



Responses of Coral-Associated Bacterial Communities to Local and Global Stressors

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The microbial contribution to ecological resilience is still largely overlooked in coral reef ecology. Coral-associated bacteria serve a wide variety of functional roles with reference to the coral host, and thus, the composition of the overall microbiome community can strongly influence coral health and survival. Here, we synthesize the findings of recent studies ($n = 45$) that evaluated the impacts of the top three stressors facing coral reefs (climate change, water pollution and overfishing) on coral microbiome community structure and diversity. Contrary to the species losses that are typical of many ecological communities under stress, here we show that microbial richness tends to be higher rather than lower for stressed corals (i.e., in ~60% of cases), regardless of the stressor. Microbial responses to stress were taxonomically consistent across stressors, with specific taxa typically increasing in abundance (e.g., *Vibrionales*, *Flavobacteriales*, *Rhodobacterales*, *Alteromonadales*, *Rhizobiales*, *Rhodospirillales*, and *Desulfovibrionales*) and others declining (e.g., *Oceanospirillales*). Emerging evidence also suggests that stress may increase the microbial beta diversity amongst coral colonies, potentially reflecting a reduced ability of the coral host to regulate its microbiome. Moving forward, studies will need to discern the implications of stress-induced shifts in microbiome diversity for the coral hosts and may be able to use microbiome community structure to identify resilient corals. The evidence we present here supports the hypothesis that microbial communities play important roles in ecological resilience, and we encourage a focus on the microbial contributions to resilience for future research.

Keywords: coral, bacteria, global change biology, environmental stress, symbiosis, global warming, pollution, overfishing

INTRODUCTION

Corals are diverse meta-organisms that contain not only the conspicuous dinoflagellate partner *Symbiodinium* but also a microbiome assembled of bacterial, archaeal, viral, and other eukaryotic microorganisms (Rosenberg et al., 2007; Ainsworth et al., 2010; Thompson et al., 2014). Host specific differences in microbiome composition suggest that some bacterial members of the microbiome are mutualistic (Ainsworth et al., 2015); thus, many recent efforts have focused on identifying these bacteria and their specific metabolic roles in coral health (**Table 1**). These abundant coral-associated bacterial communities are distinct (**Box 1**) from the surrounding habitat, containing taxa that drastically differ from free-living seawater microbes (Rohwer et al., 2001; Carlos et al., 2013).

TABLE 1 | Overview of the proposed beneficial roles of different coral-associated bacteria.

Role	Description	Example taxa	References
Metabolism	Provide nitrogen to <i>Symbiodinium</i>	<i>Cyanobacteria</i> (potentially <i>Synechococcus</i> and <i>Prochlorococcus</i>)	Lesser et al., 2004
	Provide nitrogen to coral larvae's <i>Symbiodinium</i>	<i>Cyanobacteria</i>	Lesser et al., 2007
	Provide nitrogen to the coral larvae	<i>Altermonas</i> sp. and <i>Vibrio alginolyticus</i>	Ceh et al., 2013a
	Provide nitrogen to <i>Symbiodinium</i> and the coral	<i>Rhizobiales</i>	Ceh et al., 2013a; Lema et al., 2014
	Provide nitrogen and sulphur to the holobiont	<i>Gammaproteobacteria</i> , specifically <i>Vibrio</i> sp.	Olson et al., 2009
	Sulphur cycling	<i>Rhizobiales</i>	Lema et al., 2012
	Cycling sulphur, carbon, nitrogen and phosphorous cycling to the holobiont, metal homeostasis, organic remediation, antibiotic resistance, secondary metabolism	Unknown	Wegley et al., 2007
Protection	20% of cultured bacteria had antibiotic activity against other strains and pathogens	<i>Photobacterium</i> , <i>Halomonas</i> , <i>Exiguobacterium</i> , <i>Bacillus</i> , <i>Altermonas</i>	Ritchie, 2006
	~70% of culturable isolates from corals demonstrated inhibition to <i>Burkholder</i> agar diffusion assays	<i>Vibrionales</i> , <i>Alteromonadales</i> (e.g., <i>Pseudoaltermonas</i>), <i>Bacteroidetes</i>	Rypien et al., 2010
	Cultured isolates from corals demonstrated inhibition of four coral pathogens and three fungi	<i>Bacillus</i> , <i>Pseudomonas</i>	EIAhwany et al., 2013
	Opportunistic <i>Proteobacteria</i> increased when <i>Actinobacteria</i> were below ~2.5% relative abundance	<i>Actinobacteria</i>	Zaneveld et al., 2016
	8% of coral commensals inhibited glycosidases (needed for growth) and of catabolic enzymes in a coral pathogen, <i>Serratia marcescens</i>	<i>Exiguobacterium</i>	Krediet et al., 2012
	Predatory bacteria consume the coral pathogens <i>Vibrio corallyticus</i> and <i>V. harveyi</i>	<i>Halobacteriovorax</i> sp.	Welsh et al., 2016
	Displayed antimicrobial activity against other coral cultured isolates	<i>Pseudoaltermonas</i>	Kvennefors et al., 2011
Recruitment	Cultures and filtrates significantly increased larval settlement suggesting an extracellular factor	<i>Roseivivax</i> sp. 46E8 (<i>Alphaproteobacterium</i>)	Sharp et al., 2015

Aspects of coral biology also influence microbiome structure and function. Similar to humans, compartmentalization of the microbiome generates distinct microbial communities in the coral animal, within the surface mucus layer, tissues, skeleton, and gut (Sweet et al., 2010; Ainsworth et al., 2015; Apprill et al., 2016) and some particularly associated with *Symbiodinium* (Ainsworth et al., 2015). Coral-associated bacteria can be transferred vertically from parent to larva (Sharp et al., 2012) or they can be horizontally acquired from the environment (Apprill et al., 2009; Sharp et al., 2010), including when adult corals release bacteria (e.g., *Altermonas* and *Roseobacter*) as a by-product of broadcast spawning (Ceh et al., 2013b). Although recent research has focused on the role of microbiomes in coral adaptation (Gilbert et al., 2012; Glasl et al., 2016), coral reef management still largely ignores the role of microbial communities, with the exception of *Symbiodinium*, in coral resilience (McClanahan et al., 2012). With rapid advances in DNA sequencing technologies, more studies are able to capture the influence of stressors on the coral microbiome, but no study to date has reviewed these impacts. Here, we

conduct a synthesis of the results from 45 relevant studies that evaluated how three key stressors threatening coral reefs (i.e., climate change, water pollution and overfishing) altered coral microbiomes. In addition, we provide hypotheses as to how the microbiome may provide corals with resistance to these stressors.

Overview of the Beneficial Roles That Bacteria Play in Corals

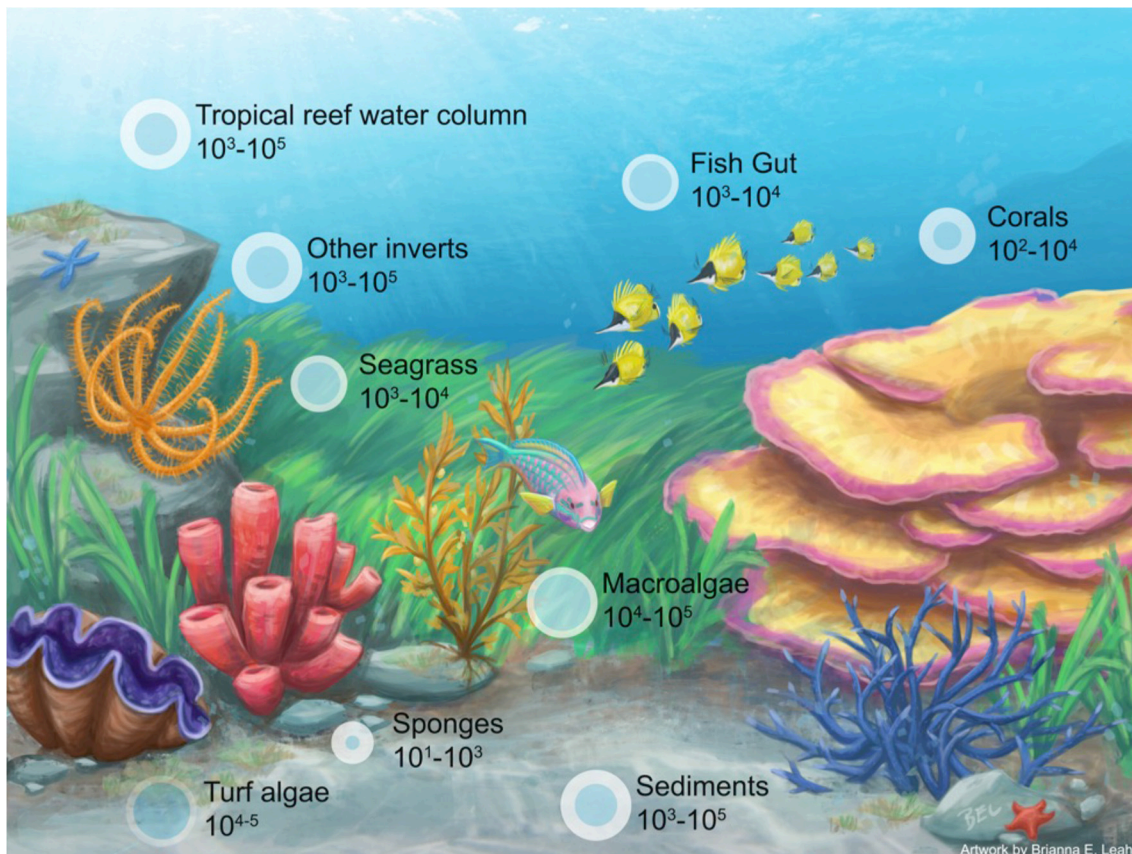
Different coral-associated bacteria are hypothesized to play varying roles in coral health, nutrition and development (Table 1). Recent reviews have proposed the term “Beneficial Microorganisms for Corals” (BMC) to define microbial symbionts that maintain coral health (Peixoto et al., 2017), outlined microbiome roles in coral health and resilience (Bourne et al., 2016) and suggested that coral reef microbial communities serve as indicators of environmental stress and coral health (Glasl et al., 2017). Coral-associated microbial communities contribute to carbon cycling (Kimes et al., 2010), sulfur cycling (Wegley et al., 2007; Raina et al., 2009),

BOX 1 | Are coral microbiomes unusually diverse?

Coral are sometimes referred as “highly” diverse meta-organisms. Yet this is a somewhat subjective statement that likely has arisen when coral microbiomes are compared to other well studied mutualistic symbiotic model systems that are highly canalized (Dubilier et al., 2008). It is now well accepted that microorganisms colonize most marine species, yet a systematic comparison among marine organisms is currently lacking. For example, sponge tissues contain between 10 and 1,000 bacterial OTUs (Bourne and Webster, 2013), a species richness value well within the range for corals. A recent assessment of tropical reef algal microbiomes also demonstrate that algae contain even more diverse bacterial communities than corals (Barott et al., 2011). The number of bacterial OTU's in corals can range up to 10^2 – 10^4 compared to 10^1 – 10^3 for sponges and 10^2 for *Hydra* (Blackall et al., 2015), although as just discussed these richness estimates vary across species, habitat, and host compartment. With these context dependent numbers, it is thus difficult to say whether corals have a higher richness of microbial taxa than other marine species. For example, turf and CCA each exhibited overall higher numbers of OTUs (18,926 and 9,559) than the three coral species compared (*Acropora hyacinthus*, *A. rosaria*, and *Porites lutea*) (951, 2,331, 4,018) (Hester et al., 2016). Similarly, algal (i.e., *Dictyota bartayresiana*, *Halimeda opuntia*, turf algae, and CCA) microbiomes were generally more diverse overall [ranging from 6.22 to 7.82 (Shannon Index)] than those in corals (ranging from 2.84 to 4.51) (Barott et al., 2011). Therefore, more comparisons among coral species and marine meta-organisms are needed to determine if corals or certain coral species actually have highly diverse microbial communities.

Additionally, when comparing the composition and dynamics of the coral microbiome to other marine hosts, it is important to differentiate between stable and sporadic members of the community. It is likely that stable members play more important roles in promoting the health and longevity of the host while transient members might contribute to only the function of the host under explicit environmental conditions or alternatively play negative and antagonistic roles in the system (albeit, stable members could also act as opportunistic pathogens). Stable microbes should exhibit consistent relative abundances in the host vs. the sporadic members who will vary in their prevalence and relative abundance among individuals of the same host (Hester et al., 2016). Sporadic members may opportunistically associate with the coral and not play a beneficial role. In three coral species there was a high number of stable members to sporadic members: *A. hyacinthus* (stable = 902, sporadic = 49), *A. rosaria* (stable = 2,188, sporadic = 143), *P. lutea* (stable = 3,662, sporadic = 356) (Hester et al., 2016).

Another way to evaluate this is to conduct “core” microbiome analysis at various levels of stringency. This prevalence-based metric has been used to infer which members of a coral's microbiome are mutualistic or opportunistic. In an evaluation of the core coral microbiome (i.e., phylotype presence in 30% of the samples), *Acropora granulosa*'s core microbiome consisted of 159 out of 1,508 phylotypes, *Leptoseris* spp. 204 out of 1,424, and *Montipora capitata* 350 out of 1,433 (Ainsworth et al., 2015). Importantly, most of these core microbiome members were highly diverse yet found in very low relative abundance compared to the entire community. Thus, it is important to consider rare microbiome members, as these may be the beneficial resident members researchers are interested in. In another longitudinal study from three coral species from South Florida, the core coral mucus microbiome consisted of 13 bacterial orders at a >95% prevalence score (Zaneveld et al., 2016). In this case, the “core” microbiome highly depends on the level of stringency used.



BOX FIGURE 1 | Depiction of a coral reef and associated microbiomes with organismal hosts [i.e., invertebrates (Bourne et al., 2013; Tianero et al., 2014; Hakim et al., 2016), seagrass (Ettinger et al., 2017; Fahimipour et al., 2017), fish (Ghanbari et al., 2015; Givens et al., 2015; Parris et al., 2016), corals (Barott et al., 2011; Blackall et al., 2015; Hester et al., 2016), macroalgae (Barott et al., 2011; Burke et al., 2011; Egan et al., 2013; Brodie et al., 2016), sponges (Bourne and Webster, 2013; Blackall et al., 2015), turf algae (Hester et al., 2016)] and environmental parameters [i.e., reef water (McCliment et al., 2012), sediment (Ettinger et al., 2017)]. The size of the bubble indicates a more species rich microbiome (based on OTUs).

phosphorous fixation, metal homeostasis, organic remediation (Zhang et al., 2015), production of antibiotics (Ritchie, 2006) and secondary metabolism (Zhang et al., 2015). For example, diazotrophs (i.e., nitrogen-fixing microbes) form species-specific associations with corals and may provide limiting fixed nitrogen to the algal partner of corals, *Symbiodinium*, and to the coral animal itself (Lesser et al., 2004, 2007; Lema et al., 2012). In the early coral life stages, bacteria provide nitrogen directly to larvae's *Symbiodinium* (Ceh et al., 2013a) and potentially to the coral larvae (Lema et al., 2014). Bacteria also play an important role in larval recruitment and settlement, for example, *Alphaproteobacterium*, *Roseivivax* sp. 46E8 significantly increases larval settlement of *Porites astreoides* (Sharp et al., 2015).

Many coral-associated bacteria defend the coral by exuding antimicrobial compounds to prevent invasions by pathogens or other exogenous bacteria (Table 1). For example, nearly 70% of cultivable isolates from *Montastrea annularis* inhibited the growth of other bacteria and 11.6% inhibited the growth of the known coral pathogen, *Vibrio shiloi* (Rypien et al., 2010). Approximately 20% of cultivable isolates from *Acropora palmata* demonstrated antibiotic activity against other strains and pathogens (Ritchie, 2006). Isolates from a soft coral, *Sarcophyton glaucum*, inhibited the growth of four coral pathogens and three fungi (ElAhwany et al., 2013). It was also found that under increased algal cover and temperatures, the relative abundances of *Actinobacteria* decreased while opportunistic *Proteobacteria* increased within the coral microbiome, suggesting that opportunists can take advantage of the absence of inhibition (Zaneveld et al., 2016). Eight percent of native coral bacteria inhibited the growth of the pathogen *Serratia marcescens*, with *Exiguobacterium* sp. inducing 10–100 fold reductions in growth within coral mucus (Krediet et al., 2012). Concurrently, the coral pathogen, *Vibrio corallilyticus*, has antimicrobial activity of its own, suggesting that it may use inhibition to colonize the coral (Kvennefors et al., 2011). There are also some resident bacteria that actively predate upon these pathogens within the coral mucus (Welsh et al., 2016). In summary, given the wide variety of roles vital to holobiont functioning that are played by coral-associated bacteria, any disruption or destabilization may influence host fitness and ecosystem functioning.

RESPONSES OF THE CORAL MICROBIOME TO STRESSORS THREATENING CORAL REEFS

Overview of Papers Synthesized

Here, we synthesized 45 relevant studies that each (1) were peer-reviewed (2) examined coral-associated bacteria and (3) measured how these bacteria were affected by climate change, water pollution or overfishing (Table 2). We included a broad range of methodologies as many researchers use different methods and we aimed to evaluate the field from a broad perspective. Over half of the studies focused on climate change ($n = 27$) and almost one quarter focused on water pollution

($n = 10$); only a small proportion addressed overfishing ($n = 4$) or more than one stressor at a time ($n = 4$) (Figure 1). The majority of the studies were published in the last 5 years (Figure 1). Geographically, almost all of the overfishing and water pollution studies occurred in the Caribbean compared with studies on climate change, which had a more global distribution of study sites (Figure 1).

The genera *Acropora* and *Porites* were the most represented corals within these studies, accounting for nearly 50% of all corals evaluated (Figure 2A). Massive *Porites* species may be “stress-tolerant” corals, as they are slow growing and may be able to survive harsher environments (Darling et al., 2012). *Acroporids* are considered “competitive” corals, meaning that they are fast-growing and dominate reefs in productive environments; they are also the most sensitive to environmental change (Darling et al., 2012). As a result, there was a bias toward studying climate change on competitive life history strategies, specifically *Acropora* in Australia (Figure 2B).

We note here that we report bacterial taxa at the levels of Phylum, Class and Order to provide consistency across the array of studies given that many of them reported their data in different ways and to different taxonomic levels. Additionally, researchers used varying metrics of community structure to evaluate the impact of stressors including: richness (i.e., total number of species), alpha diversity (i.e., the total number of species and their relative abundances, generally the Shannon and Simpson Index), evenness (i.e., distribution of species relative abundances) and beta diversity (i.e., difference in community composition).

Stressors Tend to Increase Coral Microbiome Richness/Alpha Diversity

While a consequence of human impacts on macro-scale communities is often species loss, the emerging evidence from our analysis suggests that similar impacts more commonly lead to an increase in bacterial richness or alpha diversity within coral-associated microbial communities (~60% of the time, Table 3). Invasion is likely the mechanism underlying these increases, with stress events appearing to disrupt the functioning microbiome and facilitating an invasion of microbes not typically resident on corals, thus increasing the overall number of microbiome members (Welsh et al., 2015). For example, corals closer to human disturbance have been shown to harbor higher bacterial diversity than those farther from the disturbance (Morrow et al., 2012a). Similarly, corals in lowered pH had higher microbial diversity (Meron et al., 2011) and microbial diversity increased in overfishing and eutrophication treatments (Jessen et al., 2013). Lastly, it was found that upon algal contact, the coral microbiome increased in species richness (Zaneveld et al., 2016). These results also are contrary to the patterns found in the human gut microbiome, in which stress lowers microbial alpha diversity by allowing opportunistic and pathogenic taxa to dominate the community (Lozupone et al., 2012). This might be explained by the nature of the human gut microbiome being a more closed system compared with corals that are constantly bathed in the distinct microbial assemblages of seawater. We hypothesize that when corals are disturbed, their ability to regulate and/or exclude

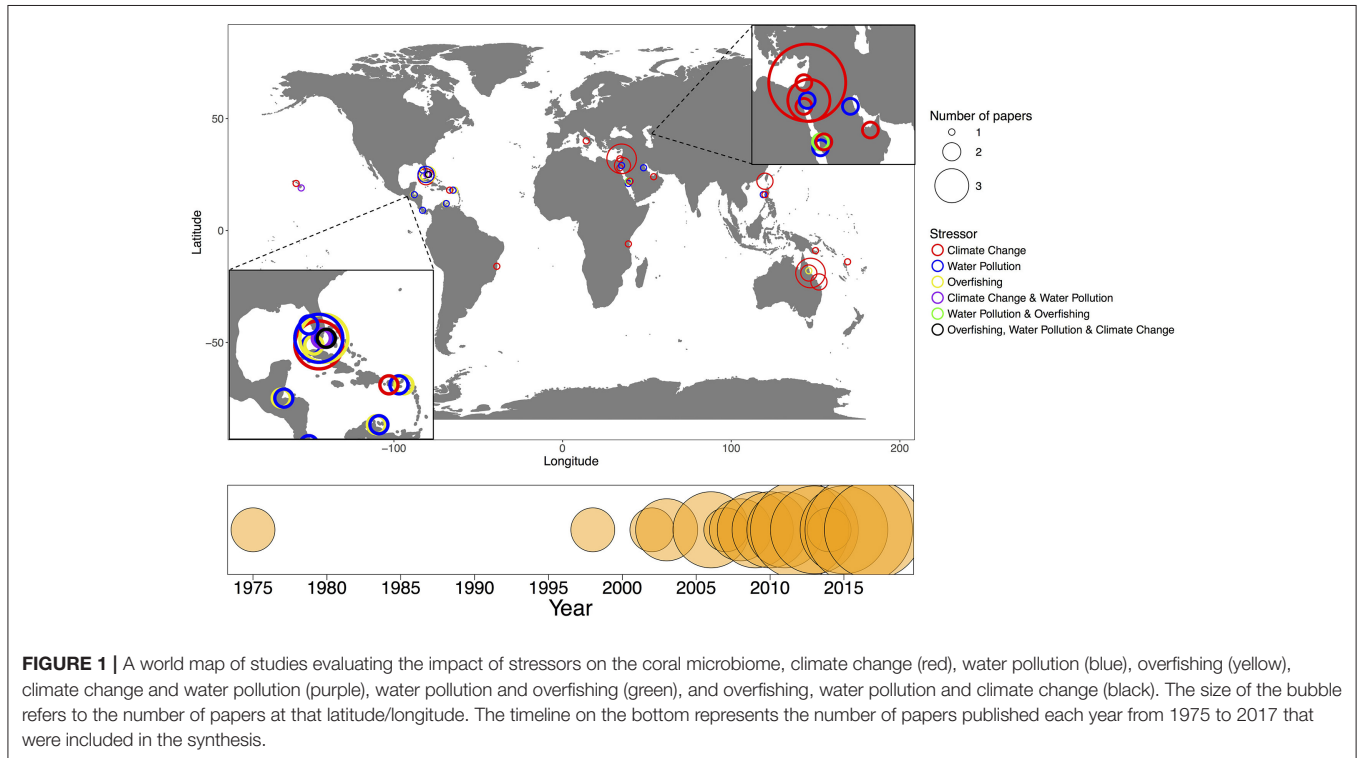
TABLE 2 | Overview of the 45 papers that evaluated the influence of climate change, water pollution and overfishing on the coral microbiome, coral species evaluated, the method they used to capture effects on the microbial community (e.g., DGGE, denaturing gradient gel electrophoresis; TRFLP, terminal restriction fragment length polymorphism; PFGE, pulsed-field gel electrophoresis), and whether the paper had data that we included on changes in bacterial taxa (i.e., **Figure 3**) or microbial diversity (i.e., **Table 3**).

Author	Coral Species	Microbial community assessment method	Taxa changes?	Microbial diversity?
CLIMATE CHANGE				
Littman et al., 2010	<i>Acropora tenuis</i>	DGGE of 16S	y	n
Littman et al., 2011	<i>Acropora millepora</i>	Metagenomics	y	n
Salerno et al., 2011	<i>Porites compressa</i>	TRFLP of 16S	y	n
Meron et al., 2011	<i>Acropora eurystoma</i>	16S rRNA clones, DGGE of 16S	y	y
Webster et al., 2012	<i>Acropora millepora</i>	DGGE of 16S	y	n
Frydenborg et al., 2013	<i>Acropora palmata</i>	Culturing	y	n
Santos et al., 2014	<i>Mussismilia harttii</i>	DGGE of 16S, qPCR	y	y
Morrow et al., 2015	<i>Acropora millepora</i> , <i>Porites cylindrica</i>	454 16S rRNA amplicons	y	y
Tout et al., 2015	<i>Pocillopora damicornis</i>	454 16S rRNA amplicons, qPCR	y	y
Webster et al., 2016	<i>Acropora millepora</i> , <i>Seriatopora hystrix</i>	454 16S rRNA amplicons	y	n
Lee et al., 2016	<i>Acropora muricata</i>	454 16S rRNA amplicons	y	y
Tracy et al., 2015	<i>Gorgonia ventalina</i> , <i>Orbicella faveolata</i>	454 16S rRNA amplicons	y	y
Meron et al., 2012	<i>Balanophyllia europaea</i> , <i>Cladocora caespitosa</i>	16S rRNA clones	y	y
Banin et al., 2003	<i>Oculina patagonica</i>	Culturing	n	n
Ben-Haim et al., 2003	<i>Pocillopora damicornis</i>	Culturing	n	n
Ainsworth and Hoegh-Guldberg, 2009	<i>Acropora aspera</i> , <i>Stylophora pistillata</i>	FISH Microscopy	n	n
Bourne et al., 2007	<i>Acropora millepora</i>	RFLP of 16S, DGGE of 16S, colony blotting	y	y
Kushmaro et al., 1998	<i>Oculina patagonica</i>	Culturing	y	n
Ritchie, 2006	<i>Acropora palmata</i>	Culturing, 16S rRNA clones	y	n
Ben-Haim and Rosenberg, 2002	<i>Pocillopora damicornis</i> , <i>Acropora formosa</i> , <i>Acropora</i> sp., <i>Cycloseries</i> sp., <i>Fungiidae</i>	Culturing, 16S rRNA clones	n	n
Koren and Rosenberg, 2006	<i>Oculina patagonica</i>	16S rRNA clones	n	n
Koren and Rosenberg, 2008	<i>Oculina patagonica</i>	Culturing, 16S rRNA clones	n	n
Cardini et al., 2016	<i>Acropora hemprichii</i> , <i>Stylophora pistillata</i>	Measured microbial N ₂ fixation	n	n
Ziegler et al., 2017	<i>Acropora hyacinthus</i>	Illumina 16S rRNA amplicons	y	n
Lee et al., 2017	<i>Acropora muricata</i>	Illumina 16S rRNA amplicons	y	n
Hadaidi et al., 2017	<i>Porites lobata</i>	Illumina 16S rRNA amplicons, qPCR	n	n
Gajigan et al., 2017	<i>Acropora digitifera</i>	Illumina 16S rRNA amplicons	y	y
CLIMATE CHANGE AND WATER POLLUTION				
Vega Thurber et al., 2009	<i>Porites compressa</i>	Metagenomics	y	n
Welsh et al., 2016	<i>Agaricia</i> sp., <i>Porites</i> sp., <i>Siderastrea siderea</i>	454 16S rRNA amplicons, culturing, microscopy, predation assays	n	n
WATER POLLUTION				
Sutherland et al., 2010	<i>Acropora palmata</i> , <i>Siderastrea siderea</i> , <i>Solenastrea bournoni</i>	PFGE of 16S	n	n
Looney et al., 2010	<i>Acropora palmata</i> , <i>Montastraea faveolata</i> , <i>Siderastrea siderea</i>	Culturing	n	n
Morrow et al., 2012a	<i>Montastraea faveolata</i> , <i>Porites astreoides</i>	DGGE of 16S, 454 16S rRNA amplicons	y	y
Röthig et al., 2016	<i>Fungia granulosa</i>	Illumina 16S rRNA amplicons	y	y
Kline et al., 2006	<i>Montastraea annularis</i>	Culturing	n	n
Klaus et al., 2007	<i>Montastraea annularis</i>	TRFLP of 16S	n	n
Garren et al., 2009	<i>Porites cylindrica</i>	16S rRNA clones, DGGE of 16S	n	n
Ziegler et al., 2016	<i>Pocillopora verrucosa</i> , <i>Acropora hemprichii</i>	Illumina 16S rRNA amplicons	y	y
Mitchell and Chet, 1975	<i>Platygyra</i>	Culturing	n	n
Al-Dahash and Mahmoud, 2013	<i>Porites compressa</i> , <i>Acropora clathrata</i>	DGGE of 16S, culturing	y	y
WATER POLLUTION AND OVERFISHING				
Jessen et al., 2013	<i>Acropora hemprichii</i>	454 16S rRNA amplicons	y	n

(Continued)

TABLE 2 | Continued

Author	Coral Species	Microbial community assessment method	Taxa changes?	Microbial diversity?
OVERFISHING				
Vega Thurber et al., 2012	<i>Porites astreoides</i>	TRFLP of 16S	y	y
Barott et al., 2012	<i>Montastraea annularis</i>	454 16S rRNA amplicons	y	y
Morrow et al., 2013	<i>Montastraea faveolata</i> , <i>Porites astreoides</i>	DGGE of 16S	n	n
Morrow et al., 2017	<i>Porites cylindrica</i>	Illumina 16S rRNA amplicons, culturing	y	y
OVERFISHING, WATER POLLUTION AND CLIMATE CHANGE				
Zaneveld et al., 2016	<i>Siderastrea siderea</i> , <i>Porites</i> sp., <i>Agaricia</i> sp.	454 16S rRNA amplicons	y	y



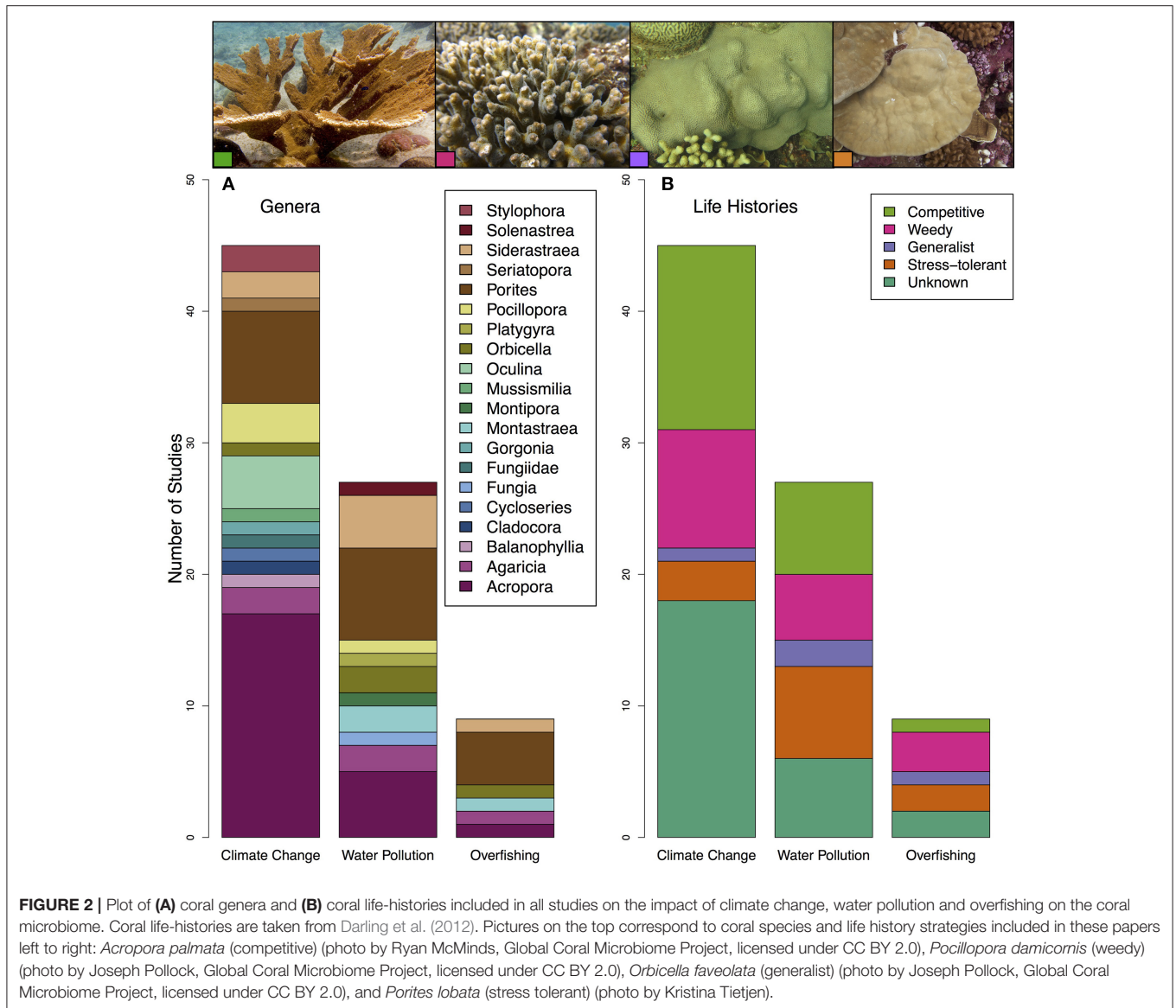
incoming microbial taxa from the surrounding environment may be reduced. However, this is not always the case, as other studies have demonstrated no significant change or a decrease in microbial diversity under these three stressors (Meron et al., 2012; Tracy et al., 2015; Morrow et al., 2017). These conflicting results likely are the result of variability in coral microbiome responses across coral host species, locations and stressors. Additionally, these diversity changes may reflect differences in experimental design.

Stressors Decrease the Stability and Increase Beta Diversity of Microbiome Community Structure

In addition to increased richness, there is mounting evidence that stressors induce changes to coral microbiome evenness and beta diversity. Changes in evenness indicates shifts in microbial species dominance, and evenness has been found to decrease in

the rhizosphere with added disturbance (van der Voort et al., 2016). An increase in beta diversity in response to stress may indicate a destabilized microbiome in mammals (Moeller et al., 2013; Zaneveld et al., 2017) with the host being unable to regulate its microbiome. In corals, both temperature extremes and contact with macroalgae were shown to increase microbiome beta diversity (Zaneveld et al., 2016). Similarly, microbiome composition in shallow polluted sites was more variable from coral to coral than at the control sites (Klaus et al., 2007). Changes in salinity also impacted community evenness. For example it was found that the microbiome of hypersaline-treated corals shifted from a community dominated by a single OTU (*Rhodobacteraceae*) to a more even one in which *Pseudomonas veronii* was the most abundant taxon (Röthig et al., 2016).

Overfishing on reefs can lead to reduced grazing pressure, by decreasing herbivorous fish abundance, and increasing competition between corals and macroalgae for space (Morrow et al., 2013). Macroalgae are hypothesized to outcompete



corals via a variety of mechanisms including alterations to the microbiome (Smith et al., 2006; Morrow et al., 2012b), faster growth rates, shading, allelopathic interactions (Rasher and Hay, 2010), and abrasion and preventing coral recruitment (Jompa and McCook, 2003). For example, macroalgal contact with the coral *Porites astreoides* caused multiple changes in the coral microbiome including increased dispersion (i.e., beta diversity), disappearance of a potentially mutualistic *Gammaproteobacteria*, changes in abundance for taxa already present, establishment of new taxa, and growth of algae-associated microbes within the coral (Vega Thurber et al., 2012). Macroalgal contact has also been shown to shift the coral microbiome to become more similar to the macroalgal microbiome (Morrow et al., 2013).

A counter example to the overall trend of stress-induced community shifts is provided by a study on *A. millepora* and *Seriatozona hystrix* microbiomes, which demonstrated stability in microbiome composition in the face of both lowered pH

and increased temperatures. While *S. hystrix*'s microbiome did show some variability, the overarching conclusion was that corals demonstrated a more stable and robust microbiome compared to other key calcifying reef taxa such as foraminifera and crustose coralline algae (Webster et al., 2016).

Stressors Decrease the Abundance of the Proposed Bacterial Symbiont, *Endozoicomonas*

The studies we synthesized consistently found that the bacterial order, *Oceanospirillales*, especially the genus *Endozoicomonas*, was underrepresented in corals during stress events, particularly during climate anomalies (Figure 3). This may be problematic for corals as *Endozoicomonas* is a proposed beneficial symbiont to corals. Two studies used CARD-FISH and FISH probes, respectively, to reveal that *Endozoicomonas* was located deep

TABLE 3 | Changes in microbiome alpha diversity or richness due to stress from climate change, water pollution and overfishing (+, higher diversity; –, lower diversity; 0, no difference).

Stressor	Summary of findings	Coral species	Lab or field?	Overall	References
CLIMATE CHANGE					
Thermal Stress	Higher diversity (Shannon) within a coral colony during bleaching compared to pre- and post-bleaching	<i>Acropora millepora</i>	Field	+	Bourne et al., 2007
	Diazotroph diversity (Chao1, Shannon) and richness significantly increased 3-fold with +2.5° and +4°C increases	<i>Mussismilia harttii</i>	Lab	+	Santos et al., 2014
	Diversity (Chao1) was significantly higher under heat stress (31°C)	<i>Pocillopora damicornis</i>	Lab	+	Tout et al., 2015
	<i>G. ventalina</i> microbial diversity (Shannon) was significantly lower during the warming event comparing to pre-warming, <i>O. faveolata</i> was not significantly different to pre-warming	<i>Gorgonia ventalina, Orbicella faveolata</i>	Field	–0	Tracy et al., 2015
	Richness and diversity (Chao1, Simpson) increased with increasing temperatures	<i>Acropora muricata</i>	Lab	+	Lee et al., 2016
	Alpha diversity (Chao1, Inverse Simpson) decreased but richness stayed the same (32°C)	<i>Acropora digitifera</i>	Lab	–0	Gajigan et al., 2017
Ocean Acidification	Increase in alpha diversity (Shannon) at lower pH	<i>Acropora eurystoma</i>	Lab	+	Meron et al., 2011
	No significant changes except alpha diversity (Shannon) significantly decreased in <i>C. caespitosa</i> skeleton	<i>Cladocora caespitose, Balanophyllia europaea</i>	Field	– 0,0,0	Meron et al., 2012
	<i>P. cylindrica</i> had lower alpha diversity (Shannon, Chao1) at low pH while <i>A. millepora</i> showed no significant change	<i>Porites cylindrica, Acropora millepora</i>	Lab	–,0	Morrow et al., 2015
WATER POLLUTION					
Proximity to Humans	<i>P. astreoides</i> and <i>M. faveolata</i> had higher diversity (Shannon) at sites closer to shore (i.e., < 5km)	<i>Porites astreoides, Montastrea faveolata</i>	Field	+,+	Morrow et al., 2012a
	Alpha diversity (Chao1, Shannon, Simpson) and richness in <i>A. hemprichii</i> was significantly higher at sites impacted by sedimentation and sewage, <i>P. verrucosa</i> showed no significant difference. Both showed no significant difference at wastewater outfall	<i>Acropora hemprichii, Pocillopora verrucosa</i>	Field	+,0,0,0	Ziegler et al., 2016
High Salinity	Corals within the long-term salinity treatment increased in microbial diversity 3-fold (Chao1) and 10-fold (Inverse Simpson)	<i>Fungia granulosa</i>	Lab	+	Röthig et al., 2016
Oil Pollution	The number of bands increased after microcosm experiments exposed corals to 1 ml and 20 ul of crude oil	<i>Porites compressa, Acropora clathrata</i>	Field	+	Al-Dahash and Mahmoud, 2013
WATER POLLUTION AND OVERFISHING					
Eutrophication and Herbivore Exclusion	Diversity (Inverse Simpson, Chao1) increased over time in all stress treatments: herbivore exclusion, nutrient enrichment and herbivore exclusion * nutrient enrichment	<i>Acropora hemprichii</i>	Field	+,+,+	Jessen et al., 2013
OVERFISHING					
Macroalgae Contact	Richness increased next to all algae, and Chao1 was significantly higher in all treatments (i.e., corals touching <i>Dictyota menstrualis, Galaxaura obtusata, Halimeda tuna, Lobophora variegata, Sargassum polyceratum</i>)	<i>Porites astreoides</i>	Field	+,+,+,+,+	Vega Thurber et al., 2012
	Diversity (Shannon) increased next to CCA and <i>Dictyota bartayresiana</i> ; Decreased next to <i>Halimeda opuntia</i> and turf algae	<i>Montastraea annularis</i>	Field	+, +, –, –	Barott et al., 2012

(Continued)

TABLE 3 | Continued

Stressor	Summary of findings	Coral species	Lab or field?	Overall	References
	Diversity (Shannon) was lower but not significantly different in coral fragments exposed to extracts from <i>Lobophora</i> sp.	<i>Porites cylindrica</i>	Lab	0	Morrow et al., 2017
OVERFISHING, POLLUTION, CLIMATE CHANGE					
Thermal Stress, Nutrients, Macroalgae Contact	Richness increased next to algae	<i>Siderastrea siderea</i> , <i>Porites</i> sp., <i>Agaricia</i> sp.	Field	+	Zaneveld et al., 2016

within the coral tissues, suggesting an intimate association with coral hosts (Bayer et al., 2013; Neave et al., 2016). Additionally, the first cultivable *Endozoicomonas* from corals suggests *Endozoicomonas montiporae* CL-33 helps corals under stress through preventing mitochondrial dysfunction and promoting gluconeogenesis (Ding et al., 2016). Additionally, researchers have proposed that *Endozoicomonas* plays a role in sulfur cycling (Raina et al., 2009), nutritional symbiosis (La Rivière et al., 2013) and protecting *Symbiodinium* from bleaching pathogens (Pantos et al., 2015). By comparing cultured and culture-independent genomes of *Endozoicomonas*, researchers demonstrated that *Endozoicomonas* likely plays a role in protein and carbohydrate transport for the host and may have diversified and adapted with their hosts (Neave et al., 2017). However, they also demonstrated that *Endozoicomonas* has a large genome, suggesting it has a free-living stage. Not only might the observed decrease in these potentially symbiotic taxa during stress events threaten coral resistance to stress, it also may influence coral resilience after the stress is alleviated if *Endozoicomonas* does not return to its original abundance and function. In a study of volcanic CO₂ seeps where the seawater has naturally reduced pH, researchers found that *Acropora millepora* and *Porites cylindrica* contained significantly different microbial communities compared to the same coral species at a control site (>500 m away); for *A. millepora* this was mainly due to a 50% decrease of this proposed mutualist *Endozoicomonas* (Morrow et al., 2015). These coral species were also less abundant at the volcanic seeps, potentially due to this loss of symbiont in their microbiomes. In a separate study, *Endozoicomonas* was significantly reduced at low pH in *A. millepora* showing that this stressor can cause loss of these symbionts (Webster et al., 2016). Other symbiotic taxa in addition to *Endozoicomonas* are likely to decline as well under stress. At anthropogenic impacted reefs (i.e., close to metropolitan cities), the main coral symbiotic taxon in *Pocillopora verrucosa* (*Endozoicomonaceae*) and *A. hemprichii* (*Alteromonadales*) declined in relative abundance (Ziegler et al., 2016).

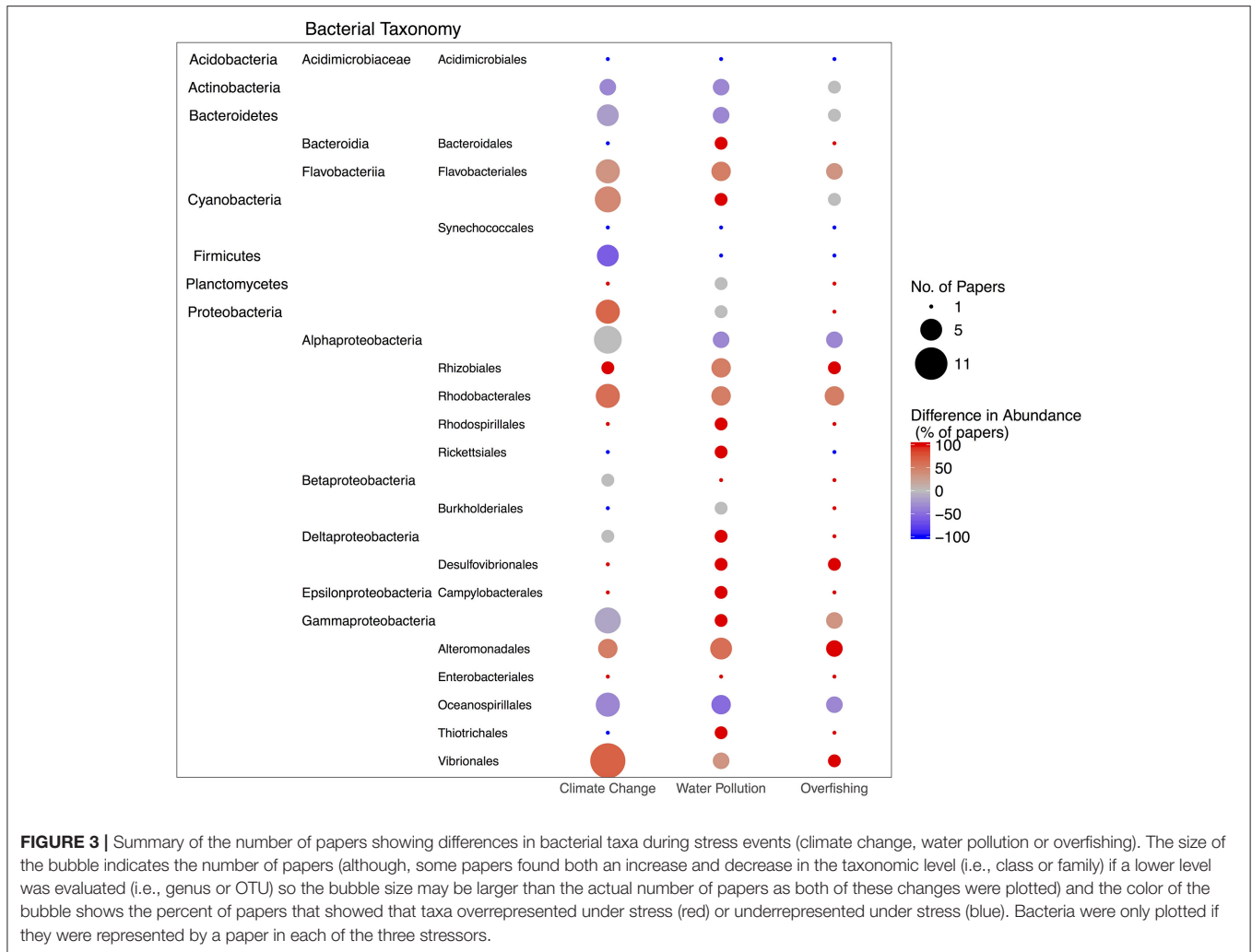
Stressors Increase Opportunistic and Pathogenic Bacterial Taxa in the Coral Microbiome

Stressed corals may have a reduced ability to regulate their microbiomes and thus have reciprocal increases in potentially pathogenic and opportunistic microbial taxa (Figure 3). The overrepresented taxa during all three types

of stressor we evaluated were: *Vibrionales*, *Flavobacteriales*, *Rhodobacterales*, *Alteromonadales*, *Rhizobiales*, *Rhodospirillales*, and *Desulfovibrionales* (Figure 3). The Order *Rhodobacterales*, for example, are fast growing opportunistic bacteria (Teeling et al., 2012) that have been found in both healthy and stressed corals (Meron et al., 2011; Sharp et al., 2012), potentially blooming under periods of stress when there is open niche space (Welsh et al., 2015). OTUs within the Order *Flavobacteriales* were shown to make up a large percentage of white band disease associated OTUs (Gignoux-Wolfsohn and Vollmer, 2015). Thus, these potentially pathogenic, opportunistic taxa may flourish when the coral is stressed and cannot regulate its microbiome.

In comparison, a meta-analysis of 16S sequences from 32 papers, showed that the microbiome of bleached corals differed from that of healthy corals primarily in having a higher proportion of two specific taxa: *Vibrionas* and *Acidobacterias* (Mouchka et al., 2010). An increase in *Vibrionales* under climate change stress is unsurprising as the cultivable *Vibrio* strain AK-1 was shown to induce coral bleaching (Kushmaro et al., 1998) (albeit the coral, *Oculina patagonica*, may have developed resistance to this bacteria; Mills et al., 2013) and *Vibrionales* are a common taxa to increase under conditions of thermal stress (Bourne et al., 2007; Frydenborg et al., 2013; Tout et al., 2015). Importantly, the coral microbiome may have a temperature tolerance threshold, as it was found that bacterial community structure only changes after an elevation of temperature greater than 1°C; all exposures at temperatures lower than this threshold showed no evidence of community alterations (Salerno et al., 2011). Thus, coral microbiomes may buffer thermal anomalies within that lower temperature range.

Bleached corals also exhibit different bacterial communities than “healthy” corals (Koren and Rosenberg, 2008). For example, during a bleaching event in Australia, the coral microbiome showed an increase in genes associated with virulence factors (Littman et al., 2011). Correspondingly, during heat stress experiments, the known pathogen *V. coralliilyticus* increased in abundance by four orders of magnitude (Tout et al., 2015). One likely mechanism for these observed changes are strong competition between native commensals and pathogenic bacteria (i.e., *V. shiloi* and *V. coralliilyticus*) on corals, with temperature stress mediating the growth of the foreigners. This has been supported by work within *Acropora palmata*, where high temperatures tend to select for pathogens in the coral microbiome (Frydenborg et al., 2013). Increased temperatures also correlated with increased expression of virulence genes (Banin et al., 2003), lysis of coral cells (Ben-Haim et al., 2003),



and infection (Kushmaro et al., 1998; Ben-Haim and Rosenburg, 2002) by coral pathogenic bacteria. However, *Porites lobata* has been found to have a relatively stable microbiome between bleached and healthy colonies, suggesting its mucus microbiome plays a protective role within bleached corals (Hadaidi et al., 2017).

Furthermore, increased *Vibrio* and other taxa occur prior to visual bleaching signs (Bourne et al., 2007; Lee et al., 2016), suggesting some predictable changes in the bacterial community could forewarn which corals may bleach. The abundance of Vibrionales within the microbiome may also be regulated by factors other than temperature, including what strain of *Symbiodinium* is hosted by the coral (Littman et al., 2010).

Importantly, the increases in potentially pathogenic or opportunistic taxa found in our analysis (Figure 3) may be due to a variety of mechanisms such as the induction of temperature sensitive virulence cassettes found in pathogens, enhanced growth rates under higher temperatures, or altered microbial-host signals during stress. Thermally stressed corals often increase production of the

metabolites like dimethylsulphoniopropionate (DMSP), which is normally exuded by corals (Raina et al., 2013) and their symbionts (Steinke et al., 2011). It is hypothesized that DMSP is used as a chemoattractant by bacterial pathogens to locate thermally stressed corals (Garren et al., 2014).

While in most cases stressors altered coral microbial community structure, shifts do not always occur. For example, *O. faveolata*'s microbiome did not significantly shift when the host bleached (Tracy et al., 2015). Furthermore, coral-associated microbial communities did not undergo major shifts when transplanted to a natural lower pH environment and did not harbor microbial pathogens (Meron et al., 2012). This study (Meron et al., 2012), suggests that for these two coral species (i.e., *Balanophyllia europaea* and *Cladocora caespitosa*), reduced pH does not pose a significant threat to coral health. Importantly, environmental conditions can buffer these microbiome changes, specifically with high water flow buffering coral microbiome changes under high temperatures (Lee et al., 2017).

Climate Change, Water Pollution and Overfishing Increase Disease Associated Bacteria

In addition to community structure changes, stressors can also increase disease on coral reefs (Brandt et al., 2013; Vega Thurber et al., 2013). For example, exposure of corals to lower pH resulted in microbiome communities reminiscent of those associated with diseased and stressed corals as they contained more *Vibrionaceae* and *Altermonadaceae* (Vega Thurber et al., 2009; Meron et al., 2011). Additionally, reduced pH significantly changed the microbial communities in *A. millepora* with the loss of *Proteobacteria* sequences typically associated with healthy corals while *Gammaproteobacteria*, which are often associated with diseased and stressed corals, increased (Webster et al., 2012).

Given that coral reefs occur in oligotrophic environments, added nutrients can dramatically influence ecosystem functioning and alter microbial communities in ways that appear to favor disease. In Florida, human sewage supplied a strain of *Serratia marcescens* (a common fecal enterobacterium) into reef water and corallivorous snails acted as a vector, therefore inducing white-pox like diseases in *Acropora palmata*, *Siderastrea siderea*, and *Solenastrea bournoni* (Sutherland et al., 2010). Furthermore, the addition of glucose or inorganic nutrients improved the survival of *S. marcescens* in *A. palmata* (Looney et al., 2010). Under this water pollution stress, as with thermal stress (Littman et al., 2011), the microbial communities shifted toward a higher prevalence of heterotrophic bacteria relative to autotrophic bacteria (Dinsdale et al., 2008). Microbiome taxa in polluted sites can be more pathogenic, as demonstrated by a study in which exposure to pollutants increased coral mortality except when antibiotics were added, suggesting a bacterially mediated cause of death (Mitchell and Chet, 1975). As the proximity and size of human populations increases adjacent to coral reefs, so does the likelihood of land-based runoff, and evidence continues to demonstrate that corals living closer to shore have higher abundances of disease-related bacteria (Morrow et al., 2012a), and coral disease correlates with poor water quality and high nutrient levels (Furby et al., 2014). Nevertheless, the coral microbiome also demonstrates resilience against water pollution, when coral fragments were transplanted under eutrophic aquaculture pens, the coral microbiome shifted toward known pathogens but then showed no physical signs of disease and after 22 days the communities shifted back to their original state (Garren et al., 2009).

Overfishing may alter coral microbiomes indirectly, with decreases in herbivorous fish populations being one means by which algal growth can be facilitated at the expense of corals. For example, overfishing in Jamaica, in concert with warming and hurricanes, caused coral cover to decrease from 50 to 5% and an increase to 90% macroalgae cover (Hughes, 1994). Shifts to an algae dominated state can influence the coral microbiome by changing the water column microbial composition, increasing algal interactions (Morrow et al., 2013) and triggering coral disease (Nugues et al., 2004). Increased coral interactions with turf algae have been associated with an increase in pathogens and virulence genes (Barott et al., 2011). These authors also

proposed that fleshy algae can alter reefs by increasing both bacterial respiration and pathogenic invasion (Barott et al., 2012). Moreover, algae may act as reservoirs for coral pathogens (Sweet et al., 2013) and thus enhance disease events. Algae harbor distinctly different microbial communities than corals (Barott et al., 2011; Vega Thurber et al., 2012) and produce more carbon exudate that can stimulate heterotrophic microbial growth in reef waters (Haas et al., 2011). Algae also produce dissolved organic matter (DOM) that is enriched in dissolved neutral sugars (DNS). These sugars can spur the growth of fast-growing bacteria in the water column, the result of which is a community with less bacterial diversity and dominated by copiotrophic bacteria like *Vibrionaceae* and *Pseudoaltermonadaceae* that typically carry virulence factors (Nelson et al., 2013). Conversely, corals exude DOM that selects for high bacterial diversity in the water column dominated by *Alphaproteobacteria* and few representatives with virulence factors (e.g., *Hyphomonadaceae* and *Erythrobacteraceae*) (Nelson et al., 2013). Other stressors in addition to climate change can also increase virulence sequences, for example increased nutrients, DOC, temperature or pH can all increase the abundance of virulence genes in the coral holobiont (Vega Thurber et al., 2009).

Overfishing also alters fish populations and induces trophic cascades (Jackson et al., 2001), and changes in fish functional roles can influence the reef-associated microbial communities. For example, within the territory of the damselfishes, *Stegastes apicalis* and *S. nigricans*, there were 2–3-fold increases in coral pathogens in the microbiome and a higher prevalence of corals with signs of black band disease. These *Stegastes* species normally exclude macroalgae and cultivate filamentous algae, thus providing a trophic link among fish behavior, coral pathogen reservoirs and coral disease (Casey et al., 2014). Other fishes (i.e., *Chaetodontidae*) may also act directly as disease vectors (Raymundo et al., 2009), however, functionally diverse fish communities have been suggested to alleviate coral disease (Raymundo et al., 2009) and five *Chaetodontidae* and one *Labridae* species actually slowed the progression of blackband disease (Cole et al., 2009). Furthermore, damage to corals from abandoned fishing lines, is correlated with a 4-fold increase in coral disease and thus can somewhat explain the reduction in coral disease prevalence between marine reserve and non-reserve areas (Lamb et al., 2015).

Biases within the Available Data

There are several caveats associated with the data synthesized here, specifically evaluating changes in bacterial composition from disparate studies. These biases stem from uneven sequence library sizes, the use of different primer sets, low DNA amplification, and most importantly the use of different methods for assessment of microbiome response (e.g., culturing, 16S amplicons, metagenomes). Researchers in microbiology use a wide array of methodologies, which can make it difficult to compare studies quantitatively. At the same time, studies often reported only bacterial composition through relative abundance measures, and are therefore not directly quantifying bacterial cells within the coral microbiome. For example, if a study

measures a decrease in a bacterial taxon, that taxon could be staying in consistent quantity while all other members of the microbiome are increasing. Thus, it is important to remember these biases when inferring from these data and keep in mind they are a broad qualitative overview of what happens to the coral microbiome under stress.

EVIDENCE THAT CORAL MICROBIOMES MEDIATE HOST RESISTANCE TO STRESSORS

Some of the strongest evidence in support of the hypothesis that coral microbes provide their hosts with resilience or resistance to stressors comes from studies using antibiotics. For example, antibiotic treatment of thermally stressed corals caused tissue loss, significant declines in photosynthetic efficiency (Gilbert et al., 2012) and increased coral susceptibility to *Vibrio shiloi* infection and bleaching (Mills et al., 2013; although see Bellantuono et al., 2012). Furthermore, when corals were subjected to antibiotics and subsequently transplanted back onto the reef, those corals bleached and eventually died compared with the control corals that did not receive antibiotics (Glasl et al., 2016).

Early investigations into the role of DSMP cycling suggest that the coral microbiome likely plays an important role in coral resistance to stress. Coral-associated bacteria implicated in sulfur cycling (e.g., *Endozoicomonas*, *Halomonas*) (Raina et al., 2009; Todd et al., 2010) may help corals acclimate to climate change by protecting *Symbiodinium* from photosynthesis derived oxidative stress, as sulfur compounds such as DMSP and its breakdown products can act as antioxidants for marine algae (Sunda et al., 2002). As such, in bleaching corals, it was shown that there is a strong negative correlation between the abundance of bacterial pathogens and the abundance of the proposed symbiont *Endozoicomonas* (Pantos et al., 2015).

Nitrogen fixation and regulation by coral microbiome residents may also play an important role in coral resistance to stress. *Symbiodinium* depend on nitrogen for growth (Béraud et al., 2013), diazotroph abundance increases with higher seawater temperatures (Santos et al., 2014), and nitrogen fixation within corals increases with higher temperatures (Cardini et al., 2016). However, the mechanism behind and outcome of this relationship remains an active area of research. For example, it was recently suggested that these bacterial diazotrophs may in fact harm corals during heat stress by increasing the N:P ratio within the cells, causing a destabilization of the host-*Symbiodinium* partnership and thus inducing or prolonging holobiont bleaching events above normal levels (Rädecker et al., 2015). Yet diazotrophs still may play an important role in buffering the coral holobiont under water pollution stress by fixing nitrogen. In eutrophication experiments, nitrogen fixing and denitrifying bacteria increased in abundance in the coral *Acropora hemprichii*, but there were no significant changes to holobiont physiology (Jessen et al., 2013).

Finally, coral-associated bacteria may support coral resistance to algal growth simulated by overfishing given that resident

bacteria defend the coral from microbial invasions (Rypien et al., 2010; Shnit-Orland et al., 2012; Welsh et al., 2016), thus potentially providing protection from algae altering the coral microbiome (Vega Thurber et al., 2012). There are clearly multiple mechanisms that influence these microbial roles and, as demonstrated above, a conflicting base of evidence. Recent research further supports the hypothesis that the microbiome plays a role in coral resistance, with coral microbiomes adapting to environmental conditions during reciprocal transplants and microbiomes that were previously exposed to a more variable and warmer environment having higher resistance during heat stress experiments (Ziegler et al., 2017). Clarity into these dynamics will likely grow as evidence increases and we suggest that these are key research topics to better understand the roles played by microbes in coral resistance to stress.

CONCLUSIONS AND FUTURE DIRECTIONS

Our understanding of how the coral microbiome contributes to reef health is rapidly evolving, with the studies synthesized herein providing insight into how microbial communities respond to environmental change and hypotheses regarding the potential mechanisms underlying microbial support of coral resistance to stress. When stressors induce changes in coral-associated bacterial communities their beneficial functions to the coral holobiont can be lost. Thus, the composition of the coral microbiome could help to inform resource managers about which corals are most likely to successfully resist stressors, but this information has not yet been compiled. However, our results suggest that stressed corals have more taxonomically diverse microbiomes and increased beta diversity between coral colonies, potentially due to the stressed corals' inability to regulate incoming microbial members. At the same time, in stressed corals the opportunistic bacterial taxa *Flavobacteriales*, *Rhodobacterales* and *Vibrionales* are generally overrepresented, while the proposed coral symbiont, *Endozoicomonas* and related species, is underrepresented. Our results suggest metrics of microbiome diversity should be further investigated, especially beta diversity dispersion, which has only recently been applied to coral microbiome studies as a measure of microbiome stability between coral colonies (Zaneveld et al., 2016). Researchers should also utilize metrics of phylogenetic diversity through metrics like Faith's phylogenetic diversity, mean pairwise distance, and variation of pairwise distance (Tucker et al., 2017) to better understand the coral microbiome. In the future, resource managers may be able to identify stressed corals by the presence of opportunistic microbe taxa (Pollock et al., 2011) and by increased microbiome alpha and beta diversity, even if the coral has not yet shown physical signs of stress or deterioration.

To assist these trajectories, researchers need a better understanding of coral microbiome variability (e.g., temporal, spatial, seasonal, coral host species), to assemble databases of the microbiomes during different coral states (i.e., what is the normal microbiome for a coral species?), and determine the function of these bacteria for the coral host. With climate

projections predicting that future conditions will increase disease susceptibility, pathogen abundance and virulence on coral reefs (Maynard et al., 2015) and diverging predicted responses of marine microbes to anthropogenic change (Hutchins and Fu, 2017), it is critical that researchers continue to advance understanding of the relationships between corals and their microbiomes, and how these change under stress. Promisingly, ongoing research suggests that we may have the ability to increase coral adaptation to these stressors by modifying the coral-associated microbial community (van Oppen et al., 2015) or by using coral probiotics (Krediet et al., 2013). This review and an ever-growing body of evidence suggest that conservationists may be able to screen for corals with resilient microbiomes to determine where best to focus management priorities as threats to coral reefs continue to accumulate.

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AUTHOR CONTRIBUTIONS

JMI wrote the first draft of the manuscript, synthesized the papers, and created the figures. All authors contributed to the writing and revisions of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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