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EDITED BY

Mark A. Elgar,
The University of Melbourne, Australia

REVIEWED BY

Saúl Huitzil,
Northwestern University, United States
Michael P. Doane,
Flinders University, Australia

*CORRESPONDENCE

Cody S. Clements
✉ cclments9@gatech.edu

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Disentangling the impacts of macroalgae on corals via effects on their microbiomes

Cody S. Clements* and Mark E. Hay

School of Biological Sciences and Center for Microbial Dynamics and Infection, Georgia Institute of Technology, Atlanta, GA, United States

Tropical reefs are commonly transitioning from coral to macroalgal dominance, but the role of macroalgae in coral decline remains inadequately understood. A growing body of research suggests that algae may harm corals via disruptions to the homeostasis of the coral holobiont, including resident microbial communities, but the processes that mediate these potential microbial effects and the spatial scales at which they operate are uncertain. Resolving the relative importance and context dependencies of microbially-mediated algal-coral competition is critical for understanding and predicting coral dynamics as reefs further degrade. In this review, we examine the current state of knowledge surrounding algal impacts on corals via disruption of their microbiomes, with a particular focus on the mechanisms hypothesized to mediate microbial effects, the scales at which they are thought to operate, and the evidence from laboratory- and field-based studies for their existence and ecological relevance in the wild. Lastly, we highlight challenges for further advancing the field.

KEYWORDS

coral reef, coral, microbiome, macroalgae, coral-algal competition, microbial interactions, dysbiosis

1. Introduction

Microbiomes can alter the development, health, function, and behavior of humans and other hosts (Markle et al., 2013; McFall-Ngai et al., 2013; Gensollen et al., 2016). This realization generated an understandable interest in investigating the potential impacts of host microbiomes and their dynamics on the ecological health and function of a wide range of species playing critical roles in the structure and function of natural ecosystems (Ritchie, 2006; Barott and Rohwer, 2012; Krediet et al., 2013; McDevitt-Irwin et al., 2017). This is especially true for scleractinian corals, which are the foundation species of tropical reefs but have declined precipitously in recent decades as a variety of anthropogenic stressors increased in frequency and severity (e.g., overfishing, ocean warming, pollution, etc.; Bellwood et al., 2004; Hughes et al., 2010, 2018; Jackson et al., 2014). Mutualistic interactions among the coral animal, the symbiotic dinoflagellates that reside in and transfer photosynthates to the coral host, and a number of external symbionts, including crabs, shrimps, and fishes that protect corals from predators or competitors in return for a safer living space were already known and appreciated (Glynn, 1983; Stachowicz and Hay, 1999; Dixon and Hay, 2012). However, the possibility that this already “tangled bank” of symbiotic interactions might also depend on a wealth of undescribed mutualisms involving unappreciated microbes offered a new vision of deep biological complexities that proved irresistible for microbiologists and coral reef investigators (e.g., Ritchie, 2006; Vega Thurber et al., 2009; Barott and Rohwer, 2012; Haas et al., 2016;

Clements et al., 2020b). If appropriate microbiomes are critical to the wellbeing of this crucial group of foundation species, then understanding, and possibly remedying, microbial imbalances on corals might offer novel means for conserving or restoring reefs (Santoro et al., 2021; Voolstra et al., 2021).

These new insights initiated a wealth of studies involving coral microbiomes. Because corals were often replaced by macroalgae as reefs degraded, many investigations focused on the potential impacts of macroalgae on coral microbiomes and the role that algal-microbiome interactions might play in coral demise. We overview hypotheses and information on these interactions below. We do not attempt to be comprehensive of all studies to date, but rather try to elaborate major findings, issues, and remaining challenges.

Coral decline is often accompanied by increases in benthic algae, which compete with corals for space and now dominate the benthic landscape on numerous tropical reefs (Hughes, 1994; Mumby and Steneck, 2008; Roff and Mumby, 2012; Rasher et al., 2013). In general, competition with algae is expected to further exacerbate coral decline as macroalgae proliferate and interactions with remaining corals increase in frequency and intensity (Mumby et al., 2007; Bonaldo and Hay, 2014). Numerous studies have demonstrated that algal competitors suppress coral growth (River and Edmunds, 2001; Clements et al., 2018, 2020b), fecundity (Foster et al., 2008; Monteil et al., 2020), recruitment (Birrell et al., 2008), and survival (Box and Mumby, 2007); however, the extent to which algal competition is a driver of coral stress and demise versus a response to coral stress and demise due to other causes is uncertain (Bruno et al., 2009; Dudgeon et al., 2010; Mumby et al., 2012; Schmitt et al., 2019). These drivers may also be context dependent (e.g., Bruno et al., 2007; Mumby et al., 2007; Mumby and Steneck, 2008; Rasher et al., 2011; Vega Thurber et al., 2012; Clements et al., 2020b), making the general role of algae in suppressing corals via impacts on coral microbiomes uncertain.

Despite uncertainties, it has become common to assume that changes in coral microbiomes may be a driver of coral demise rather than a response to coral stresses from other sources (Barott and Rohwer, 2012; Haas et al., 2016; Nelson et al., 2022). The difficulties of separating microbial causes of coral demise from microbial responses to coral demise are complicated by a general inability to identify microbial pathogens causing coral diseases despite considerable efforts to do so (Barott and Rohwer, 2012; Vega Thurber et al., 2020). In many cases, coral diseases are correlated with a polyculture of different microbes; some may be pathogens, some detritivores responding to the dead tissues, a mix of both, or normally benign coral associates that become opportunistic detritivores or pathogens when corals are compromised by other stresses (Vega Thurber et al., 2020). Despite our enthusiasm for understanding the role that microbes may play in coral dynamics and responses to stress, it is necessary to remember that predictable co-occurrence need not indicate a *cause* rather than a *consequence* of demise. A consistent change in coral microbiomes as corals sicken need not indicate that the microbial changes are a *cause* rather than a *consequence* of the coral's demise. Additionally, it is common for studies of microbial shifts on reefs, or of the pathways the microbes are up-regulating (pathogenicity, etc.), to assume these shifts or changes in metabolism will lead to coral demise without investigating co-occurring changes in corals. Of the 45 studies we found addressing how shifts in microbes on coral reefs might impact corals, fewer than half (44%) assessed for effects on co-occurring corals (Supplementary Table S1).

Extensive investigations into the dynamics of coral-algal competition have been undertaken in recent decades—ranging from experimental field manipulations pairing corals and algae or excluding herbivores to assess the effects of algal proliferation, to broader scale correlations of coral recruitment and survivorship on algal-dominated versus coral-dominated reefs (Birrell et al., 2008; Beatty et al., 2018). Within some of these efforts, there was an interest in linking observed algal effects to the complex association between the coral animal and its associated microorganisms (protists, bacteria, archaea, fungi, and viruses)—collectively referred to as the coral microbiome. These associates can be integral to a variety of host functions that facilitate or hinder coral growth, health, and survival. Among the most well-known facilitators of coral health are endosymbiotic *Symbiodinium* algae that provide photosynthates to the coral host, but increasing evidence suggests that other associates such as bacteria also play integral roles in metabolism, nutrient dynamics, resistance to pathogens, and immune response (Thompson et al., 2014; Bourne et al., 2016), and may help corals tolerate or adapt to stressful conditions (Rosado et al., 2019; Santoro et al., 2021). Conversely, stresses associated with algal competition may disrupt these relationships, potentially compromising coral health (Zaneveld et al., 2017). These competing notions (microbiome changes as adaptive for versus detrimental to the holobiont) make it impossible to interpret the fitness-related consequences of microbiome change without a better “natural history” of the functional role of individual microbes, or consortia of microbes, to the well-being of the holobiont. An adequate natural history understanding is not presently available.

Harmful algal effects to corals observed at the macroscale, such as reduced coral growth, survival, and recruitment (Vermeij et al., 2009; Bulleri et al., 2018), commonly, but not always (Clements et al., 2020a,b), co-occur with alterations to the coral holobiont—often via changes in composition, abundances, or dispersion of resident microbes that are thought to be indicative of microbial dysbiosis (i.e., increases in harmful or loss of beneficial microbes; Vega Thurber et al., 2012; Zaneveld et al., 2017). Algal-induced microbiome changes are hypothesized to occur via several mechanisms that vary in their mode of action, and as a consequence, the potential extent and severity of their impacts. These are thought to include contact-mediated mechanisms that likely act at localized scales of centimeters or less near the coral-algal interface (Brown and Carpenter, 2015; Jorissen et al., 2016; Clements et al., 2020a,b), as well as via algal release into the water of compounds that may be advected to corals centimeters to meters downstream of algal competitors (Barott and Rohwer, 2012). Each has substantially different implications for potential trajectories of coral reef decline and recovery.

Algae have been implicated in disrupting the coral holobiont (e.g., reduced *Symbiodinium* densities; Quan-Young and Espinoza-Avalos, 2006), with most research to-date focused on disruptions to coral microbiomes (Rosenberg et al., 2007; McDevitt-Irwin et al., 2017). Indeed, microbially-mediated competition is now commonly stated to be among the primary processes involved in coral-algal interactions and a potential driver of coral decline (Barott and Rohwer, 2012; McDevitt-Irwin et al., 2017). However, the degree to which altered coral microbiomes are: i) a cause of coral decline, ii) a response to coral decline caused by other stresses, or iii) an adaptive response of the coral to alter its microbiome to better fit the new ecological conditions and enhance holobiont fitness is often unclear. The mechanisms by which algae affect coral holobionts appear

multifactorial, context-dependent, and not mutually exclusive. Resolving their ecological relevance and the spatial scales at which competing algae impact microbiome dynamics remains a challenge that has important implications for efforts to predict, manage, and restore coral populations on increasingly degraded reefs.

Below, we discuss the current state of knowledge surrounding algal effects on coral holobionts, with a special focus on whether, how, and under what conditions macroalgal effects on corals are mediated via impacts on coral microbiomes. Our goal is to examine the ecological scales at which these processes operate, the evidence to-date for their effects on corals, and how these may differ under the lab settings that facilitate careful monitoring versus the field conditions under which corals and macroalgae actually live and interact. We are particularly interested in exploring the relative importance of contact-versus water-mediated interactions in driving changes to coral microbial communities, as well the potential adaptive capacity and resilience of the coral host to such disruptions. These distinctions may prove critical for understanding the likelihood of various conservation measures proving effective under field conditions.

2. Algal effects via contact versus effects at a distance

The spatial scale at which algal-coral interactions occur and how this may vary with species combinations or environmental context can be critical for understanding these interactions. If contact is required, then corals may be able to counter or limit algal impacts via offensive sweeper tentacles (Wellington, 1980) or commensal crustaceans or fishes that remove nearby macroalgae (Stachowicz and Hay, 1999; Dixon and Hay, 2012). In contrast, if algae can damage corals at a distance by releasing water-soluble compounds that destabilize critical microbiomes on corals downstream (Barott and Rohwer, 2012), then ecological countermeasures by corals or their symbionts may be ineffective, leaving the longer-term option of evolving resistance to these effects as the primary avenue of response. In summary, it is important to understand whether algae function more as: i) “toxic paint brushes” damaging corals only on contact, ii) “sewage outfalls,” spilling organic pollutants that damage downstream corals at a distance, or iii) some of both, depending on environmental circumstances and species combinations.

Numerous field- and laboratory-based studies have demonstrated adverse effects for corals that are directly contacted by macroalgae (McCook et al., 2001; Rasher and Hay, 2010; Bonaldo and Hay, 2014; Vieira et al., 2016b; Clements et al., 2018), with an increasing number also documenting concurrent shifts in coral microbiomes (Vega Thurber et al., 2012; Morrow et al., 2013; Zaneveld et al., 2016; Pratte et al., 2018; see Supplementary Table S1). Experiments focused on the mechanistic basis of these microbial dynamics or their ecological impacts are less common, but increasing evidence suggests that direct mechanisms such as algal abrasion or shading (Clements et al., 2020b), as well contact-mediated transfer of hydrophobic allelochemicals (Rasher and Hay, 2010; Rasher et al., 2011; Morrow et al., 2012, 2017), organic matter, or microbial pathogens (Nugues et al., 2004; Barott et al., 2012; Sweet et al., 2013; Vieira et al., 2016a), are capable of inducing microbiome changes that may, or may not, constitute dysbiosis (i.e., change can be damaging or an adaptive response).

Though it has been suggested that physical mechanisms play only a minor role in coral-algal competition (Barott and Rohwer, 2012; but see Box and Mumby, 2007), recent field-based manipulations demonstrated that biologically inert algal mimics reduced coral growth and photosynthetic efficiency, and altered resident microbial communities in a comparable manner to live algae common to degraded reefs (Morrow et al., 2012; Clements et al., 2020b), including species known to damage corals via allelopathy (*Galaxaura* spp.; Rasher and Hay, 2010; Rasher et al., 2011). Tank-based studies have also reported comparable effects on coral microbiomes between mimics and live algae, but this varied based on the coral-algal species pairs tested and was not consistently reflected in the physiological metrics being assessed (i.e., percent tissue bleaching, photosynthetic efficiency; Fong et al., 2020). Under ecologically realistic scenarios, contact-mediated stressors likely work in concert to alter the coral holobiont, potentially facilitating dysbiotic after-effects (e.g., pathogen invasion), but this will depend on the species involved and interaction context. It is also useful to recognize that microbiome changes need not be detrimental to a coral. Changes could be neutral or even beneficial allowing the coral to adapt to new stresses via its microbial associates. One way of addressing this is to measure correlates of coral fitness (e.g., growth or photosynthesis) as changes in microbiome dynamics are assessed under realistic field conditions. This is relatively rare—with only seven of the 45 studies in Supplementary Table S1 (~16%) conducting such experiments.

The potential for algae to harm corals at a distance through changes to coral microbiomes has gained considerable attention in the past two decades and is hypothesized to be an important contributor to coral decline (Barott and Rohwer, 2012; Haas et al., 2016; Nelson et al., 2022). Early lab studies demonstrated that algae held in small containers and separated from immediately adjacent coral by filters that should prevent passage of microbes caused coral damage without direct contact; this effect was suppressed or nullified by the addition of antibiotics (Smith et al., 2006). The coral damage in these experiments was associated with a decline in oxygen where corals were immediately adjacent to macroalgae, suggesting that dissolved organics (e.g., dissolved organic carbon = DOC) leaking from algae were fueling microbial growth, lowering O₂, and stressing or killing adjacent coral tissue via hypoxia. This, and related experiments (Haas et al., 2011, 2013, 2016; Nelson et al., 2011, 2013; Walsh et al., 2017), lead to positing the DOC, disease, and algae model (DDAM), suggesting that algae release bioavailable DOC into surrounding waters, that the released compounds stimulate growth and respiration of reef microbes, that the released DOC may produce effects centimeters to meters downstream (Barott and Rohwer, 2012), and that this harms corals via hypoxia (Haas et al., 2011). In this scenario, microbial community changes do not simply correlate with macroscale changes in reef benthic communities, but actively promote feedback loops that suppress corals and accelerate transitions towards degraded reefs dominated by macroalgae.

The above models are supported by laboratory investigations demonstrating microbial changes in seawater of various algal-associated dissolved organic compounds (Kline et al., 2006; Haas et al., 2011, 2013; Nelson et al., 2013) and adverse effects on corals at distances of centimeters or less (Jorissen et al., 2016; Fong et al., 2020). Limited field collections ($n = 2-4$) of water within, or near, the benthic boundary layer above an area dominated by a coral, macroalga, turf alga, or a zoanthid found differences in water microbiomes across these

collections and that all differed from water samples collected three meters above these substrates (Walsh et al., 2017), indicating localized but not reef-wide impacts. Walsh et al. (2017) also probed for functions and noted halos of microbiomes above turf algae were expressing functions suggesting pathogenic activity. However, many pathogens have a narrow host range and pathogenicity to corals, or damage to corals of any sort, was not assessed. Even when one probes for function, detects activation of pathogenicity, and knows the host that can be infected, there is no assurance that this will result in successful host attack. Microbial physiology alone is insufficient as a proof of coral damage; one needs to actually assess damage to nearby corals. Numerous studies do not do this (Supplementary Table S1). Several field studies do not find corals being damaged by seaweeds unless there is direct contact (Rasher and Hay, 2010; Rasher et al., 2011; Clements et al., 2018, 2020b), thus the potential effects of seaweeds on corals or their microbiomes across distance needs confirmation under field conditions. Of the 45 studies in Supplementary Table S1, only five tested for effects on coral microbiomes via dissolution over a distance (see Supplementary Table S1). Two were conducted in the field under natural conditions of flow and found no effects at cm scales (Barott et al., 2012; Clements et al., 2020b); two lab studies in closed containers demonstrated water-soluble effects (Smith et al., 2006; Fong et al., 2020) and one correlative field study found patterns suggestive of such effects (Briggs et al., 2021).

Several issues may constrain laboratory studies conducted in still enclosures or in containers with limited flow from translating to the field where flow, advection, turbulence, and various biotic processes may diminish or completely counter effects noted under laboratory conditions. As examples: i) DOC concentrations will accumulate in lab containers in a manner that might rarely occur given flow conditions in the field, ii) fragmenting macroalgae to place them in lab containers may cause more leakage of DOC or other algal metabolites than occurs under intact conditions in the field, and iii) if microbes are stimulated by DOC from algae, it is likely that they will colonize algal surfaces and draw DOC down as it emerges rather than leaving it to drift downstream to be used by other microbial competitors. This latter possibility is supported by a 4-year study of DOC and bacterioplankton concentrations in oceanic water as it passed from the ocean over the reef crest, lagoon, and fringing reefs in Moorea, French Polynesia, with the latter areas all supporting large areas of macroalgae. In this investigation, Nelson et al. (2011) found that both DOC and bacterioplankton declined significantly, rather than increasing, as low DOC oceanic water moved across these algal-rich reefs. A possible explanation is that microbial populations inhabiting the considerable surface areas of macroalgae were able to not only consume all DOC released by the macroalgae, but to also draw down further the low DOC concentrations from the oceanic waters. If this is the case, then DOC from macroalgae is unlikely to be affecting coral microbiomes at a distance.

A careful field study on reefs in Moorea, French Polynesia, found that algal-coral interactions and the effects of these on microbial concentrations in the water were highly context dependent and varied as a function of flow conditions, the types of algae involved, whether the up-stream or down-stream side of the coral was considered, etc. (Brown and Carpenter, 2015). These authors concluded that algal release of DOC and its negative effects on corals via microbially-mediated hypoxia, could likely occur, but only under constrained conditions of low flow, very small spatial scales, and certain algal-coral

combinations (e.g., turf algae that could hold DOC in the diffusive boundary layer on the down current side of a massive coral). Field sampling by Walsh et al. (2017) also found effects on water sample microbiomes taken within centimeters of macroorganisms, but not at meter scales. More critically, when numerous macroalgae and corals were paired in the field on reefs in Fiji or Caribbean Panama, almost all algal damage to corals was detectable only on coral portions experiencing direct algal contact (i.e., in most pairings, no detectable damage occurred only millimeters away) and the damage seen in algal-coral pairings could be replicated via extracts of non-polar metabolites that would not be dispersed via dissolution into water (Rasher and Hay, 2010; Rasher et al., 2011).

Bolstering this effect of direct contact versus compounds dispersed via DOC dissolution, when corals (*Acropora millepora* and *Porites cylindrica*) were transplanted into dense algal beds, their growth was significantly suppressed, but when macroalgae were cleared for only centimeters around them—preventing direct contact—there was no effect on coral growth (Clements et al., 2018). Unfortunately, these investigations did not evaluate algal effects on coral microbiomes, but the types of tissue bleaching and death seen in earlier lab-based experiments (Smith et al., 2006) were not apparent in these field assays unless macroalgae were physically contacting corals.

A more recent lab-based experiment involving three coral species (*Merulina ampliata*, *Montipora stellata*, and *Pocillopora acuta*) found that microbiome composition of one species (*M. stellata*) was altered when in close proximity (~5 cm) to macroalgae (*Lobophora* sp. and *Hypnea pannosa*) in 3-liter tanks, but adverse effects on coral physiology (e.g., percent tissue bleaching, photosynthetic efficiency) required direct algal contact (Fong et al., 2020). Similarly, photosynthesis and growth of corals (*A. millepora*) in the field were suppressed when corals were in direct contact with live algae (*Sargassum polycystum* or *Galaxaura filamentosa*) or inert algal mimics, but were unaffected when algae or algal mimics were 1.5 cm distance away from corals and contact was prevented (Clements et al., 2020b). Coral microbiomes were also largely unaffected in composition, variability, or diversity by any of the treatments; however, a few uncommon taxa did differ among treatments. These experiments suggest that under most ecologically realistic field conditions, the negative impacts of macroalgae on corals are limited to contact and rarely affected by DOC liberated by the macroalgae.

3. Coral microbiome stability on algal-versus coral-dominated reefs

Determining the relevant ecological scales at which negative algal impacts operate not only depends on characteristics inherent to algae (e.g., ability to stimulate copiotrophic microbial activity via algal-induced DOC) and the abiotic environment (e.g., flow dynamics), but also the ability of the coral to maintain holobiont homeostasis despite external, potentially stressful, conditions (Sunagawa et al., 2010; Webster et al., 2016; Zhou et al., 2016; Marcelino et al., 2017; O'Brien et al., 2018; Reigel et al., 2021; Díaz-Almeyda et al., 2022). Studies assessing differences in microbiomes of corals from algal- versus coral-dominated reefs have yielded mixed results but suggest that some corals are regulating their microbiomes despite macroalgal dominance and that coarse-resolution microbial metrics alone may be ill-suited for assessing potential algal effects. For example, Beatty

et al. (2018) found that neither adults nor larvae of the coral *Pocillopora damicornis* differed significantly in microbiome composition between adjacent coral- and algal- dominated reefs in Fiji, but adult *P. damicornis* microbiomes were more variable (i.e., greater beta-dispersion) and enriched in low abundance (<2%) of potentially pathogenic taxa from the family Vibrionaceae (e.g., *Vibrio shilonii*).

As reported in other studies, Beatty et al. (2019) found that microbiome composition of benthic seawater differed between adjacent coral- and algal-dominated reefs, but in contrast to what might be expected in these differing environments, the community composition of microbiomes from three coral species (*A. millepora*, *P. damicornis*, and *P. cylindrica*) collected from these differing locations did not differ within species. However, one species (*A. millepora*) did exhibit greater microbiome dispersion, reduced abundance of a putative beneficial Endozoicimonaceae indicator taxon, and reduced ability to suppress a common coral pathogen (*Vibrio coralliilyticus*) when corals were sampled from macroalgal-dominated reefs versus coral-dominated reefs. When fragments of the same three coral species were reciprocally transplanted between paired coral- and algal-dominated reefs, two species (*A. millepora* and *P. damicornis*) exhibited differences in microbiome composition based on the type of site from which they were collected (both species) or transplanted to (*P. damicornis* only; Beatty et al., 2022). These differences were again largely driven by reduced relative abundances of Endozoicimonaceae and enrichment of Vibrionaceae sequences.

Together, the findings outlined above suggest that some corals maintain broad-scale microbiome community composition despite marked, and sometimes dramatic (Beatty et al., 2019, 2022), differences in macroalgal abundance and in the surrounding benthic and water column microbial community. They also suggest that relevant algal effects may involve more nuanced differences in coral microbiomes than coarse-scale metrics such as community composition (i.e., small or modest changes in rare microbes may produce important effects). Similar findings have been reported for other marine organisms, such as sponges and macroalgae, which can exhibit overall microbiome stability and minor shifts in less abundant taxa despite occurring on reefs differing in algal abundance and in water column microbiomes (Chen and Parfrey, 2018; Campana et al., 2021). It also is consistent with other studies that found stressor-induced changes to coral microbiomes (e.g., via corallivory, temperature, fish feces) were spatially and temporally constrained (Clements et al., 2020a; Ezzat et al., 2021), and dovetails with macroscale assessments of coral well-being (e.g., growth) that suggest algal effects require direct contact (Clements et al., 2018, 2020b) and that negative effects cease relatively quickly following algal removal (Clements et al., 2018; van Duyl et al., 2023).

Furthermore, none of the aforementioned comparisons precluded contact between coral and algae within algal-dominated sites and thus did not assess potential contact- versus water-mediated effects. We are aware of only one correlative field-based study that has attempted to assess microbial community changes as a function of benthic algal cover and algal contact. The authors' reported a mix of coral microbiome responses, including antagonistic effects of algal contact and macroalgal cover for broad-scale metrics such as microbiome composition and dispersion, as well as changes in relative abundances of specific microbes that were more pronounced based on algal contact than cover (Briggs et al., 2021). Higher-resolution investigations, including assessments of the "core microbiome"

(Ainsworth et al., 2010, 2015; Bourne et al., 2016), more specific indicator taxa, or other microbial metrics (e.g., potency of pathogen-suppressing extracts; Beatty et al., 2019, 2022), may be necessary to reconcile disparate findings and adequately evaluate coral responses to changes in reef state and how these vary with direct contact versus close proximity.

4. Outstanding questions and challenges

Despite the considerable progress in studies of algal impacts on coral holobionts, questions remain concerning the mechanistic basis of algal-coral-microbiome interactions, their impacts on coral fitness, and how this may be impacting conservation, management, and restoration of degraded reefs. The majority of correlative studies assessing the relationship between algal cover and reef "microbialization" have focused on sampling and assessing differences in the microbiomes of water slightly above the substrate on coral-versus algal-dominated reefs (Haas et al., 2011, 2013, 2016; Nelson et al., 2013; Walsh et al., 2017; Meirelles et al., 2018; Silva et al., 2021)—but not to corals themselves (see Supplementary Table S1)—making it difficult to discern whether and how proposed models of indirect algal effects (e.g., DDAM) translate to microbial changes within the coral holobiont, or whether such changes have negative effects on coral fitness. These knowledge gaps represent a formidable challenge for future efforts to understand the impacts of algae on coral holobionts, but also an opportunity to foster greater integration and collaboration between field- and lab-based experimentalists whose complementary approaches can strengthen both fields via collaboration.

4.1. Understanding context-dependence

The ecologically relevant scales at which algae alter coral microbiomes, and the consequences of microbiome change for the host holobiont may have dramatically different implications for trajectories of coral decline or resilience. Laboratory-based experiments suggest that algae can influence coral microbiomes at limited distances (≤ 5 cm; Jorissen et al., 2016; Fong et al., 2020) via water-mediated mechanisms, but manipulative field experiments to-date have yet to detect similar effects at this spatial scale (Brown and Carpenter, 2015; Clements et al., 2020b); thus, the ecological relevance of water-mediated processes thought to operate in the wild (e.g., DDAM; Haas et al., 2016) remain uncertain. Indirect algal effects on microbiomes *in situ* appear likely, but will depend on interaction context and may occur under only a limited set of conditions (Brown and Carpenter, 2015). Rigorous field studies under variable conditions of flow, turbulence, and advection need to be conducted to bound the conditions under which algal effects at a distance may occur.

4.2. A natural history of microbes is needed

We know too little of the real effects of particular microbes in nature. This is readily evident in coral reef ecosystems, which are being dramatically impacted by disease, but in many cases the specific causative

microbial agent(s) of disease remain unknown (Mera and Bourne, 2018; Vega Thurber et al., 2020). Our considerably greater understanding of human microbial pathogens has taken centuries and large amounts of human and financial capital to achieve since Pasture's initial studies. The history of successes and failures in human studies can help inform marine approaches (Pollock et al., 2011). Erecting and understanding the natural history and epidemiology of coral diseases will not be easy and may require reevaluating traditional etiological paradigms. For example, recent calls to move beyond the "one pathogen—one disease" model of coral disease (Vega Thurber et al., 2020) have followed from insights first gleaned from studies of human health, such as the polymicrobial nature of many diseases (Nelson et al., 2012; Lamont and Hajishengallis, 2015), the pathobiont concept (Chow et al., 2011), and the role of dysbiosis as an indicator of disease (Zaneveld et al., 2017) versus adaptation via microbiome alterations. Studies have begun and should continue to utilize these alternative frameworks for assessing algal effects.

4.3. Not "who is there?," but "what are they doing?"

To more rigorously understand the critical roles that microbial associates may play in coral health and function, we need to move beyond studies of descriptive co-occurrence to rigorous demonstrations of cause-effect relationships and the mechanisms involved in microbiome impacts on coral hosts. We need to go beyond broad-scale sequencing and evaluate active and core members of the microbiome, as well as the functions microbes are up- or down-regulating in different contexts. However, just as not all predator attacks are successful, not all microbes that induce pathogenicity or similar traits will successfully invade and infect a coral host. We will not understand the importance and dynamics of coral-microbiome interactions unless both host and microbes are studied synchronously and under realistic ecological conditions. [Supplementary Table S1](#) suggests that we can improve on this. High prevalence in healthy corals does not negate a microbe's pathogenic potential (Shaver et al., 2017; Klimes et al., 2019), and even common commensals or mutualists may turn into pathogens under certain conditions (Seyedsayamdost et al., 2011). Multidisciplinary approaches are already underway to tackle these questions (Bourne et al., 2016; Barreto et al., 2021), including in studies of coral-algal interactions (Roach et al., 2020).

4.4. Cause versus effect

Disentangling cause versus effect is a problem that consistently confounds efforts to investigate links between various stressors and microbiome dynamics across a range of disciplines (Fischbach, 2018). This is further complicated by the multifactorial nature of stressors facing

corals on most modern reefs (Bellwood et al., 2004). At present, we cannot consistently differentiate microbiome changes that destabilize the host and cause coral death, from microbiome changes that are a response to coral demise due to other drivers or from changes that may involve the coral adapting to a changing environment by "trading-out" microbial associates. In numerous cases, it is not even clear if coral disease/demise is due to changes in bacterial, fungal, ciliates, flatworms, or other coral associates (Mera and Bourne, 2018; Barton et al., 2020; Vega Thurber et al., 2020). In these instances, field experiments with compounds targeting these different groups may be useful. Making advances on the three challenges listed above may allow us to begin to separate and understand microbiome dynamics that are driving coral demise from those that are a response to coral stress or demise. Achieving that goal will represent a significant advance in the field.

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All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1083341/full#supplementary-material>

References

- Ainsworth, T. D., Krause, L., Bridge, T., Torda, G., Raina, J.-B., Zakrzewski, M., et al. (2015). The coral core microbiome identifies rare bacterial taxa as ubiquitous endosymbionts. *ISME J.* 9, 2261–2274. doi: 10.1038/ismej.2015.39
- Ainsworth, T. D., Thurber, R. V., and Gates, R. D. (2010). The future of coral reefs: a microbial perspective. *Trends Ecol. Evol.* 25, 233–240. doi: 10.1016/j.tree.2009.11.001
- Barott, K. L., Rodriguez-Mueller, B., Youle, M., Marhaver, K. L., Vermeij, M. J. A., Smith, J. E., et al. (2012). Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proc. Biol. Sci.* 279, 1655–1664. doi: 10.1098/rspb.2011.2155
- Barott, K. L., and Rohwer, F. L. (2012). Unseen players shape benthic competition on coral reefs. *Trends Microbiol.* 20, 621–628. doi: 10.1016/j.tim.2012.08.004

- Barreto, M. M., Ziegler, M., Venn, A., Tambutté, E., Zoccola, D., Tambutté, S., et al. (2021). Effects of ocean acidification on resident and active microbial communities of *Stylophora pistillata*. *Front. Microbiol.* 12:707674. doi: 10.3389/fmicb.2021.707674
- Barton, J. A., Bourne, D. G., Humphrey, C., and Hutson, K. S. (2020). Parasites and coral-associated invertebrates that impact coral health. *Rev. Aquac.* 12, 2284–2303. doi: 10.1111/raq.12434
- Beatty, D. S., Clements, C. S., Stewart, F. J., and Hay, M. E. (2018). Intergenerational effects of macroalgae on a reef coral: major declines in larval survival but subtle changes in microbiomes. *Mar. Ecol. Prog. Ser.* 589, 97–114. doi: 10.3354/meps12465
- Beatty, D. S., Clements, C. S., Valayil, J. M., Jarvis, S. Y., Ritchie, K. B., Stewart, F. J., et al. (2022). Variance of coral anti-pathogen defense in response to transplantation between coral- and macroalgal-dominated reefs. *Coral Reefs* 41, 1417–1431. doi: 10.1038/s41598-018-27891-3
- Beatty, D. S., Valayil, J. M., Clements, C. S., Ritchie, K. B., Stewart, F. J., and Hay, M. E. (2019). Variable effects of local management on coral defenses against a thermally regulated bleaching pathogen. *Sci. Adv.* 5:eaa1048. doi: 10.1126/sciadv.aay1048
- Bellwood, D. R., Hughes, T. P., Folke, C., and Nystrom, M. (2004). Confronting the coral reef crisis. *Nature* 429, 827–833. doi: 10.1038/nature02691
- Birrell, C. L., McCook, L. J., Willis, B. L., and Diaz-Pulido, G. A. (2008). Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* 20081322, 25–63. doi: 10.1201/9781420065756.ch2
- Bonaldo, R. M., and Hay, M. E. (2014). Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLoS One* 9:e85786. doi: 10.1371/journal.pone.0085786
- Bourne, D. G., Morrow, K. M., and Webster, N. S. (2016). Insights into the coral microbiome: underpinning the health and resilience of reef ecosystems. *Annu. Rev. Microbiol.* 70, 317–340. doi: 10.1146/annurev-micro-102215-095440
- Box, S. J., and Mumby, P. J. (2007). Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar. Ecol. Prog. Ser.* 342, 139–149. doi: 10.3354/meps342139
- Briggs, A. A., Brown, A. L., and Osenberg, C. W. (2021). Local versus site-level effects of algae on coral microbial communities. *R. Soc. Open Sci.* 8:210035. doi: 10.1098/rsos.210035
- Brown, A. L., and Carpenter, R. C. (2015). Water flow influences the mechanisms and outcomes of interactions between massive *Porites* and coral reef algae. *Mar. Biol.* 162, 459–468. doi: 10.1007/s00227-014-2593-5
- Bruno, J. F., Selig, E. R., Casey, K. S., Page, C. A., Willis, B. L., Harvell, C. D., et al. (2007). Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol.* 5:e124. doi: 10.1371/journal.pbio.0050124
- Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., and Schutte, V. G. W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90, 1478–1484. doi: 10.1890/08-1781.1
- Bulleri, F., Thiault, L., Mills, S. C., Nugues, M. M., Eckert, E. M., Corno, G., et al. (2018). Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. *Mar. Ecol. Prog. Ser.* 597, 65–77. doi: 10.3354/meps12583
- Campana, S., Demey, C., Busch, K., Hentschel, U., Muyzer, G., and de Goeij, J. M. (2021). Marine sponges maintain stable bacterial communities between reef sites with different coral to algae cover ratios. *FEMS Microbiol. Ecol.* 97:fiab115. doi: 10.1093/femsec/fiab115
- Chen, M. Y., and Parfrey, L. W. (2018). Incubation with macroalgae induces large shifts in water column microbiota, but minor changes to the epibiota of co-occurring macroalgae. *Mol. Ecol.* 27, 1966–1979. doi: 10.1111/mec.14548
- Chow, J., Tang, H., and Mazmanian, S. K. (2011). Pathobionts of the gastrointestinal microbiota and inflammatory disease. *Curr. Opin. Immunol.* 23, 473–480. doi: 10.1016/j.coi.2011.07.010
- Clements, C. S., Burns, A. S., Stewart, F. J., and Hay, M. E. (2020a). Parasite-host ecology: the limited impacts of an intimate enemy on host microbiomes. *Anim. Microbiome* 2:42. doi: 10.1186/s42523-020-00061-5
- Clements, C. S., Burns, A. S., Stewart, F. J., and Hay, M. E. (2020b). Seaweed-coral competition in the field: effects on coral growth, photosynthesis and microbiomes require direct contact. *Proc. Biol. Sci.* 287:20200366. doi: 10.1098/rspb.2020.0366
- Clements, C. S., Rasher, D. B., Hoey, A. S., Bonito, V. E., and Hay, M. E. (2018). Spatial and temporal limits of coral-macroalgal competition: the negative impacts of macroalgal density, proximity, and history of contact. *Mar. Ecol. Prog. Ser.* 586, 11–20. doi: 10.3354/meps12410
- Diaz-Almeyda, E. M., Ryba, T., Ohdera, A. H., Collins, S. M., Shafer, N., Link, C., et al. (2022). Thermal stress has minimal effects on bacterial communities of thermotolerant *Symbiodinium* cultures. *Front. Ecol. Evol.* 10:764086. doi: 10.3389/fevo.2022.764086
- Dixon, D. L., and Hay, M. E. (2012). Corals chemically cue mutualistic fishes to remove competing seaweeds. *Science* 338, 804–807. doi: 10.1126/science.1225748
- Dudgeon, S. R., Aronson, R. B., Bruno, J. F., and Precht, W. F. (2010). Phase shifts and stable states on coral reefs. *Mar. Ecol. Prog. Ser.* 413, 201–216. doi: 10.3354/meps08751
- Ezzat, L., Merolla, S., Clements, C. S., Munsterman, K. S., Landfield, K., Stensrud, C., et al. (2021). Thermal stress interacts with surgeonfish feces to increase coral susceptibility to dysbiosis and reduce tissue regeneration. *Front. Microbiol.* 12:608. doi: 10.3389/fmicb.2021.620458
- Fischbach, M. A. (2018). Microbiome: focus on causation and mechanism. *Cells* 174, 785–790. doi: 10.1016/j.cell.2018.07.038
- Fong, J., Deignan, L. K., Bauman, A. G., Steinberg, P. D., McDougald, D., and Todd, P. A. (2020). Contact- and water-mediated effects of macroalgae on the physiology and microbiome of three Indo-Pacific coral species. *Front. Mar. Sci.* 6:831. doi: 10.3389/fmars.2019.00831
- Foster, N. L., Box, S. J., and Mumby, P. J. (2008). Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. *Mar. Ecol. Prog. Ser.* 367, 143–152. doi: 10.3354/meps07594
- Gensollen, T., Iyer, S. S., Kasper, D. L., and Blumberg, R. S. (2016). How colonization by microbiota in early life shapes the immune system. *Science* 352, 539–544. doi: 10.1126/science.aad9378
- Glynn, P. W. (1983). Increased survivorship on corals harboring crustacean symbionts. *Marine Biology* 74, 105–111.
- Haas, A. F., Fairouz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., et al. (2016). Global microbialization of coral reefs. *Nat. Microbiol.* 1:16042. doi: 10.1038/nmicrobiol.2016.42
- Haas, A. F., Nelson, C. E., Rohwer, F., Wegley-Kelly, L., Quistad, S. D., Carlson, C. A., et al. (2013). Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ* 1:e108. doi: 10.7717/peerj.108
- Haas, A. F., Nelson, C. E., Wegley Kelly, L., Carlson, C. A., Rohwer, F., Leichter, J. J., et al. (2011). Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS One* 6:e27973. doi: 10.1371/journal.pone.0027973
- Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551. doi: 10.1126/science.265.5178.1547
- Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., et al. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359, 80–83. doi: 10.1126/science.aan8048
- Hughes, T. P., Graham, N. A. J., Jackson, J. B. C., Mumby, P. J., and Steneck, R. S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25, 633–642. doi: 10.1016/j.tree.2010.07.011
- Jackson, J., Donovan, M., Cramer, K., and Lam, V. (2014). *Status and Trends of Caribbean Coral Reefs: 1970–2012*. Washington, D.C. Global Coral Reef Monitoring.
- Jorissen, H., Skinner, C., Osinga, R., de Beer, D., and Nugues, M. M. (2016). Evidence for water-mediated mechanisms in coral-algal interactions. *Proc. Biol. Sci.* 283:20161137. doi: 10.1098/rspb.2016.1137
- Kline, D. I., Kuntz, N. M., Breitbart, M., Knowlton, N., and Rohwer, F. (2006). Role of elevated organic carbon levels and microbial activity in coral mortality. *Mar. Ecol. Prog. Ser.* 314, 119–125. doi: 10.3354/meps314119
- Klinges, J. G., Rosales, S. M., McMinds, R., Shaver, E. C., Shantz, A. A., Peters, E. C., et al. (2019). Phylogenetic, genomic, and biogeographic characterization of a novel and ubiquitous marine invertebrate-associated Rickettsiales parasite, *Candidatus Aquarickettsia rohweri*, gen. nov., sp. nov. *ISME J.* 13, 2938–2953. doi: 10.1038/s41396-019-0482-0
- Krediet, C. J., Ritchie, K. B., Paul, V. J., and Teplitski, M. (2013). Coral-associated micro-organisms and their roles in promoting coral health and thwarting diseases. *Proc. Biol. Sci.* 280:20122328. doi: 10.1098/rspb.2012.2328
- Lamont, R. J., and Hajishengallis, G. (2015). Polymicrobial synergy and dysbiosis in inflammatory disease. *Trends Mol. Med.* 21, 172–183. doi: 10.1016/j.molmed.2014.11.004
- Marcelino, V. R., Morrow, K. M., van Oppen, M. J. H., Bourne, D. G., and Verbruggen, H. (2017). Diversity and stability of coral endolithic microbial communities at a naturally high pCO₂ reef. *Mol. Ecol.* 26, 5344–5357. doi: 10.1111/mec.14268
- Markle, J. G. M., Frank, D. N., Mortin-Toth, S., Robertson, C. E., Feazel, L. M., Rolle-Kampczyk, U., et al. (2013). Sex differences in the gut microbiome drive hormone-dependent regulation of autoimmunity. *Science* 339, 1084–1088. doi: 10.1126/science.1233521
- McCook, L. J., Jompa, J., and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417. doi: 10.1007/s003380000129
- McDevitt-Irwin, J. M., Baum, J. K., Garren, M., and Vega Thurber, R. L. (2017). Responses of coral-associated bacterial communities to local and global stressors. *Front. Mar. Sci.* 4:262. doi: 10.3389/fmars.2017.00262
- McFall-Ngai, M., Hadfield, M. G., Bosch, T. C. G., Carey, H. V., Domazet-Lošo, T., Douglas, A. E., et al. (2013). Animals in a bacterial world, a new imperative for the life sciences. *Proc. Natl. Acad. Sci. U. S. A.* 110, 3229–3236. doi: 10.1073/pnas.1218525110
- Meirelles, P. M., Soares, A. C., Oliveira, L., Leomil, L., Appolinario, L. R., Francini-Filho, R. B., et al. (2018). Metagenomics of coral reefs under phase shift and high hydrodynamics. *Front. Microbiol.* 9:2203. doi: 10.3389/fmicb.2018.02203

- Mera, H., and Bourne, D. G. (2018). Disentangling causation: complex roles of coral-associated microorganisms in disease. *Environ. Microbiol.* 20, 431–449. doi: 10.1111/1462-2920.13958
- Monteil, Y., Teo, A., Fong, J., Bauman, A. G., and Todd, P. A. (2020). Effects of macroalgae on coral fecundity in a degraded coral reef system. *Mar. Pollut. Bull.* 151:110890. doi: 10.1016/j.marpolbul.2020.110890
- Morrow, K. M., Bromhall, K., Motti, C. A., Munnn, C. B., and Bourne, D. G. (2017). Allelochemicals produced by brown macroalgae of the *Lobophora* genus are active against coral larvae and associated bacteria, supporting pathogenic shifts to *vibrio* dominance. *Appl. Environ. Microbiol.* 83:e02391-16. doi: 10.1128/AEM.02391-16
- Morrow, K. M., Liles, M. R., Paul, V. J., Moss, A., and Chadwick, N. E. (2013). Bacterial shifts associated with coral–macroalgal competition in the Caribbean Sea. *Mar. Ecol. Prog. Ser.* 488, 103–117. doi: 10.3354/meps10394
- Morrow, K. M., Ritson-Williams, R., Ross, C., Liles, M. R., and Paul, V. J. (2012). Macroalgal extracts induce bacterial assemblage shifts and sublethal tissue stress in Caribbean corals. *PLoS One* 7:e44859. doi: 10.1371/journal.pone.0044859
- Mumby, P. J., Hastings, A., and Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature* 450, 98–101. doi: 10.1038/nature06252
- Mumby, P. J., and Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.* 23, 555–563. doi: 10.1016/j.tree.2008.06.011
- Mumby, P. J., Steneck, R. S., and Hastings, A. (2012). Evidence for and against the existence of alternate attractors on coral reefs. *Oikos* 122, 481–491. doi: 10.1111/j.1600-0706.2012.00262.x
- Nelson, C. E., Alldredge, A. L., McCliment, E. A., Amaral-Zettler, L. A., and Carlson, C. A. (2011). Depleted dissolved organic carbon and distinct bacterial communities in the water column of a rapid-flushing coral reef ecosystem. *ISME J.* 5, 1374–1387. doi: 10.1038/ismej.2011.12
- Nelson, A., De Soyza, A., Perry, J. D., Sutcliffe, I. C., and Cummings, S. P. (2012). Polymicrobial challenges to Koch's postulates: ecological lessons from the bacterial vaginosis and cystic fibrosis microbiomes. *Innate Immun.* 18, 774–783. doi: 10.1177/1753425912439910
- Nelson, C. E., Goldberg, S. J., Kelly, L. W., Haas, A. F., Smith, J. E., Rohwer, F., et al. (2013). Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. *ISME J.* 7, 962–979. doi: 10.1038/ismej.2012.161
- Nelson, C. E., Wegley Kelly, L., and Haas, A. F. (2022). Microbial interactions with dissolved organic matter are central to coral reef ecosystem function and resilience. *Annu. Rev. Mar. Sci.* 15:431. doi: 10.1146/annurev-marine-042121-080917
- Nugues, M. M., Smith, G. W., Hooi donk, R. J., Seabra, M. I., and Bak, R. P. M. (2004). Algal contact as a trigger for coral disease. *Ecol. Lett.* 7, 919–923. doi: 10.1111/j.1461-0248.2004.00651.x
- O'Brien, P. A., Smith, H. A., Fallon, S., Fabricius, K., Willis, B. L., Morrow, K. M., et al. (2018). Elevated CO₂ has little influence on the bacterial communities associated with the pH-tolerant coral, massive *Porites* spp. *Front. Microbiol.* 9:2621. doi: 10.3389/fmicb.2018.02621
- Pollock, F. J., Morris, P. J., Willis, B. L., and Bourne, D. G. (2011). The urgent need for robust coral disease diagnostics. *PLoS Pathog.* 7:e1002183. doi: 10.1371/journal.ppat.1002183
- Pratte, Z. A., Longo, G. O., Burns, A. S., Hay, M. E., and Stewart, F. J. (2018). Contact with turf algae alters the coral microbiome: contact versus systemic impacts. *Coral Reefs* 37, 1–13. doi: 10.1007/s00338-017-1615-4
- Quan-Young, L. I., and Espinoza-Avalos, J. (2006). Reduction of zooxanthellae density, chlorophyll a concentration, and tissue thickness of the coral *Montastrea faveolata* (Scleractinia) when competing with mixed turf algae. *Limnol. Oceanogr.* 51, 1159–1166. doi: 10.4319/lo.2006.51.2.1159
- Rasher, D. B., and Hay, M. E. (2010). Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc. Natl. Acad. Sci. U. S. A.* 107, 9683–9688. doi: 10.1073/pnas.0912095107
- Rasher, D. B., Hoey, A. S., and Hay, M. E. (2013). Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94, 1347–1358. doi: 10.1890/12-0389.1
- Rasher, D. B., Stout, E. P., Engel, S., Kubanek, J., and Hay, M. E. (2011). Macroalgal terpenes function as allelopathic agents against reef corals. *Proc. Natl. Acad. Sci. U. S. A.* 108, 17726–17731. doi: 10.1073/pnas.1108628108
- Reigel, A. M., Paz-García, D. A., and Hellberg, M. E. (2021). Microbiome of a reef-building coral displays signs of acclimation to a stressful shallow hydrothermal vent habitat. *Front. Mar. Sci.* 8:652633. doi: 10.3389/fmars.2021.652633
- Ritchie, K. B. (2006). Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. *Mar. Ecol. Prog. Ser.* 322, 1–14. doi: 10.3354/meps322001
- River, G. F., and Edmunds, P. J. (2001). Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *J. Exp. Mar. Bio. Ecol.* 261, 159–172. doi: 10.1016/S0022-0981(01)00266-0
- Roach, T. N. F., Little, M., Arts, M. G. I., Huckleba, J., Haas, A. F., George, E. E., et al. (2020). A multiomic analysis of in situ coral-turf algal interactions. *Proc. Natl. Acad. Sci. U. S. A.* 117, 13588–13595. doi: 10.1073/pnas.1915455117
- Roff, G., and Mumby, P. J. (2012). Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* 27, 404–413. doi: 10.1016/j.tree.2012.04.007
- Rosado, P. M., Leite, D. C. A., Duarte, G. A. S., Chaloub, R. M., Jospin, G., Nunes da Rocha, U., et al. (2019). Marine probiotics: increasing coral resistance to bleaching through microbiome manipulation. *ISME J.* 13, 921–936. doi: 10.1038/s41396-018-0323-6
- Rosenberg, E., Koren, O., Reshef, L., Efrony, R., and Zilber-Rosenberg, I. (2007). The role of microorganisms in coral health, disease and evolution. *Nat. Rev. Microbiol.* 5, 355–362. doi: 10.1038/nrmicro1635
- Santoro, E. P., Borges, R. M., Espinoza, J. L., Freire, M., Messias, C. S. M. A., Villela, H. D. M., et al. (2021). Coral microbiome manipulation elicits metabolic and genetic restructuring to mitigate heat stress and evade mortality. *Sci. Adv.* 7. doi: 10.1126/sciadv.abg3088
- Schmitt, R. J., Holbrook, S. J., Davis, S. L., Brooks, A. J., and Adam, T. C. (2019). Experimental support for alternative attractors on coral reefs. *Proc. Natl. Acad. Sci. U. S. A.* 116, 4372–4381. doi: 10.1073/pnas.1812412116
- Seyedsayamdost, M. R., Case, R. J., Kolter, R., and Clardy, J. (2011). The Jekyll-and-Hyde chemistry of *Phaeobacter gallaeciensis*. *Nat. Chem.* 3, 331–335. doi: 10.1038/nchem.1002
- Shaver, E. C., Shantz, A. A., McMinds, R., Burkepile, D. E., Vega Thurber, R. L., and Silliman, B. R. (2017). Effects of predation and nutrient enrichment on the success and microbiome of a foundational coral. *Ecology* 98, 830–839. doi: 10.1002/ecy.1709
- Silva, L., Calleja, M. L., Ivetic, S., Huete-Stauffer, T., Roth, F., Carvalho, S., et al. (2021). Heterotrophic bacterioplankton responses in coral- and algae-dominated Red Sea reefs show they might benefit from future regime shift. *Sci. Total Environ.* 751:141628. doi: 10.1002/ecy.1709
- Smith, J. E., Shaw, M., Edwards, R. A., Obura, D., Pantos, O., Sala, E., et al. (2006). Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol. Lett.* 9, 835–845. doi: 10.1111/j.1461-0248.2006.00937.x
- Stachowicz, J. J., and Hay, M. E. (1999). Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* 80, 2085–2101. doi: 10.1890/0012-9658(1999)080[2085:MACPTR]2.0.CO;2
- Sunagawa, S., Woodley, C. M., and Medina, M. (2010). Threatened corals provide underexplored microbial habitats. *PLoS One* 5:e9554. doi: 10.1371/journal.pone.0009554
- Sweet, M. J., Bythell, J. C., and Nugues, M. M. (2013). Algae as reservoirs for coral pathogens. *PLoS One* 8:e69717. doi: 10.1371/journal.pone.0069717
- Thompson, J. R., Rivera, H. E., Closek, C. J., and Medina, M. (2014). Microbes in the coral holobiont: partners through evolution, development, and ecological interactions. *Front. Cell. Infect. Microbiol.* 4:176. doi: 10.3389/fcimb.2014.00176
- van Duyl, F. C., van Bleijswijk, J. D. L., Wuchter, C., Witte, H. J., Coolen, M. J. L., Bak, R. P. M., et al. (2023). Recovery patterns of the coral microbiome after relief of algal contact. *J. Sea Res.* 191:102309. doi: 10.1016/j.seares.2022.102309
- Vega Thurber, R., Burkepile, D. E., Correa, A. M. S., Thurber, A. R., Shantz, A. A., Welsh, R., et al. (2012). Macroalgae decrease growth and alter microbial community structure of the reef-building coral. *Porites astreoides*. *PLoS One* 7:e44246. doi: 10.1371/journal.pone.0044246
- Vega Thurber, R., Mydlarz, L. D., Brandt, M., Harvell, D., Weil, E., Raymundo, L., et al. (2020). Deciphering coral disease dynamics: integrating host, microbiome, and the changing environment. *Front. Ecol. Evol.* 8:575927. doi: 10.3389/fevo.2020.575927
- Vega Thurber, R., Willner-Hall, D., Rodriguez-Mueller, B., Desnues, C., Edwards, R. A., Angly, F., et al. (2009). Metagenomic analysis of stressed coral holobionts. *Environ. Microbiol.* 11, 2148–2163. doi: 10.1111/j.1462-2920.2009.01935.x
- Vermeij, M. J. A., Smith, J. E., Smith, C. M., Vega Thurber, R., and Sandin, S. A. (2009). Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. *Oecologia* 159, 325–336. doi: 10.1007/s00442-008-1223-7
- Vieira, C., Engelen, A. H., Guentas, L., Aires, T., Houlbreque, F., Gaubert, J., et al. (2016a). Species specificity of bacteria associated to the brown seaweeds *Lobophora* (Dictyotales, Phaeophyceae) and their potential for induction of rapid coral bleaching in *Acropora muricata*. *Front. Microbiol.* 7:316. doi: 10.3389/fmicb.2016.00316
- Vieira, C., Thomas, O. P., Culioli, G., Genta-Jouve, G., Houlbreque, F., Gaubert, J., et al. (2016b). Allelopathic interactions between the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae) and scleractinian corals. *Sci. Rep.* 6:18637. doi: 10.1038/srep18637
- Voolstra, C. R., Suggett, D. J., Peixoto, R. S., Parkinson, J. E., Quigley, K. M., Silveira, C. B., et al. (2021). Extending the natural adaptive capacity of coral holobionts. *Nat. Rev. Earth Environ.* 2, 747–762. doi: 10.1038/s43017-021-00214-3
- Walsh, K., Haggerty, J. M., Doane, M. P., Hansen, J. J., Morris, M. M., Moreira, A. P. B., et al. (2017). Aura-biomes are present in the water layer above coral reef benthic macro-organisms. *PeerJ* 5:e3666. doi: 10.7717/peerj.3666

- Webster, N. S., Negri, A. P., Botté, E. S., Laffy, P. W., Flores, F., Noonan, S., et al. (2016). Host-associated coral reef microbes respond to the cumulative pressures of ocean warming and ocean acidification. *Sci. Rep.* 6:19324. doi: 10.1038/srep19324
- Wellington, G. M. (1980). Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. *Oecologia* 47, 340–343. doi: 10.1007/BF00398527
- Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., et al. (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat. Commun.* 7:11833. doi: 10.1038/ncomms11833
- Zaneveld, J. R., McMinds, R., and Vega Thurber, R. (2017). Stress and stability: applying the Anna Karenina principle to animal microbiomes. *Nat. Microbiol.* 2:17121. doi: 10.1038/nmicrobiol.2017.121
- Zhou, G., Yuan, T., Cai, L., Zhang, W., Tian, R., Tong, H., et al. (2016). Changes in microbial communities, photosynthesis and calcification of the coral *Acropora gemmifera* in response to ocean acidification. *Sci. Rep.* 6:35971. doi: 10.1038/srep35971