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# The nature and taxonomic composition of coral symbiomes as drivers of performance limits in scleractinian corals

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## ABSTRACT

All plants and animals host complex communities of taxonomically diverse microbial assemblages (viruses, Archaea, Bacteria, micro-eukaryotes) that contribute to the functional attributes of the host organism. Scleractinian corals represent particularly provocative subjects for study in this context because they are morphologically complex and associate with a broad diversity of macro invertebrates and vertebrates as well as microorganisms. Representatives of all these taxonomic groupings have been shown to contribute to the function of corals through direct or indirect provisioning and cycling of nutrients, waste removal, defense, and stress tolerance, traits that influence the fitness and environmental thresholds of individual coral colonies. How the taxonomic composition, functional limits and interactive nature of members of these communities vary among and within host species, and scale up to influence community level processes that drive ecosystem structure and function through time and space is unknown; these communities are, however, taxonomically variable among individual corals. Here we draw on the published literature to discuss the ecological and functional significance of the broad and variable taxonomic symbioses found closely associated with corals. Using a comparative approach, we hypothesize that the intra-specific and inter-specific variations in response of corals to environmental disturbance is linked to differences in the specificity, nature and composition of these symbiotic assemblages and reflect variation in the architectural complexity (micro and macro) and capacity of corals to provision habitat. We describe individual coral colonies as symbiomes, unique micro-ecosystems bounded by the physical limits of the coral colony whose performance limits reflect the taxonomic range of the associates (micro and macro) found within the colony. We explicitly recognize the fact that corals represent complex ecological communities composed of organisms that have the potential to compete, as well as interact with one another and the host as commensals, mutualists and parasites, states that likely to be dynamic with nature, context and environment.

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## 1. Introduction

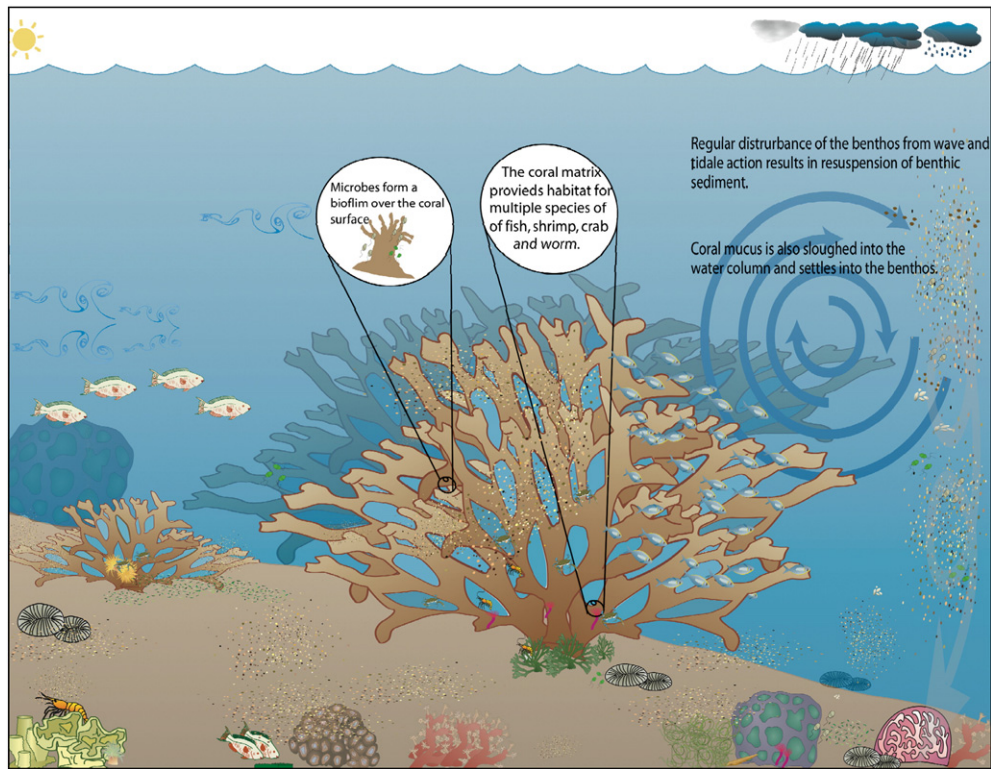
Coral reefs are productive and diverse tropical marine ecosystems framed by massive three-dimensional structures created by the deposition of calcium carbonate skeletons by individual coral colonies (Goreau and Goreau, 1959). These skeletons are hugely variable in form, reflecting innate characteristics of different coral species that scale with age, and are in some cases, plastic with respect to environmental conditions (Todd, 2008). The architectural complexity created by coral communities that combine to form coral reefs, provides a plethora of habitats to support an enormous diversity of organisms from all kingdoms of life. The capacity of coral reefs to host such broad biodiversity represents a defining feature of these

important coastal ecosystems (Grottoli et al., 2006; Rohwer et al., 2002; Schwarz et al., 2008; Stella et al., 2010).

Like the reef, each coral colony serves as habitat for a diverse assemblage of macro- and micro-eukaryotes, Bacteria, Archaea and viruses (Rohwer et al., 2001). This biodiversity occupies a variety of niches both within coral tissues and skeletons, closely associated with the surface of the coral and the mucus layers, and in the waters within or under the branches, lobes and plates of the coral colony (Ainsworth et al., 2010; Bourne and Munn, 2005; Lampert et al., 2006; Stella et al., 2010; Sunagawa et al., 2010). Each member of these multi-species assemblages or symbioses has the potential to interact with the coral host to a lesser or greater extent, and to contribute or detract from the overall fitness and long-term survival of the coral colony (Pratchett, 2001; Rohwer et al., 2001; Stella et al., 2010), impacts that scale up to affect reef structure and ecosystem processes (Fig. 1). We use the term symbiosis here to describe close enduring associations between individuals of different species (Bouchard, 2009) recognizing that

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**Fig. 1.** Schematic illustrating that corals provide habitat for a taxonomically diverse assemblage of macro and microorganisms that all have the capacity to contribute to the functional performance of the coral colony.

these interactions can change in time, space and environment, to be beneficial, neutral and also negative (see Table 1 for terms and definitions). For example, functional attributes of the intimate unions between corals and unicellular dinoflagellates in the genus *Symbiodinium* drive high rates of productivity and calcium carbonate deposition that create the structure of the reef (Yellowlees et al., 2008). The nature and taxonomic composition of these interactions are spatially and temporally variable among and within coral species, and can be dramatically influenced by changes in the abiotic environment. Differences in the taxonomy of *Symbiodinium* manifest in physiological variation that influences environmental thresholds, and as such, the relative abundance of specific *Symbiodinium* types hosted by individual coral colonies has profound implications for the persistence of an individual coral through time, and in the face of environmental disturbance (reviewed in Stat et al., 2006).

The functional underpinnings of associations between *Symbiodinium* and corals are by far the most comprehensively studied to date, however, Bacteria, endolithic algae, and a diversity of invertebrates and vertebrates have also been shown to contribute to the performance of the coral by provisioning and cycling of nutrients, defending the colony and increasing thermal tolerance (e.g. Cleveland et al., 2011; Fine and Loya, 2002; Holbrook et al., 2008; Stewart et al., 2006). This suggests that the complex assemblages hosted by corals confer benefits to the coral hosts and as a collective, have the potential to contribute to the functional range, environmental thresholds and resilience of corals and reefs.

Corals exhibit high intra and inter-specific variability in response to environmental disturbance, a trait that scales up to influence reef wide ecology (Loya et al., 2001). Here we develop a discussion framed by the idea that the performance of individual corals reflects physiological limits imposed upon the colony by the combined activities of the broad taxonomic diversity of organisms found in symbiosis with each coral colony. We propose (1) that each coral can be described by the term *symbiome*, a polygenomic super-organism

or system that encompasses all enduring associations (micro and macro) bounded by the physical limits of the colony (Sapp, 2003<sup>1</sup>); (2) that the nature and composition of the multispecies assemblage reflect the diversity of habitats within the symbiome as well as community level process such as competition and resource limitation; (3) that the multispecies assemblages in coral symbiomes interact with each other and the host in mutualistic, commensal, and parasitic states that are potentially dynamic over space, time and environment; and, (4) that symbiomes in branching corals are more complex than in massive corals, complexity that translates into positive fitness traits (for instance growth rates) under normal conditions, but that may also contribute to the increased sensitivity to branching corals under environmental stress.

## 2. Defining the functional unit in corals

The universal importance of symbiotic associations to organism (and ecosystem) function is broadly recognized (McFall-Ngai, 2008). Defining what comprises a biological individual and what contributes to its functional limits is complicated in any system, but is particularly challenging in corals because they are architecturally complex and morphologically variable, and the peripheral limits of the colony encompass a variety of compartments with very different environmental characteristics (e.g. skeleton, gastrodermal tissues, mesoglea, ectodermal tissues, mucus layers and interstitial waters). Each of these compartments is composed of niches that are spatially and temporally dynamic and that have the capacity to support a large and

<sup>1</sup> This term was first introduced by Sapp (2003) to describe microbial symbioses (see discussions in Sapp, 2003, 2004). We use his original conceptual framework, but apply the term more broadly here to describe and discuss the full taxonomic range of interactions closely associated with, and functionally relevant to, corals.

taxonomically broad diversity of symbionts, uniquely suited to the specifics of each environmental setting. The microbial component of this diversity is now widely recognized as being fundamentally important to the functionality of corals (see Knowlton and Rohwer, 2003; Rohwer et al., 2001), and the coral and closely associated microbial assemblages are collectively described as the coral holobiont. A significant portion of symbiotic diversity in corals is, however, non-microbial and falls outside the definition of the coral holobiont. Many of these non-microbial symbionts have been shown to confer benefits to the coral host, however, the collective role that this diverse and highly variable component of coral associated communities plays in establishing the performance limits of the coral has not yet been considered. Here we operationally describe and discuss individual coral colonies as symbiomes rather than holobionts to indicate that we are considering the functional and ecological significance of the broader taxonomic range of organisms found in symbiotic relationships with corals, rather than the associated microbial communities alone.

Defining which members of the communities within the physical boundaries of a coral at any one time actually represent a component of the symbiome is complex because the marine setting and reef environment create a high level of connectivity that links much of the biodiversity found closely associated with corals to the water column and benthos (Fig. 1). It has been suggested that the term biological individual should be defined as organism interactions that are functionally integrated and linked by a common fate under environmental challenge (Bouchard, 2009; Wilson and Sober, 1989). For corals, this concept creates an interesting framework for discussion because they are frequently examined in the context of their responses to environmental stress and exhibit both within and among species variability in their vulnerability and responses to local and climatic disturbances. An extreme example of implications of common fate on reefs is seen in the differential impacts of large storms, where many fragile branching corals are smashed, buried and die, while the less fragile and/or massive forms weather the storm and survive. The habitat created by the fragile branching forms is destroyed by this disturbance and the closely associated species that engage in enduring relationship with these corals, particularly those occupying habitats within the tissues and skeletons, presumably also perish, while those associated with surviving corals persist. Thus those members of the multi-species assemblage that share a common fate with their coral hosts would be considered as part of the biological individual under this definition.

**Table 1**  
Terms and definitions.

<i>Commensalism:</i>	An interaction that is beneficial to one member and neutral to the other member.
<i>Ecto- epi- or exosymbiosis:</i>	A surface associated, or surface living, symbiotic interaction.
<i>Endosymbiosis:</i>	An internalized symbiotic interaction that occurs within tissue, cells and cellular spaces.
<i>Eukaryote:</i>	An organism where the cells and organelles are membrane bound.
<i>Facultative symbiosis:</i>	An enduring association that is beneficial, but not essential for survival of the organisms.
<i>Mutualism:</i>	An enduring association that is mutually beneficial.
<i>Obligate mutualism:</i>	An enduring association that is required for the survival of both symbiotic partners.
<i>Parasitism:</i>	An interaction that is beneficial to one member of a symbiosis and detrimental to the other.
<i>Pathogenesis:</i>	The development or progression of a diseased state.
<i>Prokaryote:</i>	Organism(s) lacking membrane bound organelles.
<i>Symbiosis:</i>	An enduring association between individuals of different species.
<i>Symbiome:</i>	The organismal ecosystem, bounded by the outer physical limits of the eukaryotic host and encompassing the eukaryotic host and all of its associated symbioses.
<i>Symbiomics:</i>	The study of the biochemistry, physiology, genetics, ecology and evolution of the symbiotic systems, as well as their dynamic interfaces.

The former example highlights the importance of corals as habitats and emphasizes the fact that common fate can occur despite the high degree of connectivity in reef environments. It also emphasizes the fact that the spatial and interactive nature of the association can mediate the role of connectivity in this system to influence fate outcomes. For example, small fish use the water spaces within branching corals for shelter from predators and excrete nitrogen that promotes coral growth (Holbrook et al., 2008). During storms, fish have the mobility to exploit the connectivity and move to another more protected environment and are thus unlikely to share a common fate with the original coral colony if it is destroyed. In contrast, an endosymbiotic dinoflagellate living deep inside the corals tissues has limited capacity to vacate the coral host in the event of any stress, and may actually be incapable of surviving outside the coral in the free living environment, thus connectivity is redundant in this case and the endosymbiotic dinoflagellates are much more likely to die with the coral.

These examples are extreme cases representing two ends of a spectrum in terms of residency fate outcomes and they highlight the innate complexity in the system; the fish exploits the coral as habitat, the coral and fish do not necessarily share common fate but when the organisms associate, the outcome is mutually beneficial and the partnership contributes to the functional performance of the symbiome (Cleveland et al., 2011). At the other end of the spectrum are the endosymbiotic dinoflagellates, the permanent residents, who are spatially constrained by their intracellular habitat and, in some cases, can be passed from one generation of corals hosts to the next via the coral egg. The high fidelity of these associations makes it likely that these *Symbiodinium* are obligate mutualisms, and that neither partner can survive independently of the other.

There are also, however, a whole suite of interactions in corals that are less easy to define in terms of residency status and fate outcomes. For example, corals host diverse and in some cases, specific assemblages of microbes (Rohwer et al., 2001), many of which are located in the coral's very dynamic surface mucus layer (for review see Ainsworth et al., 2010). These mucus layers are constantly being lost and replaced, a process that is profoundly accentuated during stress events (Fig. 2). Microbes resident in this mucus are continually lost to the water column and adjacent sediments (Wild et al., 2004) where their fate is unknown. This raises another important issue to consider, which is the temporal stability in a coral niche as it relates to the scale and generation times of the taxonomic entities that reside there. In the case of microbes, many have fast generation times, so their rate of turnover in the mucus layer under normal circumstance may provide ample opportunity for multiple generations to persist in close association with the corals through time and fill stable functional niches despite the dynamic nature of their habitat. Thus, they may actually represent very specific and enduring associations with their host. There are some parallels between this example and the temporally and spatially dynamic habitat created by the bobtail squid *Euprymna scolopes* for its pivotally important bacterial symbionts *Vibrio fischeri* (McFall-Ngai, 1999). The chemical nature and temporal stability of the various environmental compartments that exist in coral symbiomes (skeleton, tissues, mucus layers, interstitial waters) are not well understood, but this is an area of investigation that will inform the basic biology of corals and clarify the context in which symbiotic associations occur in coral symbiomes.

### 3. Architectural complexity and capacity of corals to provision habitat

The architectural complexity (micro and macro) of coral colonies creates a diversity of potentially unique habitats, a feature that will directly influence the capacity of a colony to interact with or host other species. The idea that corals represent symbiomes, or individuals whose functional attributes reflect the collective performance limits set by the multispecies assemblage they host, is provocative when one considers the implications of the level of architectural variability among and within coral species, and the fact that coral species assemble in very



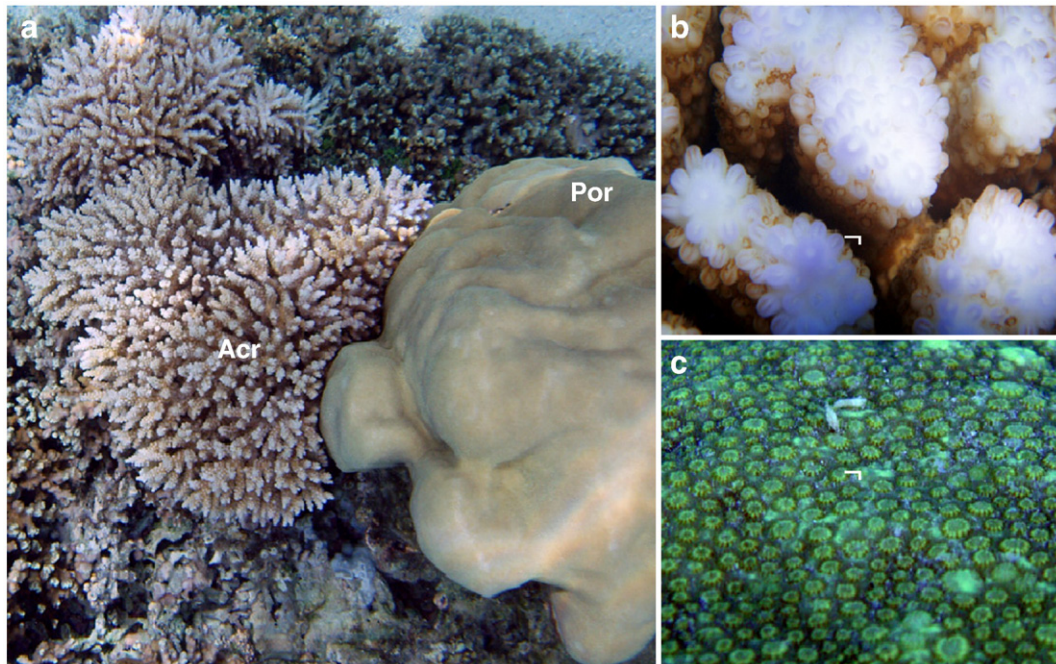


**Fig. 2.** Colonies of the patch forming branching coral *Acropora aspera* sloughing mucus into the water column and onto the adjacent benthos following exposure to environmental stress.

different ways across geographic locations. If one examines the extreme ends of the morphological continuum and compares branching forms such as representatives of the genera *Pocillopora* or *Acropora*, with massive

members of a genus like *Porites*, it is obvious that their innate capacity to provision habitat is very different (Fig. 3). The branching corals exhibit a high degree of micro and macro architectural complexity that is variable among individuals of a species, a trait that often reflects plasticity with respect to the environment and increasing three-dimensional complexity that emerges as the colony grows. In contrast, the massive *Porites* are mounding or lobed forms that are less architecturally complex at macro- and micro scales, are more uniform among individuals, show less increase in three-dimensional complexity as the coral colony grows, and are less plastic with respect to the environment (Todd, 2008). The question is then, to what degree does differences in architectural complexity of corals manifest in the taxonomic composition of the multispecies symbioses that comprise the coral symbiome? Further, how do these differences map onto the functional range and collective environmental thresholds of the individual, or symbiome, and scale up to influence the outcomes of an environmental disturbance on a given reef assemblage?

Branching and massive corals are known to have very different vulnerabilities to environmental disturbance (Loya et al., 2001), and different basic functional attributes (see results in Edmunds et al., 2011; Fitt et al., 2009; Gates and Edmunds, 1999). The branching corals are generally environmentally sensitive and fast growing, while massive corals are more stress resistant and grow slowly. How these differences in environmental thresholds and basic biology relate to the interactive nature and taxonomic breadth of the organisms that these corals form symbioses with has not been holistically studied to date. The only comparative data available for symbioses in branching and massive coral symbiomes is for endosymbiotic dinoflagellate (*Symbiodinium*) communities, and these data suggest they are very different. For example, the environmentally susceptible branching coral *Acropora millepora* hosts multiple *Symbiodinium* types representing at least two of the nine major lineages in the genus *Symbiodinium* (clades C and D; e.g. Berkelmans and van Oppen, 2006; Pochon and Gates, 2010), and these endosymbionts are acquired from the environment anew each generation. In contrast, *Porites lobata*, an environmentally robust massive member of the genus *Porites*, hosts a group of very closely related sequence types representing one lineage (clade C, internal transcribed spacer 2 sequence type C15 cluster; e.g. Lajeunesse, 2004) that are vertically transmitted from parent to offspring via the egg. The



**Fig. 3.** Morphological differences between coral species are evident at both the scale of a) the coral colony (macro morphology) and b) and c) coral polyp (micro morphology). Acr: branching Acroporid coral, Por: massive Poritid coral. White arrow indicates individual coral polyps. Photos courtesy of Hollie Putnam.

genetic distances among the *Symbiodinium* lineages hosted by *A. millepora* are equivalent to different taxonomic orders in free-living dinoflagellate groups (Stat et al., 2008) and represent ancestral types in clades C and D that are found in a broad diversity of coral hosts, and that can be cultured independently from their hosts. In contrast, the C15 *Symbiodinium* group hosted by *P. lobata* represent derived members of the most derived clade of the nine in the genus *Symbiodinium*, and are found in a very narrow range of coral hosts and have not been successfully cultured to date, despite significant attempts do so (Krueger and Gates, in prep). Although the general perception is that all members of the *Symbiodinium* genus have the capacity to interact equally well with their host, the stark differences in the overall diversity, taxonomic positions, culturability, and the strategies by which the respective coral hosts acquire their *Symbiodinium*, raises fundamental questions about just how similar they are in terms of their functional range, physiological performance and levels of specialization, integration and evolution with their respective coral hosts.

Refocusing on the implications of architectural complexity in corals, it is likely that differences in the basic diversity of the *Symbiodinium* communities hosted by *A. millepora* and *P. lobata*, reflect differences in the nature and quality of the habitats provisioned by their very contrasting growth forms. In this context, it is interesting to ask the question of whether differences in the basic diversity of *Symbiodinium* found associated with two coral species scale across taxonomic groups and is generally greater in a branching morphology such as *A. millepora*, in comparison to a massive morphology such as *P. lobata*. To our knowledge, there are no studies that compare the broader taxonomic assemblages in these two very different coral morphologies. A recent study, however, examined epifaunal (exosymbiotic) invertebrate assemblages in four branching coral species (including *A. millepora*) and revealed that they associate with between 64 and 102 different invertebrate species representing up to 12 different phyla (Stella et al., 2010). Of these, 15% were unique to coral species, suggesting some level of specialization with coral host (Stella et al., 2010). This study provides a provocative glimpse of the enormous taxonomic complexity in the multi-species assemblages found in corals and confirms that these communities vary within and among closely related species, and that at least some of these associations are unique to a given coral species and individuals within a species. The latter specialization highlights the potentially important and enduring nature of the interactions between the broader biodiversity found in corals and is compelling rationale for future studies aimed at understanding how among and within species variation in colony morphology reflects in the abundance and nature of symbiotic associations, and influences the functional range and environmental thresholds of coral symbiomes.

The above example highlights two coral species that host very different communities of a single genus (*Symbiodinium*). It is also important to consider that the composition of each of these communities will reflect not only constraints and features imposed upon them by their relationship with the host coral, but also interactions with each other and other members of the symbiome community as they compete for resources that are limiting, such as light, space or nutrients. Such interactions are likely to drive, and be evidenced by stratification, niche specialization and compartmentalization in the symbiome. Interestingly, spatial and environmental stratification has been documented in cases where multiple *Symbiodinium* types are hosted by individual coral colonies (Rowan et al., 1997). Further, bacterial communities in tissue slurries of healthy corals from the Great Barrier Reef are dominated by  $\gamma$ -proteobacteria and the mucus is known to be dominated by  $\alpha$ -proteobacteria in a variety of coral species (Bourne and Munn, 2005; Kvennefors et al., 2010), suggesting that spatial (Sweet et al., 2011), taxonomic, and potentially functional compartmentalization also occurs in coral microbial interactions. Although well studied and known to be pivotally important to structuring macro communities, the implications of inter and intra specific competitions for resources in coral symbiomes have not been explored to date, but are likely extremely important in

structuring these communities and setting the overall functional range of individual corals.

#### 4. Functional attributes associated with multispecies assemblages in corals

Research of the past decade has provided tantalizing evidence for the coral symbiome, or multispecies phenotype, to fulfill functional niches. Symbionts often provide their hosts with functional capacity that the host does not innately possess, and this extension of biological range has the potential to influence the overall success, fitness and competitive advantage of the symbiotic unit. In corals, these functional benefits include the provisioning and cycling of nutrients, defense, and thermal (stress) tolerance.

##### 4.1. Provisioning and cycling of nutrients

Nitrogen and carbon are limiting elements for growth in all marine systems but particularly in nutrient depleted tropical reef waters where corals thrive (Muscatine and Porter, 1977). As in all ecosystems, the microbial communities play a central role in provisioning and cycling nutrients in coral reefs. Despite molecular based studies that provide compelling evidence for broad associations between corals and nitrogen fixing bacteria and Archaea (Beman et al., 2007; Olson et al., 2009; Wegley et al., 2004), only a single study focusing on a single coral species has demonstrated a direct link between the presence of symbiotic microbes with the functional capacity to fix nitrogen in the coral where it presumably benefits the coral host. This is the endosymbiotic association between diazotrophic bacteria and the Caribbean coral *Montastrea cavernosa* (Lesser et al., 2004, 2007). The documented presence of diverse microbial assemblage in multiple compartments of the coral symbiome that possess the capacity to fix nitrogen, however, suggests that they play a very important role in coral biology and make this a rapidly expanding area of study in the field.

Coral colonies also benefit indirectly through the contribution of ammonia by closely associated macro-symbionts such as coral associated fish (Holbrook et al., 2008) and bivalves (Mokady et al., 1998). Although the spatial context of these associations is different, the ammonia provided by these exosymbionts results in improved coral growth, coral tissue thickness and endosymbiotic dinoflagellate density ((Meyer and Schultz, 1985)) and presumably, influences overall fitness. It is unknown how the ammonia signal is translated and utilized by the coral for growth, but this process is likely to be mediated by symbiotic microbes closely associated with corals. Indeed, the *Symbiodinium* communities are known to play a key role in recycling and assimilating ammonia produced by the host itself (Burriss, 1983). To date there has been little work focusing on the functional linkages among taxonomically different symbiotic members of coral symbiomes as it pertains to nitrogen cycling.

In terms of carbon fixation, the endosymbiotic dinoflagellates hosted by corals are major players in both coral biology and functional integrity of the ecosystem. They have been the subjects of numerous studies demonstrating their role in provisioning hosts with carbon and can support all of the host's respiratory needs. The *Symbiodinium* reside in an encysted form inside their host's gastrodermal cells and they photosynthesize and translocate newly fixed carbon to the host. Quantitative aspects of this translocation are thought to be under the control of the host, although such regulation is inferred from *in vitro* studies and has never been demonstrated *in situ* (Gates et al., 1995). It is also known that endolithic communities reside within the skeleton of coral colonies (Shashar and Stambler, 1992) and are major contributors to coral reef primary productivity (Odum and Odum, 1955). Recent evidence suggests that microbial endoliths within the coral skeleton, particularly the alga *Ostreobium* sp, provide a source of fixed carbon to the coral host (Fine and Loya, 2002). Additionally, *Ostreobium* sp. exhibit high tolerances for thermal stress (Fine et al., 2005) and capacity for photoacclimation (Fine et al., 2004) which



combines to allow for population blooms during coral bleaching and disease events (Fine et al., 2006). The populations translocate newly fixed carbon to the coral host tissues that compensates for the reduced supply of carbon from the endosymbiotic dinoflagellates during bleaching, or impairment to photophysiological function associated with disease. A recent study of four massive coral from fringing reefs in Japan and Vietnam documented differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between coral colonized and not colonized by endolithic *Ostreobium* spp. (Titlyanov et al., 2009). The results indicate that the mutualism between coral and *Ostreobium* sp. is either limited to periods of increased light associated with bleaching of the coral tissues or is highly species or location specific. Titlyanov et al. (2009) also provide evidence that the coral host may be provisioning the endolithic *Ostreobium* spp. with nutrients at other times. This study highlights the dynamic nature of the interactions between corals and *Ostreobium* spp. and suggests they can shift to interact as mutualists and parasites depending on the environmental conditions. Just how common such shifts in interactive states are in coral symbiomes is unknown, as is their impact on the physiology of the host, but is in our opinion an extremely interesting area for future research.

#### 4.2. Defense

Recently, Mao-Jones et al. (2010) developed a computational model demonstrating a stable-state shift in microbial communities from antibiotic producing to pathogenic following environmental change, and suggested that the antibiotic state contributes to robustness, and health of the host. Rypien et al. (2010) specifically demonstrated that antagonisms occur between members of healthy coral bacterial flora and suggested that the resident microbes directly control bacterial colonization, particularly that of opportunistic pathogens. The authors identified that between 52% and 63% of cultivable bacterial isolates obtained in the study showed antibiotic properties (Rypien et al., 2010), while another study (Ritchie, 2006) showed approximately 20% of the cultivable surface mucus population to be antibiotic producers. This supports the idea that particular members of bacterial communities associated with corals are beneficial, while others maybe be more functionally neutral in this particular functional niche. The universality and functional attributes of probiotic bacteria on the surface, or inside, coral hosts is not well-studied or understood at present, but is likely to be a very informative and fruitful avenue for future research.

In other systems, specific bacterial communities play a role in stimulating host immunity. For example, Kitano and Oda (2006) argue that members of the commensal bacterial flora of the mammalian gut provide benefit to the host by contributing to robustness through the stimulation of the immune system, and confer protection against pathogenesis. Microbial communities specific to digestive regions of corals have not yet been identified to date, but presumably if these communities exist and are specific to the digestive region, it is provocative to think that they function in this capacity and provide similar benefit to the host. Identifying how members of symbiome assemblages partition among microhabitats in which specific host function occurs, such as digestion in the gut, will assist in targeting members that may play a role, or mediate, host physiology and immunology, as has been demonstrated in higher organisms (for review see Ley et al., 2008).

A wide range of macro-organisms also contribute significantly to defense in the coral symbiome (Oigman-Pszczol and Creed, 2006). Recently Pantos and Bythell (2010) identified a novel coral–hydrozoan interaction occurring exclusively with *Acropora muricata* of the Great Barrier Reef, and suggested that the large battery of hydrozoan nematocytes provides enhanced defenses on the coral apical tip. Coral associated crabs are also thought to provide significant defense against crown-of-thorns predation (Pratchett, 2001; Pratchett et al., 2000) and algal overgrowth. For example, corals maintained without crab

symbionts were found to have significantly higher overgrowth (75%) than those held with crabs communities (10%; Coen, 1988). This role in algal control or reduction is particularly significant during stress events because algal blooms can occur when corals bleach and these types of interaction may be key to corals resisting overgrowth and ultimately recovery (Diaz-Pulido et al., 2009). Crabs have also been shown to play an important role in sediment removal from coral colonies (Omer and Aaron, 2009; Rinkevich et al., 1991; Stachowicz et al., 1999; Stachowicz and Hay, 1999; Stewart et al., 2006), a benefit which no doubt provides increased capacity to withstand smothering and sedimentation during runoff events.

#### 4.3. Resistance to stress

To date, most of the research on the implications of symbiosis for stress resistance in corals has focused on the endosymbiotic dinoflagellate communities. Clade D *Symbiodinium* appear to have greater thermal range than some clade C *Symbiodinium* and their presence is broadly discussed as conferring benefit to the host coral in terms of stress resistance (Baker et al., 2004). Corals that host clade D do not, however, grow as well as conspecifics that host clade C, so there are obvious functional trade-offs associated with these unions (Jones and Berkelmans, 2010; Little et al., 2004). Indeed, clade D *Symbiodinium* are often described as ‘opportunists’, a term that is used in this context to refer to a capacity to engage in symbiosis with a variety of partners, and reflects their increased abundance in thermally challenged or bleached hosts. A recent global analysis of circumstances where clade D is found in high abundance reveals that this clade associates with degraded habitats and may in fact be exploiting the compromised health of stressed coral hosts (Stat and Gates, 2011). Maintaining specific assemblages of *Symbiodinium* is not without metabolic costs and examining the immune systems of corals in different environments and when challenged with different types of *Symbiodinium* will unveil cellular behaviors that will inform the relative advantages and disadvantages of associating with organisms with different interactive and functional attributes.

Other than the endosymbiotic dinoflagellate, recent studies of coral community stress responses have focused primarily on the potential pathogenic nature of microbial interactions and the idea that shifts in the microbial community composition in corals may be a sub-lethal indicator of environmental stress. For example recent research has provided evidence that changes in both viral (Vega-Thurber et al., 2009) and fungal communities are sentinels of an environmental stress response in corals (Domart-Coulon et al., 2004; Le Campion-Alsumard et al., 1995; Ravindran et al., 2001; Wegley et al., 2007; Yarden et al., 2007). There are a number of examples in other systems where symbionts extend the capacity of a host to withstand stress. For example a tri-partite symbiosis between plant–fungi–virus has been described to confer thermal tolerance to the host plant (Marquez et al., 2007). Similarly plant–fungal symbioses are shown to provide the host increased tolerance of both biotic and abiotic stressors (see Rodriguez and Redman, 2008). Although it is clear that fungal associates and viruses play very beneficial roles in host resistance in other systems (Marquez et al., 2007), our understanding of these communities in corals is limited to their potential negative impacts. For example studies on coral associated fungi have focused on decomposition, pathogenesis, and bioerosion (Sterflinger, 2000; Tribollet et al., 2006; Tribollet and Payri, 2001) and to date there has been little focused consideration of the positive functional contributions of members of the broader diversity found associated with corals in conferring stress resistance of coral symbioses. As mentioned earlier, endolithic algae provision hosts with nutrients when the colony is bleached, and it has also been proposed that they confer photoprotection to the coral–dinoflagellate symbiosis (Yamazaki et al., 2008), thereby extending the capacity of the symbiome to withstand the impact of thermal stress and the progression of bleaching events.

## 5. Summary

Much of the effort over the last 20 years has focused on describing patterns of diversity in a few members of the symbiotic assemblages hosted by corals across a variety of spatial scales. This work is heavily weighted to the endo- and exo-symbiotic microbial diversity in corals, with an emphasis on endosymbiotic dinoflagellates, the characterization of virus-like particles and viral sequences (Davy and Patten, 2007; Patten et al., 2008; Seymour et al., 2005), and the identification of potential primary and opportunistic pathogens (Wilson et al., 2001, 2005; Munn, 2006; Davy et al., 2006; Lohr et al., 2007). Although it is known that the physiology of endosymbiotic dinoflagellates differs among members of the genus, very few studies have examined the comparative functionality of this group in their hosts and it is broadly assumed that all members of the genus interact equally with their hosts, and that they are always mutualists, despite evidence of opportunism and lower fitness in coral that host specific *Symbiodinium* lineages (Cantin et al., 2009; Jones and Berkelmans, 2010; Little et al., 2004; Mieog et al., 2009; Stat et al., 2008). By contrast, studies describing viral and microbial interactions are generally contextualized by the assumption that these symbionts have primarily negative fitness consequences for their hosts and it is only recently that the idea of beneficial bacterial, or viral, associations has begun to emerge in the coral literature (Ainsworth et al., 2010; Van Oppen et al., 2009).

To our knowledge there is no work that examines the full taxonomic diversity of organisms hosted by corals and addresses the range of potential benefits and tradeoffs associated with the combined activities of these interactions under normal and disturbed conditions. The capacity now exists, however, to integrate studies of multiple organisms simultaneously as a means to understand the function and response of the coral as a single functional symbiotic system. Such studies should consider the biochemistry, physiology, genetics, ecology and evolution of the symbiotic systems, in parallel with the dynamic interfaces between symbiotic partners. The recent expansion in studies investigating multi-partite microbial interactions in coral reef communities, coupled with the broader interest regarding the role of biodiversity in ecosystem function, is a clear indication of the widespread importance of this area of research within the coral reef field. We argue that all taxonomic components of the symbiotic assemblages hosted by corals should be considered, as all have the capacity to contribute to the functionality of the corals. Understanding the nature, persistence and functionality of coral symbionts that represent different levels of architectural complexity (within and among coral species, to encompass complexity that scales with age) over time, space, and environment will ultimately inform our understanding of functional biology and performance thresholds of corals representing structural elements that assemble very differently on reefs with location. Such efforts have the potential to provide a compelling framework for tailored modeling efforts aimed at better predicting climate change impacts on corals and reefs globally.

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## References

- Ainsworth, T.D., Thurber, R.V., Gates, R.D., 2010. The future of coral reefs: a microbial perspective. *Trends in Ecology & Evolution* 25, 233–240.
- Baker, A.C., Starger, C.J., McClanahan, T.R., Glynn, P.W., 2004. Coral reefs: corals' adaptive response to climate change. *Nature* 430, 741–741.
- Beman, J.M., Roberts, K.J., Wegley, L., Rohwer, F., Francis, C.A., 2007. Distribution and diversity of archaeal ammonia monooxygenase genes associated with corals. *Environmental Microbiology* 73, 5642–5647.
- Berkelmans, R., van Oppen, M.J.H., 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London Series B-Biological Sciences* 273, 2305–2312.
- Bouchard, F.D.R., 2009. Understanding colonial traits using symbiosis research and ecosystem ecology. *Biological Theory* 4, 240–246.
- Bourne, D.G., Munn, C.B., 2005. Diversity of bacteria associated with the coral *Pocillopora damicornis* from the Great Barrier Reef. *Environmental Microbiology* 7, 1162–1174.
- Burris, R.H., 1983. Uptake and assimilation of  $^{15}\text{NH}_4^+$  by a variety of corals. *Marine Biology* 75, 151–155.
- Cantin, N.E., van Oppen, M.J.H., Willis, B.L., Mieog, J.C., Negri, A.P., 2009. Juvenile corals can acquire more carbon from high-performance algal symbionts. *Coral Reefs* 28, 405–414.
- Cleveland, A., Verde, E.A., Lee, R.W., 2011. Nutritional exchange in a tropical tripartite symbiosis: direct evidence for the transfer of nutrients from anemonefish to host anemone and zooxanthellae. *Marine Biology* 158, 589–602.
- Coen, L.D., 1988. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. *Oecologia* 75, 198–203.
- Davy, J.E., Patten, N.L., 2007. Morphological diversity of virus-like particles within the surface microlayer of scleractinian corals. *Aquatic Microbial Ecology* 47, 37–44.
- Davy, S.K., Burchett, S.G., Dale, A.L., Davies, P., Davy, J.E., Muncke, C., Hoegh-Guldberg, O., Wilson, W.H., 2006. Viruses: agents of coral disease? *Diseases of Aquatic Organisms* 69, 101–110.
- Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., Weeks, S., Evans, R.D., Williamson, D.H., Hoegh-Guldberg, O., 2009. Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS One* 4, e5239.
- Domart-Coulon, I.J., Sinclair, C.S., Hill, R.T., Tambutte, S., Puvarel, S., Ostrander, G.K., 2004. A basidiomycete isolated from the skeleton of *Pocillopora damicornis* (Scleractinia) selectively stimulates short-term survival of coral skeletal cells. *Marine Biology* 144, 583–592.
- Edmunds, P.J., Putnam, H.M., Nisbet, R.M., Muller, E.B., 2011. Benchmarks in organism performance and their use in comparative analyses. *Oecologia* 167, 379–390.
- Fine, M., Loya, Y., 2002. Endolithic algae: an alternative source of photassimilates during coral bleaching. *Proceedings of the Royal Society B: Biological Sciences* 269, 1205–1210.
- Fine, M., Steindler, L., Loya, Y., 2004. Endolithic algae photoacclimate to increased irradiance during coral bleaching. *Marine and Freshwater Research* 115–121.
- Fine, M., Meroz-Fine, E., Hoegh-Guldberg, O., 2005. Tolerance of endolithic algae to elevated temperature and light in the coral *Montipora monasteriata* from the southern Great Barrier Reef. *Journal of Experimental Biology* 208, 75–81.
- Fine, M., Roff, G., Ainsworth, T., Hoegh-Guldberg, O., 2006. Phototrophic microendoliths bloom during coral "white syndrome". *Coral Reefs* 25, 577–581.
- Fitt, W.K., Gates, R.D., Hoegh-Guldberg, O., Bythell, J.C., Jatkar, A., Grottoli, A.G., Gomez, M., Fisher, P., Lajunesse, T.C., Pantos, O., Iglesias-Prieto, R., Franklin, D.J., Rodrigues, L.J., Torregiani, J.M., van Woesik, R., Lesser, M.P., 2009. Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: the host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology* 373, 102–110.
- Gates, R.D., Edmunds, P.J., 1999. The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* 39, 30–43.
- Gates, R.D., Hoegh-Guldberg, O., McFall Ngai, M., Bil, K.Y., Muscatine, L., 1995. Free amino exhibit anthozoan "host factor" activity: they induce the release of photosynthate from symbiotic dinoflagellates *in vitro*. *Proceedings of the National Academy of Sciences USA* 92 (16), 7430–7434.
- Goreau, T.F., Goreau, N.I., 1959. The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. *The Biological Bulletin* 117, 230–250.
- Grottoli, A.G., Rodrigues, L.J., Palardy, J.E., 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* 440, 1186–1189.
- Holbrook, S., Brooks, A., Schmitt, R., Stewart, H., 2008. Effects of sheltering fish on growth of their host corals. *Marine Biology* 155, 521–530.
- Jones, A., Berkelmans, R., 2010. Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS One* 5 (5), e10437. doi:10.1371/journal.pone.0010437.
- Kitano, H., Oda, K., 2006. Robustness trade-offs and host-microbial symbiosis in the immune system. *Molecular Systems Biology* 2, 2006.0022.
- Knowlton, N., Rohwer, F., 2003. Multispecies microbial mutualisms on coral reefs: the host as a habitat. *The American Naturalist* 162, S51–S62.
- Kvennefors, E.C., Sampayo, E., Ridgway, T., Barnes, A.C., Hoegh-Guldberg, O., 2010. Bacterial communities of two ubiquitous Great Barrier Reef corals reveals both site- and species-specificity of common bacterial associates. *PLoS One* 5, e10401.
- Lajunesse, T.C., 2004. "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution* 22, 570–581.



- Lampert, Y., Kelman, D., Dubinsky, Z., Nitzan, Y., Hill, R.T., 2006. Diversity of culturable bacteria in the mucus of the Red Sea coral *Fungia scutaria*. *FEMS Microbiology Ecology* 58, 99–108.
- Le Campion-Alsumard, T., Golubic, S., Priess, K., 1995. Fungi in corals – symbiosis or disease – interaction between polyps and fungi causes pearl-like skeleton biomineralization. *Marine Ecology Progress Series* 117, 137–147.
- Lesser, M.P., Mazel, C.H., Gorbunov, M.Y., Falkowski, P.G., 2004. Discovery of symbiotic nitrogen-fixing cyanobacteria in corals. *Science* 305, 997–1000.
- Lesser, M.P., Falcón, L.I., Rodríguez-Román, A., Enriquez, S., Hoegh-Guldberg, O., Iglesias-Prieto, R., 2007. Nitrogen fixation by symbiotic cyanobacteria provides a source of nitrogen for the scleractinian coral *Montastraea cavernosa*. *Marine Ecology Progress Series* 346, 143–152.
- Ley, R.E., Hamady, M., Lozupone, C., Turnbaugh, P.J., Ramey, R.R., Bircher, J.S., Schlegel, M.L., Tucker, T.A., Schrenzel, M.D., Knight, R., Gordon, J.I., 2008. Evolution of mammals and their gut microbes. *Science* 320 (5883), 1647–1651.
- Little, A.F., van Oppen, M.J.H., Willis, B.L., 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science* 304, 1492–1494.
- Lohr, J., Munn, C.B., Wilson, W.H., 2007. Characterization of a latent virus-like infection of the squid-Vibrio associations. *Applied and Environmental Microbiology* 73, 2976–2981.
- Loya, Y., Sakai, K., Yamazato, K., Nakano, H., Sambali, H., Van Woesik, R., 2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4, 122–131.
- Mao-Jones, J., Ritchie, K.B., Jones, L.E., Ellner, S.P., 2010. How microbial community composition regulates coral disease development. *PLoS Biology* 8, e1000345.
- Marquez, L.M., Redman, R.S., Rodriguez, R.J., Roossinck, M.J., 2007. A virus in a fungus in a plant: three-way symbiosis required for thermal tolerance. *Science* 315, 513–515.
- McFall-Ngai, M.J., 1999. Consequences of evolving with bacterial symbionts: insights from the squid-Vibrio associations. *Annual Review of Ecology and Systematics* 30, 235–256.
- McFall-Ngai, M., 2008. Are biologists in ‘future shock’? Symbiosis integrates biology across domains. *Nature Reviews Microbiology* 6, 789–792.
- Meyer, J.L., Schultz, E.T., 1985. Tissue condition and growth rate of corals associated with schooling fish. *Limnology and Oceanography* 30, 157–166.
- Mieog, J.C., Olsen, J.L., Berkelmans, R., Bleuler-Martinez, S.A., Willis, B.L., 2009. The roles and interactions of symbiont, host and environment in defining coral fitness. *PLoS One* 4 (7), e6364. doi:10.1371/journal.pone.0006364.
- Mokady, O., Loya, Y., Lazar, B., 1998. Ammonium contribution from boring bivalves to their coral host—a mutualistic symbiosis? *Marine Ecology Progress Series* 169, 295–301.
- Munn, C.B., 2006. Viruses as pathogens of marine organisms from bacteria to whales. *Journal of the Marine Biological Association U.K.* 86, 1–15.
- Muscantine, L., Porter, J.W., 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *Bioscience* 27, 454–460.
- Odum, H.T., Odum, E.P., 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok atoll. *Ecological Monographs* 25, 291–320.
- Oigman-Pszczol, S., Creed, J., 2006. Distribution and abundance of fauna on living tissues of two Brazilian hermatypic corals; *Mussismilia hispida* (Verrill, 1902) and *Siderastrea stellata* (Verrill, 1868). *Hydrobiologia* 563, 143–154.
- Olson, N.D., Ainsworth, T.D., Gates, R.D., Takabayashi, M., 2009. Diazotrophic bacteria associated with Hawaiian *Montipora* corals: diversity and abundance in correlation with symbiotic dinoflagellates. *Journal of Experimental Marine Biology and Ecology* 371, 140–146.
- Omer, M., Aaron, K., 2009. Paradoxically, prior acquisition of antioxidant activity enhances oxidative stress-induced cell death. *SO: Environmental Microbiology* 11, 2301–2309.
- Pantos, O., Bythell, J., 2010. A novel reef coral symbiosis. *Coral Reefs* 29, 761–770.
- Patten, N., Harrison, P., Mitchell, J., 2008. Prevalence of virus-like particles within a staghorn scleractinian coral (*Acropora muricata*) from the Great Barrier Reef. *Coral Reefs* 3, 569–580.
- Pochon, X., Gates, R.D., 2010. A new *Symbiodinium* clade (Dinophyceae) from soritid foraminifera in Hawai'i. *Molecular Phylogenetics and Evolution* 56, 492–497.
- Pratchett, M.S., 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. *Marine Ecology Progress Series* 214, 111–119.
- Pratchett, M., Vytopil, E., Parks, P., 2000. Coral crabs influence the feeding patterns of crown-of-thorns starfish. *Coral Reefs* 19, 36–36.
- Ravindran, J., Raghukumar, C., Raghukumar, S., 2001. Fungi in *Porites lutea*: association with healthy and diseased corals. *Diseases of Aquatic Organisms* 47, 219–228.
- Rinkevich, B., Wolodarsky, Z., Loya, Y., 1991. Coral–crab association: a compact domain of a multilevel trophic system. *Hydrobiologia* 216–217, 279–284.
- Ritchie, K.B., 2006. Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. *Marine Ecology Progress Series* 322, 1–14.
- Rodriguez, R., Redman, R., 2008. More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. *Journal of Experimental Botany* 59, 1109–1114.
- Rohwer, F., Breitbart, M., Jara, J., Azam, F., Knowlton, N., 2001. Diversity of bacteria associated with the Caribbean coral *Montastraea franksi*. *Coral Reefs* 20, 85–91.
- Rohwer, F., Seguritan, V., Azam, F., Knowlton, N., 2002. Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series* 243, 1–10.
- Rowan, R., Knowlton, N., Baker, A., Jara, J., 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388, 265–269.
- Rypien, K.L., Ward, J.R., Azam, F., 2010. Antagonistic interactions among coral-associated bacteria. *Environmental Microbiology* 12, 28–39.
- Sapp, J., 2003. *Genesis: the Evolution of Biology*. Oxford University Press, New York.
- Sapp, J., 2004. The dynamics of symbiosis: an historical overview. *Canadian Journal of Botany* 82, 1046–1056.
- Schwarz, J., Brokstein, P., Voolstra, C., Terry, A., Miller, D., Szmant, A., Coffroth, M., Medina, M., 2008. Coral life history and symbiosis: functional genomic resources for two reef building Caribbean corals, *Acropora palmata* and *Montastraea faveolata*. *BMC Genomics* 9, 97.
- Seymour, J.R., Patten, N., Bourne, D.G., Mitchell, J.G., 2005. Spatial dynamics of virus-like particles and heterotrophic bacteria within a shallow coral reef system. *Marine Ecology Progress Series* 288, 1–8.
- Shashar, N., Stambler, N., 1992. Endolithic algae within corals – life in an extreme environment. *Journal of Experimental Marine Biology and Ecology* 163, 277–286.
- Stachowicz, J.J., Hay, M.E., 1999. Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* 80, 2085–2101.
- Stachowicz, J.J., Whitlatch, R.B., Osman, R.W., 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286, 1577–1579.
- Stat, M., Gates, R.D., 2011. Clade D *Symbiodinium* in scleractinian corals: a “nugget” of hope, a selfish opportunist, an ominous sign, or all of the above? *Journal of Marine Biology* 730715.
- Stat, M., Carter, D., Hoegh-Guldberg, O., 2006. The evolutionary history of *Symbiodinium* and scleractinian hosts – symbiosis, diversity, and the effect of climate change. *Perspectives in Plant Ecology, Evolution and Systematics* 8, 23–43.
- Stat, M., Morris, E., Gates, R.D., 2008. Functional diversity in coral–dinoflagellate symbiosis. *Proceedings of the National Academy of Science* 105 (27), 9256–9261.
- Stella, J., Jones, G., Pratchett, M., 2010. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 1–17.
- Sterflinger, K., 2000. Fungi as geologic agents. *Geomicrobiology Journal* 17, 97–124.
- Stewart, H., Holbrook, S., Schmitt, R., Brooks, A., 2006. Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs* 25, 609–615.
- Sunagawa, S., Woodley, C.M., Medina, M., 2010. Threatened corals provide underexplored microbial habitats. *PLoS One* 5 (3), E9554.
- Sweet, M.J., Croquer, A., Bythell, J.C., 2011. Bacterial assemblages differ between compartments within the coral holobiont. *Coral Reefs* 30, 39–52.
- Titlyanov, E.A., Kiyashko, S.I., Titlyanova, T.V., Yakovleva, I.M., 2009.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in tissues of reef building corals and the endolithic alga *Ostreobium quekettii* under their symbiotic and separate existence. *Galaxea, Journal of Coral Reef Studies* 11, 169–175.
- Todd, P.A., 2008. Morphological plasticity in scleractinian corals. *Biological Reviews of the Cambridge Philosophical Society* 83 (3), 315–337.
- Tribollet, A., Payri, C., 2001. Bioerosion of the coralline alga *Hydrolithon onkodes* by microborers in the coral reefs of Moorea, French Polynesia. *Oceanologica Acta* 24, 329–342.
- Tribollet, A., Langdon, C., Golubic, S., Atkinson, M., 2006. Endolithic microflora are major primary producers in dead carbonate substrates of Hawaiian coral reefs. *Journal of Phycology* 42, 292–303.
- van Oppen, M.J.H., Leong, J.A., Gates, R.D., 2009. Coral–virus interactions: a double-edged sword? *Symbiosis* 47, 1–8.
- Vega-Thurber, R., Willner-Hall, D., Rodriguez-Muller, B., Desnues, C., Edwards, R.A., Angly, F., Dinsdale, E.A., Kelly, L., Rohwer, F., 2009. Metagenomic analysis of stressed coral holobionts. *Environmental Microbiology* 11, 2148–2163.
- Wegley, L., Yu, Y.N., Breitbart, M., Casas, V., Kline, D.I., Rohwer, F., 2004. Coral-associated Archaea. *Marine Ecology Progress Series* 273, 89–96.
- Wegley, L., Edwards, R., Rodriguez-Brito, B., Liu, H., Rohwer, F., 2007. Metagenomic analysis of the microbial community associated with the coral *Porites astreoides*. *Environmental Microbiology* 9, 2707–2719.
- Wild, C., Huettel, M., Kluever, A., Kremb, S.G., Rasheed, M.Y.M., Jørgensen, B.B., 2004. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428, 66–70.
- Wilson, D.S., Sober, E., 1989. Reviving the superorganism. *Journal of Theoretical Biology* 136, 337–356.
- Wilson, W.H., Francis, I., Ryan, K., Davy, S.K., 2001. Temperature induction of viruses in symbiotic dinoflagellates. *Aquatic Microbial Ecology* 25, 99–102.
- Wilson, W.H., Dale, A.L., Davy, J.E., Davy, S.K., 2005. An enemy within? Observations of virus-like particles in reef corals. *Coral Reefs* 24, 145–148.
- Yamazaki, S.S., Nakamura, T., Yamasaki, H., 2008. Photoprotective role of endolithic algae colonized in coral skeleton for the host photosynthesis. In: Allen, J.F., Gantt, E., Golbeck, J.H., Osmond, B. (Eds.), *Photosynthesis: Energy from the Sun*. Springer Netherlands, pp. 1392–1395.
- Yarden, O., Ainsworth, T.D., Roff, G., Leggat, W., Fine, M., Hoegh-Guldberg, O., 2007. Increased prevalence of ubiquitous ascomycetes in an acropoid coral (*Acropora formosa*) exhibiting symptoms of brown band syndrome and skeletal eroding band. *Applied and Environmental Microbiology* 73, 2755–2757.
- Yellowlees, D., Rees, T.A.V., Leggat, W., 2008. Metabolic interactions between algal symbionts and invertebrate hosts. *Plant, Cell & Environment* 31, 679–694.