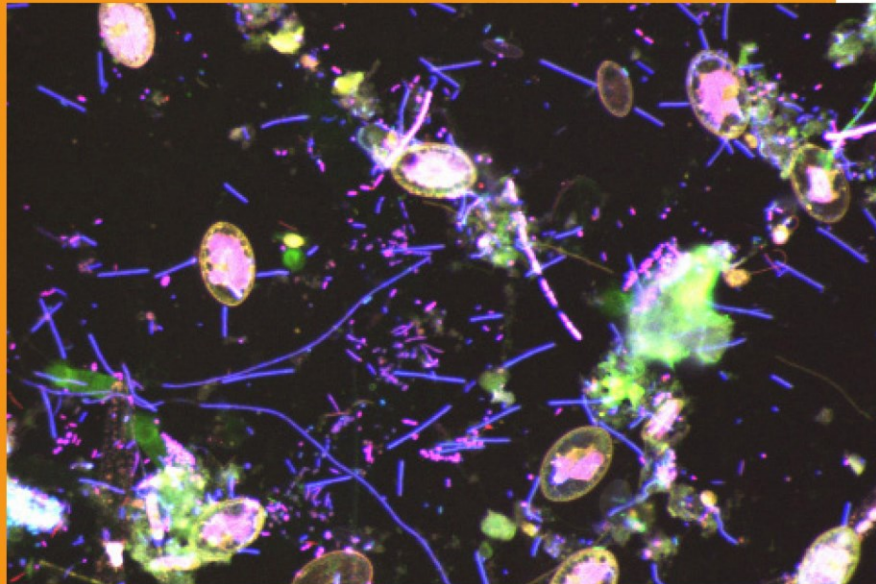

Monitoring additional values within the Reef 2050 Integrated Monitoring and Reporting Program:

Final Report of the Microbes Expert Group



Nicole Webster and Hayley Gorsuch

AIMS: Australia's tropical marine research agency

The Great Barrier Reef Marine Park Authority acknowledges the continuing sea country management and custodianship of the Great Barrier Reef by Aboriginal and Torres Strait Islander Traditional Owners whose rich cultures, heritage values, enduring connections and shared efforts protect the Reef for future generations.

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1.0 Executive Summary

Coral reefs are increasingly affected by localised impacts such as declining water quality and global pressures resulting from human-induced climate change, which severely alters the natural conditions on reefs and can push dominating benthic life forms towards the limit of their resistance and resilience.

Microorganisms play a fundamental role in the functioning and stability of coral reef ecosystems. However, environmental disturbance can trigger alterations to the composition and function of coral reef microbes, with detrimental consequences for biogeochemical cycling and the functioning of the entire coral reef ecosystem. In addition, environmental stress can alter the associated microbiome of reef organisms such as corals, disrupting the holobiont equilibrium, shifting defensive mechanisms and nutrient cycling pathways that contribute to bleaching and disease. Coral reef microorganisms can buffer or exacerbate cumulative impacts via their role in holobiont fitness as well as by modifying energy flow within the ecosystem and are therefore central to reef resilience.

Microorganisms respond very rapidly to altered environmental conditions so defining their natural variability over spatial and temporal scales is valuable for early and accurate identification of environmental disturbances. The rapid diagnostic response of microbes to environmental change is likely to confer significant advantages over traditional reef monitoring methods, which are based on visual signs of health deterioration in benthic coral reef macroorganisms.

This report outlines the functional roles microorganisms play on coral reefs, discusses the potential of microbes as early warning indicators for environmental stress and coral reef health; proposes recommendations and priorities for future research to address key knowledge gaps; and provides recommendations for incorporating microorganisms into existing monitoring programs for the Great Barrier Reef (the Reef).

2.0 Introduction

Marine microbes constitute the bulk of ocean biomass and perform the majority of oceanic photosynthesis, meaning that they directly control energy and material inputs into the marine food-web, which subsequently drives marine productivity and fishery yields (Azam et al., 1983). By performing the key chemical transformations within the ocean's major biogeochemical cycles (carbon, nitrogen, sulphur and phosphate), marine microbes also strongly mediate the ocean-atmosphere exchange of climatically important gases, which ultimately controls the global climate (Falkowski et al., 2008). However, despite their fundamental importance in the global ocean, we currently lack a basic mechanistic understanding of microbial dynamics in Australian waters, particularly for the Reef.

Within coral reefs, microbes play essential roles in a broad range of ecosystem processes. For example, their small size and fast reproduction rate make them very efficient at cycling nutrients, metabolising foreign compounds and colonising new ecological niches (Thurber et al., 2009). The bacterial communities in reef seawater, sediment, and benthic organisms are intricately linked, contributing to the tight benthic-pelagic coupling that occurs in shallow, well-mixed tropical coral reefs (Garren and Azam, 2012a). For example, particle export which can be mediated by benthic organisms such as corals sloughing large amounts of mucus, increases ecosystem productivity as it settles onto coral reef sediments or is consumed by other reef organisms thereby recycling essential nutrients back into the reef system (Wild et al., 2004). Nutrients that enter warm well-lit tropical waters are also rapidly assimilated by microorganisms and used in the synthesis of organic matter, much of which circulates as detritus and is further colonised by bacteria and other microorganisms. This organic matter is accessible to a variety of other reef organisms in the water column and benthos as a food resource (Figure 1).

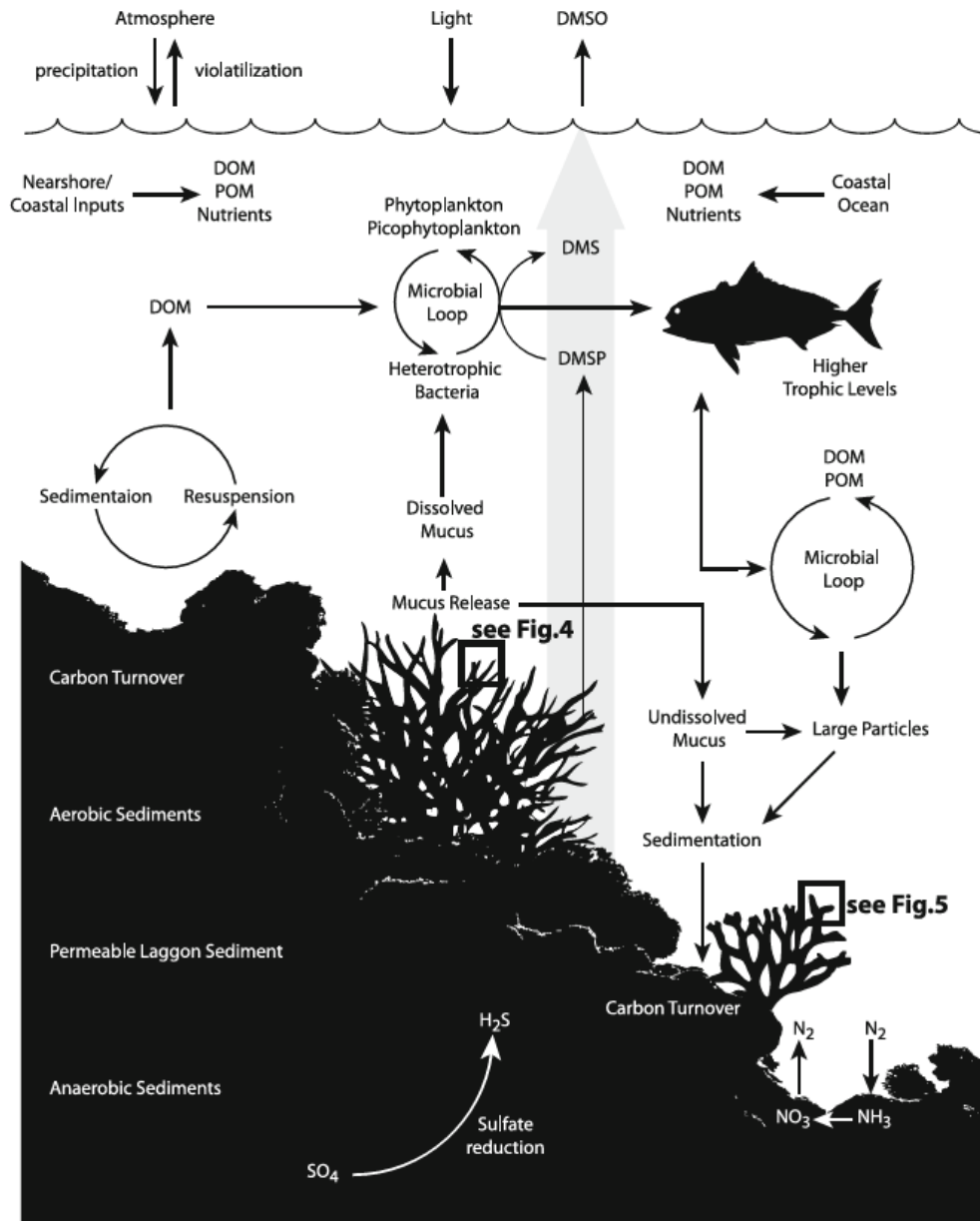


Figure 1: Simplified schematic of microbial processes on coral reefs. Coral reefs capture and recycle nutrients allowing highly productive ecosystems to thrive in relatively nutrient poor waters (reproduced from (Bourne and Webster, 2013)). Much of this productivity is driven by microbial communities that intricately couple pelagic and benthic processes. Microorganisms associated with reef benthos also contribute to their host's nutrition, waste product removal, pathogen defence and holobiont stability.

Microorganisms also form diverse symbiotic relationships with coral reef organisms, such as corals, macroalgae and sponges, for which they provide a range of functions (Figure 2). Many of the purported interactions involve cycling of essential nutrients such as carbon, nitrogen, sulphur and phosphate in addition to essential passage of trace metals, vitamins and other

cofactors. However, although the proposed symbiotic functions are extensive, examples of specific microbial symbionts being unequivocally assigned functional roles are rare. Most reef microbial symbionts are so far recalcitrant to cultivation, and the lack of a tractable host cellular assay or axenic models for experimental manipulation are major constraints to unequivocally linking microbial symbiont identity and function.

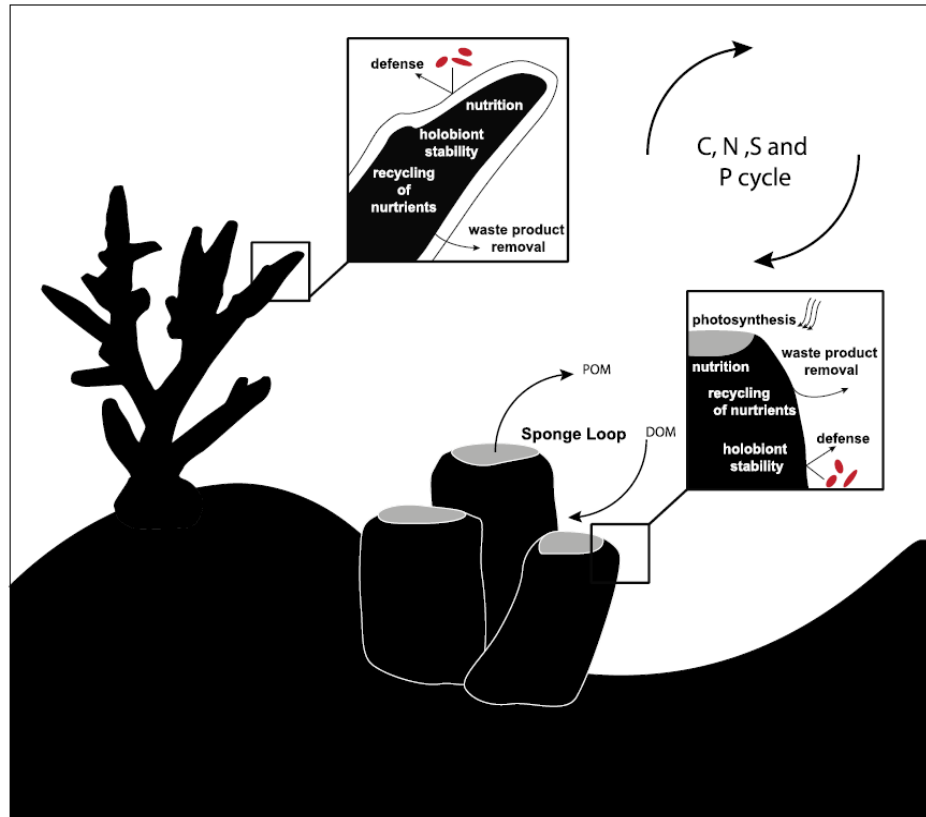


Figure 2. Simplified overview of microbial functions in reef invertebrates Microbes cycle essential nutrients that contribute to their host’s nutrition, remove waste products, contribute to pathogen defence and maintain holobiont stability (Glasl et al., 2018).

Microbial biofilms (particularly microorganisms associated with CCA) are also important as settlement cues for a variety of reef invertebrates, including corals and sponges (Negri et al., 2001, Webster et al., 2004, Webster et al., 2011, Whalan and Webster, 2014). Biofilms comprise communities of microorganisms, in addition to a matrix of extracellular polymeric compounds, which can induce larval settlement (Qian et al., 2007). Importantly, there are clear patterns of community succession in the composition of biofilms with bacteria being initial colonisers (Qian et al., 2007). For marine invertebrate larval settlement, both the age of biofilmed surfaces and the composition of the biofilm community contributes to

settlement success (Keough and Raimondi, 1995). Importantly, biofilm community composition can change when exposed to variable environmental conditions (Witt et al., 2011, Lau et al., 2005, Webster et al., 2013a, Webster et al., 2013b) with potential concomitant effects on larval settlement (Webster et al., 2013b, Qian et al., 2003). However, currently we have a very limited understanding of how larval settlement is influenced by the environmental conditions that biofilms are established at.

Microorganisms are the first responders to natural or man-made changes (including e.g. climate change, nutrient enrichment, waste discharge, oil spills) to the marine environment, and can therefore act as early warning indicators of changes in the health of ocean ecosystems. Their activities can also either augment or buffer the negative influences of human and natural impacts (Atlas and Hazen, 2011). However, due to the vast diversity of microbes and their associated metabolic processes, we cannot yet accurately estimate the net effect of microbial activity in most parts of the ocean, nor predict their response to environmental change (Ducklow and Doney, 2013). Environmental changes often cause compositional and functional shifts in microbial communities that can have flow-on consequences for microbial-mediated processes. These microbial alterations may impact the health of specific host organisms and can have repercussions for the functioning of entire coral ecosystems (Glasl et al., 2018). Disturbance-related deviations from the naturally occurring microbial communities can therefore provide useful indicators for coral reef ecosystem stability and facilitate sensitive predictions of environmental stress (Figure 3). As microbes are a widespread and diverse group of organisms, they have the potential to inform and integrate with monitoring within all other Reef 2050 Integrated Monitoring and Reporting Program (RIMReP) Program Design thematic areas.

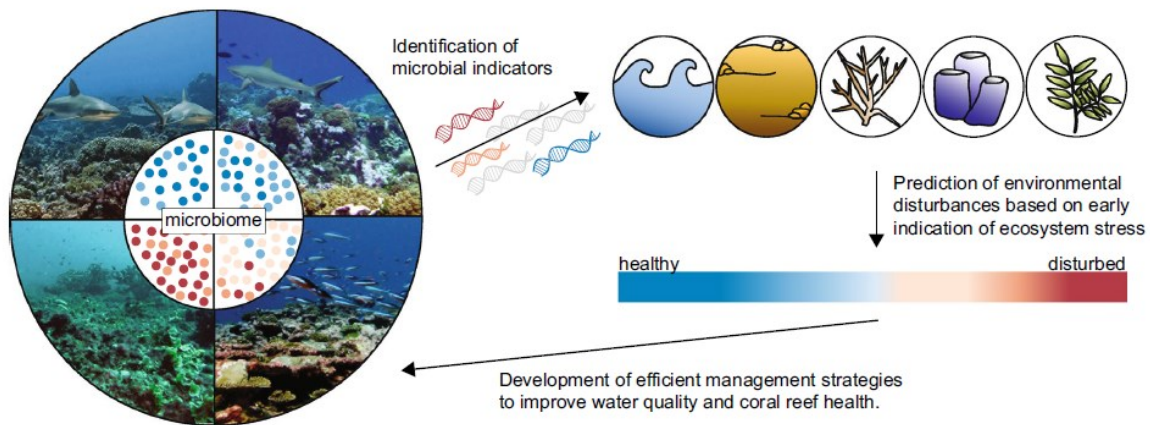


Figure 3. Microbial indicator approach to assess coral reef health (Reproduced from Glasl et al., 2017). Coral reefs are exposed to increased environmental pressures which facilitates a shift from coral to algae dominated reef systems. Accompanying the increase in environmental pressures, microbial community composition and function changes along the gradient of disturbance from a beneficial and commensal microbiome towards microbial communities dominated by opportunists and pathogens. Overall compositional and functional changes of microbial communities associated with seawater, sediment and habitat forming taxa (corals, sponges and macroalgae), but also the occurrence or loss of specific microbial taxa/function, can provide useful indications for the prevailing environmental condition. The application of microbial indicator taxa, function and/or community assemblages will allow for a rapid prediction of environmental disturbance and the health state of a coral reef.

3.0 Microbes in coral reef seawater and sediment

Microorganisms are moderately abundant (average densities of $3 - 9 \times 10^5$ cells ml^{-1}) in nutrient-poor coral reef waters, where they play diverse roles related to nutrient cycling that ultimately affect the entire reef ecosystem (Sorokin, 1973, Ducklow and Carlson, 1992, Gast et al., 1999, Gast et al., 1998). In particular, photoautotrophic phytoplankton (the picophytoplankton) are major contributors to the biomass and primary productivity of oligotrophic reef waters (Stockner, 1988). Generally, *Synechococcus* increase in abundance in more nutrient enriched conditions such as coral reef lagoonal environments (Charpy, 2005), while *Prochlorococcus* dominate the nutrient-depleted areas of the tropical oceans (Campbell et al., 1994). The contribution of these cyanobacteria to primary production is highly dependent on the hydrodynamics and physicochemical parameters of individual reef systems. On the Reef, *Synechococcus* is generally more abundant than *Prochlorococcus* at most inshore and mid-shelf reefs, with populations correlated with salinity, shelf depth, and chlorophyll a concentration rather than nutrient parameters driving the community structure (Ayukai, 1992, Crosbie and Furnas, 2001). Mid- and outer-shelf reefs of the Reef, influenced by oceanic currents, are dominated by populations of *Prochlorococcus* (Crosbie and Furnas, 2001).

A dynamic heterotrophic bacterial community dominates coral reef seawater, stimulated by increased organic matter from mucus and other nutrients released from corals (van Duyl and Gast, 2001, Sakka et al., 2002, Seymour et al., 2005, Torr ton et al., 2007, Tout et al., 2014). Bacterial communities in lagoonal reefs can be more active than bacteria from the open ocean (Rath et al., 1993, Weinbauer et al., 2010) and elevated levels of organic matter and bacteria correlate with phytoplankton biomass (Torr ton et al., 2002). In contrast, in rapidly flushing reefs, dissolved organic carbon and bacterioplankton are depleted relative to offshore waters (Nelson et al., 2011). Bacteria in rapidly flushing reef systems are also efficient scavengers and recyclers of organic matter (Nelson et al., 2011). Phytoplankton and bacterial abundance on reefs can be depleted by filter-feeding members of the benthos such as sponges (Linley and Koop, 1986, Yahel et al., 1998, Gast et al., 1999, van Duyl et al., 2002). Even within a reef, studies have shown that the number of microorganisms in the water column declines from fore reef to back reef (Ayukai, 1995). At smaller scales within the reef complex, removal and depletion of bacterioplankton and DOC is observed in coral reef cavities (Van Duyl et al., 2006, De Goeij and van Duyl, 2007) due to the high coverage of suspension feeders (Coma et al., 2001). However, an increase in bacterial abundance and actively dividing cells is observed close to coral reef surfaces (4 centimetres away). It is likely that this stimulation of bacterial abundance is caused by the diffusion of nutrient-rich mucus into the water column (Tout et al., 2014). Seasonally driven ecosystem events such as coral reproduction or algal blooms can also significantly influence the abundance, diversity, and activity of bacteria in coral reef seawater (Patten et al., 2008, Wild et al., 2008, Aprill and Rappe, 2011).

Bacterial dynamics within coral reef seawater are highly complex and dependent on many factors including (1) hydrodynamics and water residence time (rapid versus slow reef flushing by oceanic waters or nutrient-rich coastal waters), (2) benthic species abundance and diversity (high vs. low abundance of filter-feeding organisms), (3) seasonal events (coral spawning, cyclones), and (4) the scale of investigations (whole reef, within reef or microscale). Seasonal effects, such as temperature, rainfall and water quality also affect microbial community composition in shallow water reef sites (Angly et al., 2016). Integrated comparative models of reef habitats are therefore required to understand the specific parameters which affect the bacterial communities of coral reef water for individual sites (Bourne and Webster, 2013).

Coral reef sediments are typically dominated by calcareous sand, characterised by high permeability, porosity and surface area (Rasheed et al., 2003) which enables large numbers of microorganisms to settle and grow (Wild et al., 2006). Estimates of microbial abundance in coral reefs' sediment are in the order of $1-2 \times 10^9$ cells cm^{-2} (Wild et al., 2006). Reef sediment-associated microbial communities are also highly diverse, with vertical community

stratification caused by redox gradients (Rusch et al., 2009). Oxic surface sediments are often highly heterogeneous, while samples at depth are less so, supporting microscale geochemical gradients driving much of the prokaryote diversity (Gaidos et al., 2011). In Reef sediments, the communities are highly diverse with *Proteobacteria* (Alpha-, Gamma-, Delta-subdivisions), *Cytophaga-Flavobacterium-Bacteroides* (CFB), *Cyanobacteria*, *Planctomycetaceae*, *Verrucomicrobia*, and *Acidobacteriaceae* comprising the most abundant taxa (Uthicke and McGuire, 2007). Uthicke and McGuire also identified clear bacterial community differences in coral reef surface sediments collected from inshore and offshore Reef locations and proposed they be used as biological indicators for water quality (Uthicke and McGuire, 2007).

Microbial communities in coral reef sediments undertake important functional roles such as nitrogen cycling (through N₂ fixation) and the metabolism of organic matter, both of which are subsequently exported to the surrounding reef ecosystem. For example, Casareto and colleagues observed that 28 per cent of reef primary production is supported by endolithic algae within the coral rubble (Casareto et al., 2008) and Shashar and colleagues reported that 70 per cent of nitrogen fixed within sandy reef lagoon sediments gets exported to the surrounding reef (Shashar et al., 1994). Benthic bacterial and archaeal communities involved in aerobic and anaerobic ammonium oxidation (such as the orders *Nitrosomonadales* and *Nitrosopumulis*) were found to dominate the permeable sediments in Kaneohe Bay, Hawaii (Rusch et al., 2009), with the Archaea thought to play a major role in shunting fixed nitrogen away from primary producers toward denitrifiers (Gaidos et al., 2011). However it is difficult to infer functions for reef sediments between different regions or sites as each has distinct biogeochemical parameters which structure and drive the microbial communities.

3.1 Microbes within coral holobionts

At the core of a healthy reef invertebrate is a dynamic relationship with microorganisms, including enduring partnerships with an array of bacterial, archaeal, algal, fungal, protistan, and viral associates, collectively termed the coral holobiont (Rohwer et al., 2002). The coral host itself provides several microhabitats for its microbial associates, such as the surface mucus layer (Frade et al., 2016, Rohwer et al., 2002), the tissue (Bourne and Munn, 2005), the skeleton (Shashar et al., 1997) and the gastrovascular cavity (Herndl and Velimirov, 1985). Each of these microhabitats within a coral colony is associated with a distinct microbial community (Rohwer et al., 2002, Bourne et al., 2016, Sweet et al., 2011).

Bacterial communities associated with corals are clearly distinct from the bacterial communities in the surrounding environment (Frias-Lopez et al., 2002) and bacterial cell abundance within coral mucus is also 10-fold higher than in seawater (Garren and Azam,

2010). Each coral species serves as a unique habitat and is associated with a specific microbial community (Sunagawa et al., 2010), with some species maintaining stable microbiomes over large geographic scales (Rohwer et al., 2002), suggesting that the coral host plays a key role in structuring its bacterial community.

To deal with the enormous diversity of microorganisms associated with corals, and separate beneficial and opportunistic bacteria and archaea from the bulk microbial community, understanding coral holobiont stability and functionality is paramount. For instance, the mucus microbiome of healthy *Porites astreoides* colonies is dominated by *Endozoicomonadaceae*, whose loss is coupled to deterioration in holobiont health (Glasl et al., 2018, Glasl et al., 2016, Glasl et al., 2017, Meyer et al., 2014). *Endozoicomonas* also dominate the microbiome of *Stylophora pistillata* and *Pocillopora verrucosa*, however the *Endozoicomonas* genotypes vary with geography in *S. pistillata*, but remain stable over broad spatial scales in *P. verrucosa* (Neave et al., 2017). Based on meta-analysis of the core microbiomes of diverse coral species, members of *Actinobacteria* have also recently been identified as ubiquitous symbionts of corals (Ainsworth et al., 2015). A decrease in *Actinobacteria* in coral microbiomes during periods of temperature and algal stress further suggests their beneficial role in the coral holobiont (Zaneveld et al., 2016) and their putative utility as a bioindicator of environmental stress. Potential functions of the coral's microbiome vary from nutrient supply and recycling (Lesser et al., 2004, Lesser et al., 2007) to protection against pathogens (Ritchie, 2006, Rohwer et al., 2002, Raina et al., 2016, Shnit-Orland and Kushmaro, 2009). For example, the depletion of the coral's beneficial mucus microbiome affects holobiont health under *in situ* conditions (Glasl et al., 2016), suggesting that major disturbances of the surface mucus microbiome may open a niche for potentially opportunistic and/or pathogenic bacteria, which can further lead to diseases or host mortality.

While the microbiome of corals can persist over space and time (Rohwer et al., 2002), compositional and functional shifts have been observed in association with seasonal environmental variation (Li et al., 2014), host mucus-shedding dynamics (Glasl et al., 2016), thermal stress (for example coral bleaching (Bourne et al., 2008), disease (Sere et al., 2013, Meyer et al., 2014), coral's proximity to macroalgae (Barott et al., 2012, Sweet et al., 2013) and increasing environmental pollution (Garren et al., 2009, Kelly et al., 2014, Ziegler et al., 2016). For example, thermal stress leads to destabilisation of coral-algae interactions (Brown, 1997) and a shift towards an opportunistic and/or pathogenic microbial community (Ainsworth et al., 2008, Bourne et al., 2008, Littman et al., 2011).

Water quality changes associated with increased sediment and nutrient run-off can increase microbial abundance (Dinsdale et al., 2008b, D'Angelo and Wiedenmann, 2014), coral disease frequency (Bruno et al., 2003, Thurber et al., 2014) and higher macroalgal abundance on coral reefs (Kline et al., 2006). Macroalgae exudates stimulate bacterial activity and copiotrophic bacterial growth, and cause shifts in the coral microbiome attributed to increased labile DOC and toxic secondary metabolites (Barott et al., 2012, Morrow et al., 2011, Nelson et al., 2013, Sweet et al., 2013, Thurber et al., 2012, Haas et al., 2016). Environmentally induced changes in the coral microbiome generally result in higher microbial abundance and a shift away from beneficial microbes towards opportunistic and/or pathogenic bacterial taxa, such as *Vibrionaceae* and *Rhodobacteraceae* (Bourne et al., 2016, Thurber et al., 2009, Ziegler et al., 2016, Röthig et al., 2016). Increased nutrient run-off, in combination with reduced grazers (hence higher algal abundance), destabilises the coral microbiome with detrimental consequences for the host, particularly when exposed to additional stressors such as parrotfish bites and thermal stress (Zaneveld et al., 2016). The resulting imbalance in the holobiont composition (dysbiosis) can lead to functional changes of the microbiome and facilitate disease development or alterations in metabolism and/or immunity that lead to bleaching and/or necrosis, and ultimately coral death (Figure 4) (reviewed by (Bourne et al., 2016)).

3.2 Macroalgae and their microbiomes

Macroalgae have always been present in healthy coral reef ecosystems at relatively low abundance (Bruno et al., 2014). However, overfishing and eutrophication can facilitate a shift from coral dominated to algal dominated reefs (Hughes et al., 2007). The increase of macroalgal abundance on coral reefs is a threat for corals, not only because of direct competition for space but also because macroalgae have been shown to facilitate coral disease outbreaks, increase mortality and prevent larval settlement (Nugues et al., 2004, Smith et al., 2006, Sweet et al., 2013, Webster et al., 2015). Furthermore, macroalgae significantly alter their ambient environment by releasing higher amounts of labile dissolved organic carbon (DOC) compared to corals. This elevated DOC supports higher microbial growth rates, leads to a depletion of bioavailable DOC in seawater and facilitates the growth of copiotrophic and potentially pathogenic microbial taxa (Haas et al., 2016) (Nelson et al., 2013, Haas et al., 2016, Haas et al., 2011).

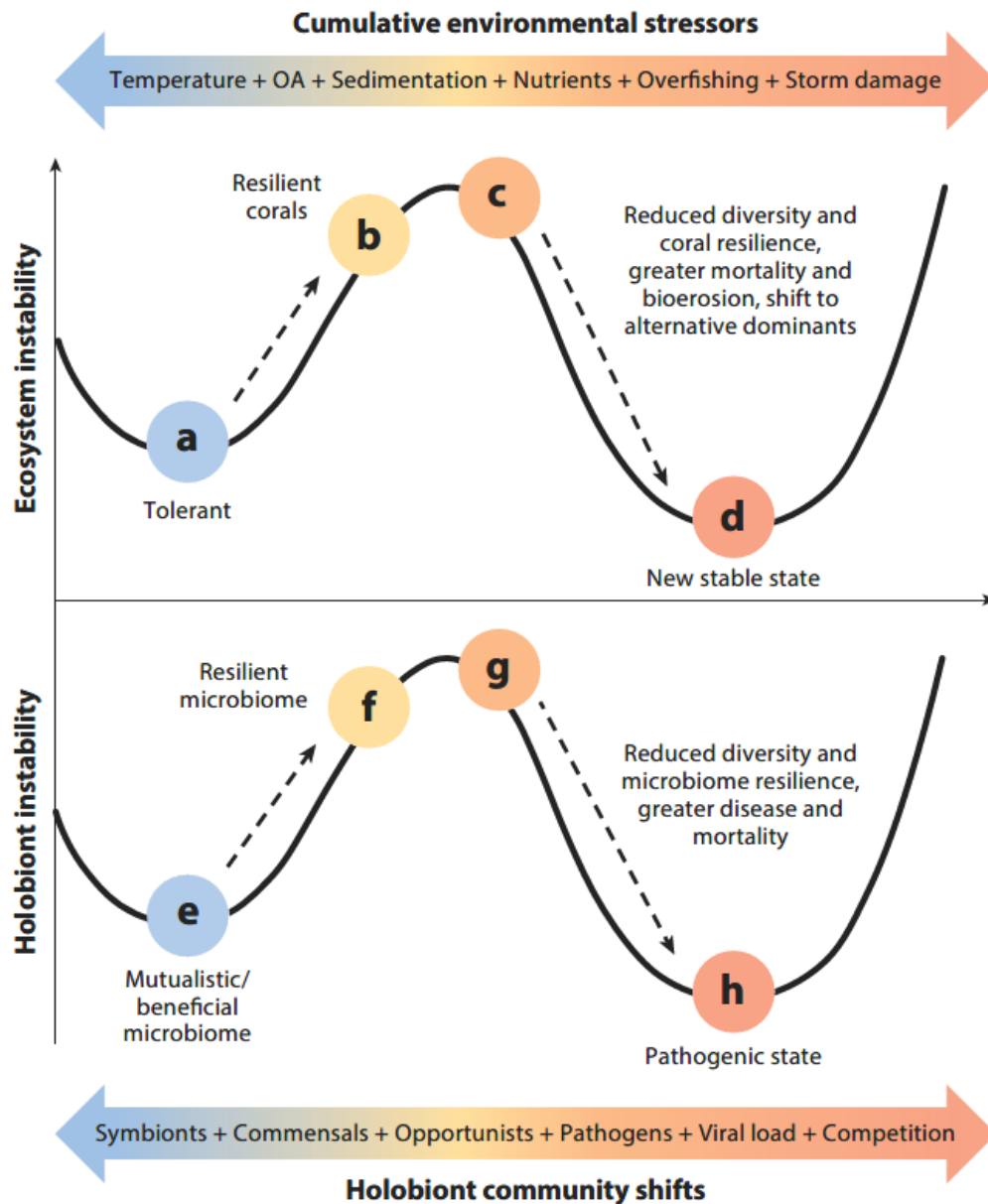


Figure 4. Effects of cumulative stressors on ecosystem and holobiont stability. Reproduced from (Bourne et al., 2016). (*Top*) Cumulative stressors can shift the stable equilibrium of reef benthos from a coral-dominated community to reefs dominated by organisms such as macroalgae or sponges. (*a*) Cumulative stressors initially select for resilient coral species. If stressors are below a critical threshold (intensity or duration), it is possible for an ecosystem to recover and return to the original stable community state. (*b,c*) However, once a tipping point is reached, there is (*d*) reduced species diversity, less resilience, and higher mortality, and potentially shifts to alternative dominant species. (*Bottom*) The concept of reef resilience applies equally to the coral microbiome. (*e*) Under low pressure, the microbiome can buffer environmental change. (*f,g*) However, with increasing pressure, the initially stable microbial community shifts from mutualism to pathogenesis. Once a tipping point is reached, (*h*) holobiont destabilisation drives further changes in the microbiome, manifesting in coral disease, reduced fitness, and mortality.

Besides their influence on the seawater microbiome, macroalgae themselves are holobionts and are associated with a highly diverse microbiome (Barott et al., 2011). Bacterial densities on the algal surface vary between 10^2 and 10^7 cells cm^2 depending on the thallus section, host species and season (Armstrong et al., 2000). The epibacterial community composition significantly differs from the community in the ambient seawater and shows high host specificity and temporal adaptation (Lachnit et al., 2009, Lachnit et al., 2011, Burke et al., 2011b, Goecke et al., 2013). In addition to the biofilm community on the surface of seaweeds, macroalgae harbor a specialised and stable endophytic bacterial community (Hollants et al., 2011a, Hollants et al., 2011b). The specificity of epibacterial communities associated with different macroalgae is currently under reconsideration; microbial functioning, rather than phylogeny, seems to be consistent within the holobiont (Burke et al., 2011a, Burke et al., 2011b). The algal microbiome significantly contributes to host morphogenesis, health and defence. Epiphytic bacteria, such as *Vibrio sp.* and *Pseudoalteromonas sp.*, provide inhibitory properties against various biofouling organisms and hence contribute to host defense against unwanted colonization (reviewed by (Egan et al., 2013). Additionally, epiphytic bacteria supply the algal host with key nutrients. Heterotrophic bacteria provide CO_2 to the photoautotrophic host, and cyanobacteria, which are dominant members of the epibacterial community, provide fixed-nitrogen (Phlips and Zeman, 1990, de Oliveira et al., 2012).

In general, little is known about the factors controlling the microbial communities within the surface biofilm of macroalgae. Bacterial richness in the biofilm of the kelp *Laminaria hyperborea* is reported to increase as the kelp ages (Bengtsson et al., 2012) and microbial community succession seems to be influenced by stochastic processes (Burke et al., 2011a, Trias et al., 2012). Furthermore, disturbances such as temperature stress are shown to disrupt algal-holobiont homeostasis, which can lead to a switch in bacterial communities from surface-associated commensals to opportunistic pathogens (Case et al., 2011).

4.0 Current Monitoring

Despite the important role of microbes in coral reef ecosystems and their ability to show fast, specific responses to environmental perturbations (Haas et al., 2016, Teeling et al., 2012, Wemheuer et al., 2015), the use of microorganisms as sensitive indicators of environmental stress in coral reef ecosystems or as predictive markers for water quality in marine systems has remained largely unexplored (Bourne et al., 2016, Glasl et al., 2016).

In 2012, the 'Marine Climate Change in Australia: Impacts and Adaptation Report Card' identified that a lack of long-term microbial datasets was a critical national knowledge gap that

hindered Australia's ability to predict potential environmental impacts (Webster and Bourne, 2012). To redress this knowledge gap, microbial monitoring of seawater was introduced to the monthly sampling program of the National Mooring Network of IMOS (Integrated Marine Observing System), which targets oceanographic phenomena in Australian coastal waters (IMOS 2016). Specifically, as part of the Australian Marine Microbiology Biodiversity Initiative (AMMBI) and in collaboration with IMOS and BioPlatforms Australia (BPA) a large, globally unique dataset of molecular observations describing the seasonal taxonomic and functional dynamics of seawater microbial assemblages was collated from monthly sampling at three IMOS National Reference Stations around Australia- Maria Island, Port Hacking and Rottneest Island. This data is currently being used to build species distribution models describing the ecological niche for hundreds of individual microbial taxa (Lev Bodrossy, CSIRO and Mark Brown, Uni NSW *Pers. Comm.*).

To compliment this planktonic dataset, benthic sampling (sediment and key habitat forming taxa) was initiated in January 2016 at three Australian sites- Sydney, Western Australia and the Reef. The project was supported by financial investment from BPA for microbial sequencing. Microbial baseline sampling for the inshore Reef has involved sampling of seawater, sediments, corals, sponges and macroalgae every four weeks at Geoffrey Bay, Magnetic Island in conjunction with collection of extensive environmental metadata (water quality metrics-: salinity/conductivity, temperature, chlorophyll a, turbidity, nutrients (TN, TP, PO₄, TC, NOX, NH₄, TOC, TIC) and coral reef health assessments). Microbial samples are currently being processed for microbial composition and function using a combination of 16S rRNA gene analysis (phylogenetic marker gene to determine the composition of the microbial communities), metagenomic analysis (describes the full genomic potential of the mixed microbial assemblages) and metatranscriptomic analysis (describes the genes that have been expressed in the mixed microbial assemblages to determine gene expression patterns for processes such as nitrification, carbon metabolism, virulence etc.). Following computational sequence analysis, a list of putative microbial indicator species or functions that tightly correlate with specific water quality parameters and/or host health states will be compiled. These putative microbial indicator species/functions will need to be validated as bioindicators using targeted experimental assays that replicate the environmental conditions (e.g. elevated nutrients, elevated sediments, elevated seawater temperature, reduced salinity) or host health states from which they were originally derived.

By 2020, it is expected that this project will provide i) a baseline of microbial community composition and function on the inshore Reef, ii) an overview of microbial stability under different environmental conditions (water quality and temperature as they change on a seasonal basis), iii) an overview of microbial stability under different health states for key taxa (disease, necrosis, bleaching etc.) and iv) identification of microbial indicators or microbial processes that are sensitive indicators of either water quality or reef health. Importantly

however, Reef microbial sampling was discontinued in December 2017 due to a lack of sufficient resources for ongoing sampling and sequencing.

5.0 Potential Indicators

Microorganisms can respond very rapidly to altered environmental conditions. Responses are not only fast, but they can be specific to the environmental perturbations to which they have been exposed. These specific responses provide a potential for diagnostic analysis of environmental conditions based on microbial indicators. This diagnostic ability would provide unique advantages over many of the other indicators in current reef monitoring programs. Existing programs, such as 'Reef Check' and 'The Global Coral Monitoring Network', use visual surveys of reef associated fish, invertebrates, substrate composition, reef damage and disease impacts to assess reef health (Hodgson, 2001, Hill and Wilkinson, 2004). However, most visual cues (e.g. tissue necrosis, mortality and shifts in community composition) only become evident in the advanced stages of coral reef ecosystem stress, when ecosystem health and resistance are already compromised. At this stage the ability to recover is dependent on the resilience of the ecosystem and the success of management interventions is jeopardised (Glasl et al., 2017). Assessing changes in reef microbial communities (species and functions) should provide an early indicator of ecosystem impacts and could therefore underpin the development of diagnostic tools to help forecast shifts in coral reef health under different environmental states. This has the potential to develop into a reliable early warning system that facilitates management intervention before severe damage occurs (Glasl et al., 2018, Glasl et al., 2017).

Changes in microbial communities due to disturbance can directly affect ecosystem processes (outlined above). Therefore, researchers have recommended including microbial community composition (e.g. 16S rRNA gene sequencing) into process models that predict ecosystem responses to global change (Allison and Martiny, 2008). Microbial function is also of particular interest since metabolic capabilities can be decoupled from the phylogenetic position of microorganisms due to convergent evolution, gene loss or horizontal gene transfer (Ochman et al., 2000, Martiny et al., 2013). Hence managing for the maintenance of specific microbial functions deemed to be indicative of ecosystem health states may be preferable to managing for the maintenance of specific indicator taxa. Phylogenetic diversity is thought to positively affect the stability of an ecosystem, as it increases the probability that complementary functional traits are present (Yachi and Loreau, 1999). However, ecosystem processes can remain constant after disturbances even when a compositional shift has been observed (Wohl et al., 2004, Banerjee et al., 2016, Allison and Martiny, 2008). Both functional and compositional changes can be assessed based on the entire community or on selected microbial indicator taxa or genes.

Reef microbiomes clearly reflect human impacts associated with land use and fishing, with higher cumulative impacts driving microbial communities towards heterotrophy (Dinsdale et al., 2008b). For instance, nutrient addition and overfishing reduce the abundance of herbivores and contribute to increased algal growth (Dinsdale and Rohwer, 2011, Sandin et al., 2010). Algal exudates are rich in dissolved sugars which can rapidly stimulate microbial growth, resulting in localised hypoxia and a community dominated by opportunistic microorganisms including putative pathogens (Nelson et al., 2013). Ecosystem microbialisation scores were therefore recently proposed to measure these impacts and compare the health of coral reefs across time and space (McDole et al., 2012). Initial analyses suggest that human impacts are altering reef energy budgets by shifting the allocation of metabolic energy from macro-organisms to microorganisms (Dinsdale et al., 2008a, Haas et al., 2013, McDole et al., 2012). However, while microbialisation has been shown to occur on a global scale (Haas et al., 2016), additional research is needed to assess relevance and adopt the approach at individual reef scales.

Priority Indicator	Justification for selection
Microbial community composition (entire community profile or individual taxa)	Once established as indicators, microbial taxa indicative of certain environmental parameters or reef health states could be easily tracked using rapid, cost effective PCR based approaches (similar to pathogen screening diagnostics). Presence / absence or relative abundance of indicator taxa can be readily tracked through time. Hence, indicator taxa can be used to describe conditions and trends, measure the effectiveness of management interventions and contribute to reporting and strategic planning efforts.
Microbial functions (entire functional profile, specific biochemical pathways or individual genes)	In addition to the justification provided above for monitoring microbial taxa, the identification of microbial functional indicators would underpin the description of trends in key ecosystem processes (e.g. nitrification, ammonium oxidation, sulfate reduction etc.). The development of functional indicators would therefore provide an enhanced capability to predict future reef states based on functional tipping points.
Microbialisation Scores	Microbialisation scores represent the percentage of combined fish and microbial predicted metabolic potential. Previous work has demonstrated a positive correlation

	<p>between reef microbialisation scores and human impact. Expanding this by combining an assessment of microbial productivity with individual coral health indicators (e.g. lipid content / energetic value of a host) could provide a measure for determining the health status of coral communities.</p>
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6.0 Recommendations

Regular focused monitoring of coral reef microorganisms would provide a rapid and sensitive platform for identifying declining ecosystem health that can complement existing management frameworks (Glasl et al., 2018). However, the potential value of microorganisms for efficiently monitoring ecosystem health remain largely unexplored, despite the fact that microbes show fast, specific (diagnostic) responses to environmental perturbations (Haas et al., 2016, Teeling et al., 2012, Wemheuer et al., 2015) which are the desirable characteristics of bio indicators.

The first step towards identification of microbial indicators to assess coral reef health is analysis of the temporal and spatial variability of microbial communities (taxa and functions) associated with certain habitats and the subsequent definition of microbial baselines. Once baselines are established, the compositional and functional response of the microbial communities upon disturbance can be investigated.

Finally, a quantitative approach that establishes links between the composition/function of reef microbes and environmental data will be required to identify microbial indicators for water quality and coral reef health. Individual microbial taxa and/or functions significantly associated with healthy versus stressed reef systems or specific environmental variables (nutrients, temperature etc.) can be identified. The inclusion of microbial monitoring approaches alongside the current coral reef monitoring framework would improve our ability to rapidly detect changes occurring in the Reef.

Phase 1.	Extend existing monitoring initiatives to include high temporal resolution sample collections targeting microbial diversity, composition and function. This would provide a cost-effective strategy to establish the first microbial reference datasets for individual reef locations.
Phase 2.	Combine microbial community data and other environmental parameters (e.g. water quality) to identify microbial indicators (taxa or functions) for diagnosis or reef health or other environmental variables (e.g. DIN, TOC, salinity, temperature etc.).

Phase 3.	Establish and test reliable, fast, low-cost and easy-to-use diagnostic protocols based on microbial indicators that can be integrated into current monitoring programs.
Phase 4.	Integrate microbial indicators into standard reef monitoring procedures.

Robust microbial baselines need to be established prior to the derivation of microbial indicators. Establishing microbial baselines would require monthly sampling at selected sites for a minimum of two years so as to determine spatial and temporal variability in microbial composition and function. While sample collection requires minimal effort and can be achieved using small vessels, laboratory analyses (cell separations, DNA extractions, sequencing), bioinformatics analyses (community profiling, metagenomics sequence analysis, genome binning, genome annotation) and data analyses (statistical testing, IndVal analysis) would require a skilled microbiologist (a minimum of 1.0 FTE) over the two year baseline period. All samples need to be collected in triplicate at each time point to enable comparative statistical analysis to underpin identification of indicators.

Operational costs for deriving microbial community profiles are ~\$65/sample (assuming 96 samples are pooled per sequencing run. Library prep/ 96 well plate =\$3000 and MiSeq V3 2x300bp sequencing run =\$2600 and DNA extraction =\$5/sample.

Operational costs for deriving microbial functional profiles are ~\$410/sample (assuming \$90 Nextera XT Prep (applicable for 96 samples) and \$8600 for HiSeq 2500 Rapid Run for 2 x 250bp (total of ~120Gb) and multiplexing 24 samples / run (5Gb per sample).

Additional operational costs associated with the collection of metadata (instrumentation + nutrient analyses).

Priority Indicator	Survey Method	Survey Location/scale (Spatial)	Survey Frequency (Temporal)	Other information
Microbial taxa	Collection of seawater, sediment and key habitat forming species.	Multiple sites (inshore / offshore; lagoon / exposed reef), where monitoring efforts are	Monthly	Co-sampling of extensive metadata (salinity, temperature,

		already underway – including collection of environmental metadata.		chlorophyll a, turbidity, nutrients and coral reef health assessments).
Microbial functions	Collection of seawater, sediment and key habitat forming species.	Multiple sites (inshore / offshore; lagoon / exposed reef), where monitoring efforts are already underway – including collection of environmental metadata.	Monthly	Co-sampling of extensive metadata (salinity, temperature, chlorophyll a, turbidity, nutrients and coral reef health assessments).

7.0 New Technologies

High diversity, high functional complexity and low cultivability has historically limited our ability to understand the marine microbial realm. However, advances in next-generation sequencing (NGS) have revolutionised the study of microbial ecology (Schuster, 2008). Specifically, 16S rRNA gene amplicon (microbial community composition) and metagenomic (microbial function) sequencing now provides a practical tool for analysis of microbial communities *in situ* to underpin the establishment of robust microbial baselines for the Reef. Baseline datasets of microbial community composition and function can be subsequently interrogated for identification of putative microbial indicators.

8.0 Future information needs

Microorganisms are fundamental contributors to reef ecosystem health through their biogeochemical capabilities and intimate symbiotic partnerships. Shifts in the composition or function of bacterial and archaeal communities can therefore provide crucial diagnostic information for future coral reef monitoring. However, before such approaches can be developed and implemented, the following basic questions need to be resolved (see Figure 5):

- (1) Which taxa and functions form the microbial baseline of healthy coral reefs?
- (2) How does the microbial community respond to environmental change?
- (3) How does the microbiome influence holobiont resistance and resilience upon disturbance?

(4) How are environmental disturbances predicted by compositional and functional changes in the microbial community?

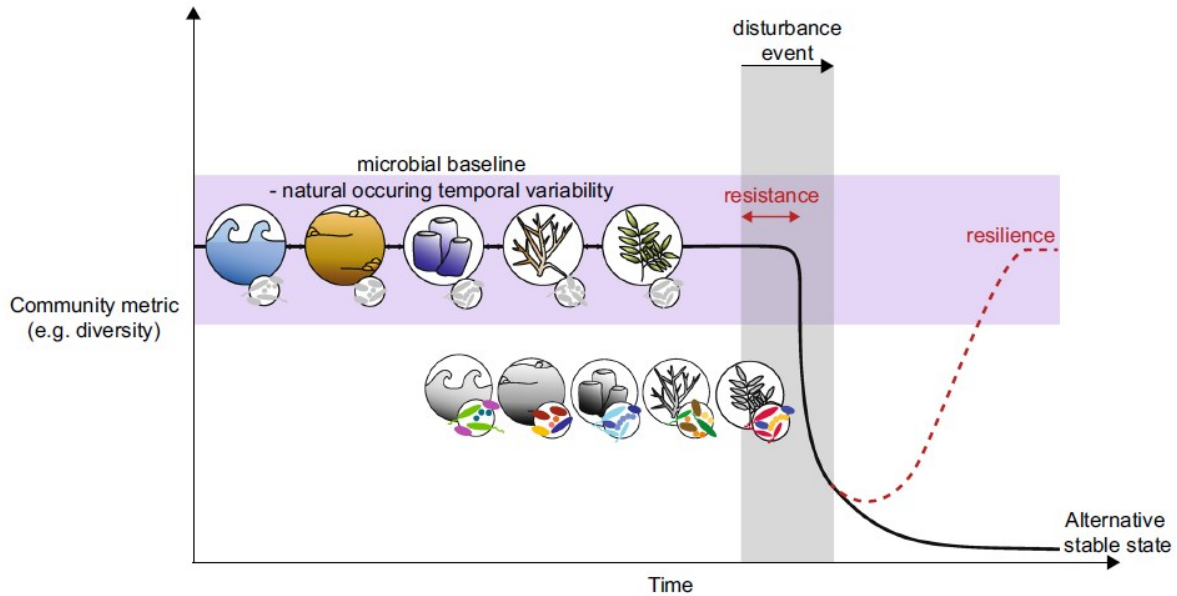


Figure 5. Schematic representation of future research directions. (Reproduced from (Glasl et al., 2017). A microbial baseline (*horizontal bar*) needs to be defined for a comprehensive range of coral reef habitats (including seawater, sediment, sponges, corals and macroalgae), over temporal periods for a particular community parameter of interest (e.g. diversity). A disturbance event (*vertical bar*) alters the environmental conditions, and triggers a shift in the microbial community associated with each habitat (*solid black line*) leading to an alternative stable state. The stability of a holobiont, which relates to its ability to act as a buffer to maintain coral reef function upon environmental alteration, is defined by the combined resistance and resilience of the microbial community. Resistance is the ability of a community to withstand a disturbance without change and resilience is the rate at which a microbial community regains its original state after disturbance. Combining the information on microbial community stability and variation will enable identification of microbial indicators leading to the early identification of imminent environmental stressors (e.g. water quality changes).

The enormous complexity of coral reefs and their associated microbial communities has resulted in studies focused on specific reef compartments. However, these habitats should not be considered as isolated from each other but rather seen as elements of a single ecosystem with a strong benthic-pelagic exchange (Lesser, 2006, Garren and Azam, 2012b). Holistic approaches that consider multiple reef habitats together are therefore urgently required to better understand the function and contribution of microorganisms to reef health and resilience.

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