temporal scales, and depth gradients, has only recently been investigated. In fact, one of the most significant findings that has arisen from recent deep sequencing of the coral microbiome is the substantial variability that is evident between individuals, species, and reef habitats – the most revealing of which is the variability that occurs between individuals [29,34,35]. For example, studies investigating ubiquitous associations across individuals find that over 60% of the identified bacterial OTUs of the coral microbiome are present in less than 10% of individuals studied, many of which include some of the most highly abundant bacteria within a single individual [29,34]. There is also substantial variation in the occurrence (and persistence) of some of the most abundant members of the microbiome. For example *Endozoicomonas* is the most abundant group in the coral microbiome but are also highly variable within and between coral species [36–38] (see review [6]). Williams *et al*. [39] have proposed that the variability between individuals seen in corals is correlated to the age of the

Glossary

Abundance: number of individuals of a species in an area, population or community. Based on 16S rRNA amplicon, sequences are considered as a proxy of individuals.
Commensal: a symbiotic relationship in which one organism is benefited and the other is not benefited or harmed.
Community: groups of organisms coexisting in the same habitat.
Community structure: composition and abundance of species in a community.
Composition: species present in a community.
Diazotrophic bacteria: bacteria capable of fixing gaseous nitrogen (N_2).
Ecosystem: interactions and dynamics of physical, chemical, and biological components in an area [90].
Endolithic: organisms boring into, and living in pores of coral skeletons.
Function: metabolic role.
Habitat: the physical space with characteristics that define niches to be occupied by organisms [90].
Holobiont: collective term to refer to a host and its symbionts from specific taxonomic groups.
Host: organism where a symbiont lives.
Microbiome: an assemblage of microorganisms, including their genomes, associated with any system (e.g., human, water column, coral).
Microhabitat: physical space in corals (Box 1) with characteristics that provide niches for bacteria.
Mutualistic: a symbiotic relationship in which both partners benefit.
Niche: ecological role and space of an organism in a community [139].
Operational taxonomic units (OTU): operational proxy of taxon when the definition of taxonomic entities is based on DNA sequence differences. OTU taxonomical definition is based on nucleotide identity (usually 97% for 16S rRNA), reflecting any taxonomic level (from phyla to species) [95].
Phylotypes: DNA sequences grouped as similar based on a specific gene marker (e.g., 16S rRNA). Individuals in the group are approximately 97–99% similar. Synonym for Operational taxonomic units (OTUs).