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INVITED PAPER

Effects of Ocean Warming on the Underexplored Members of the Coral Microbiome

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Synopsis The climate crisis is one of the most significant threats to marine ecosystems. It is leading to severe increases in sea surface temperatures and in the frequency and magnitude of marine heatwaves. These changing conditions are directly impacting coral reef ecosystems, which are among the most biodiverse ecosystems on Earth. Coral-associated symbionts are particularly affected because summer heatwaves cause coral bleaching—the loss of endosymbiotic microalgae (Symbiodiniaceae) from coral tissues, leading to coral starvation and death. Coral-associated Symbiodiniaceae and bacteria have been extensively studied in the context of climate change, especially in terms of community diversity and dynamics. However, data on other microorganisms and their response to climate change are scarce. Here, we review current knowledge on how increasing temperatures affect understudied coral-associated microorganisms such as archaea, fungi, viruses, and protists other than Symbiodiniaceae, as well as microbe-microbe interactions. We show that the coral-microbe symbiosis equilibrium is at risk under current and predicted future climate change and argue that coral reef conservation initiatives should include microbe-focused approaches.

Introduction

Coral reefs are among the most diverse and productive ecosystems on our planet. Their species richness is largely due to the three-dimensional structure produced by scleractinian corals, and soft corals to a lesser extent, which provides a habitat for more than 25% of all marine multicellular eukaryotic species (Fisher et al., 2015). Their ecological success has been attributed to the symbiotic associations they form with various microorganisms (Blackall et al., 2015; Bourne et al., 2016; Van De Water et al., 2018; van Oppen and Blackall, 2019). Amongst them, intracellular photosynthetic algae of the Symbiodiniaceae family are essential for reef coral survival, as they meet most of their host's energy requirements through translocation of photosynthate (Muscatine, 1967).

The accumulation of carbon dioxide and other greenhouse gasses, manifested as increased sea surface temperatures and ocean acidification, is severely alter-

ing marine environments. These changed conditions drastically impact the coral host animal (Stuart-Smith et al., 2018; Leggat et al., 2019), as well as coral-associated microbial communities (Vanwongterghem and Webster, 2020). The impact of elevated sea surface temperatures on coral-associated Symbiodiniaceae and bacteria has been widely studied, and can lead to shifts in existing microbial communities, acquisition of new microbial partners or even the loss of beneficial symbionts (Fig. 1). One of the most drastic examples of the latter is coral bleaching—the loss of Symbiodiniaceae from coral tissues following prolonged thermal stress (Weis, 2008; Suggett and Smith, 2020), leading to coral starvation, death, and coral reef deterioration (Hughes et al., 2018; Leggat et al., 2019). Altered environmental conditions can also lead to shifts in the specific coral-associated Symbiodiniaceae communities via “shuffling” (i.e., change in the relative abundance of Symbiodiniaceae taxa already present

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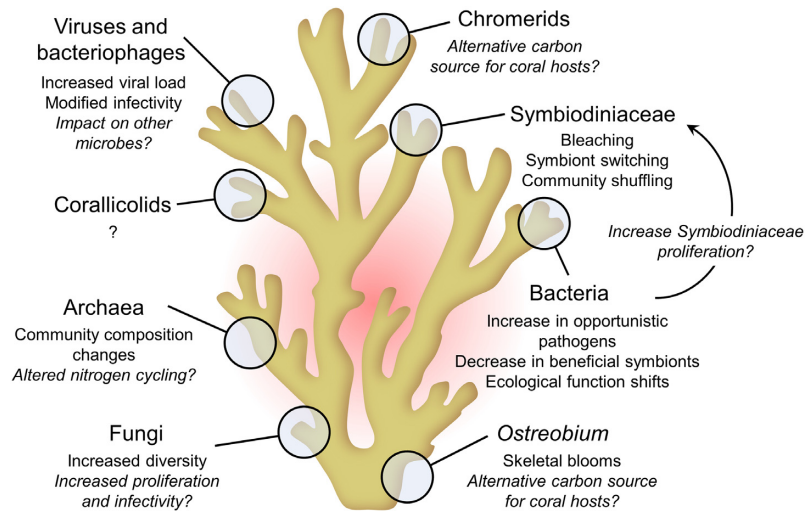


Fig. 1 Impact of elevated sea surface temperatures on known coral holobiont members. Under thermal stress, all microorganisms may be affected and in turn impact the health and functioning of the coral host or other microorganisms. Hypotheticals are italicized.

within the host) and/or “switching” (i.e., acquisition of new Symbiodiniaceae taxa from the environment) (Baker, 2003; Boulotte et al., 2016; Claar et al., 2020; Huang et al., 2020; Ros et al., 2021; Scharfenstein et al., 2022). Multiple studies have shown that some corals dominated by the Symbiodiniaceae genus *Cladocopium* become dominated by the more thermally resilient *Duruskdinium* from the environment following heat stress events (Berkelmans and van Oppen, 2006; Silverstein et al., 2015; Boulotte et al., 2016). Changes in coral-associated bacterial communities have also been observed in response to thermal stress (Fig. 1) (Ziegler et al., 2017; Grottooli et al., 2018; Savary et al., 2021), although they can remain unaffected (Wessels et al., 2017; Epstein et al., 2019; Ziegler et al., 2019). The factors underlying the flexibility or inflexibility of the microbiome during thermal stress remain unknown, but this trait appears to be coral species-specific. Ziegler et al. (2019) hypothesized that coral species with low physiological plasticity would have a more stable microbiome, and vice versa. Thermal stress is often associated with an increase in potential pathogens, such as *Vibrio* (Morrow et al., 2018), and a decrease in potentially beneficial symbionts, such as *Endozoicomonas*, in both scleractinian corals and octocorals (McDevitt-Irwin et al., 2017; Maher et al., 2020; Li et al., 2021; Savary et al., 2021; Tignat-Perrier et al., 2022). Additionally, bacterial virulence or the upregulation of bacterial virulence and secondary metabolism genes are also observed at higher temperatures (Vega Thurber et al., 2009; Littman et al., 2011; Kimes et al., 2012; Garren et al., 2015). While this is a rapidly growing field of research, more functional studies are needed to fully elucidate the impact of bacterial community changes on coral health and coral bleaching.

In addition to Symbiodiniaceae and bacteria, corals associate with a myriad of other microorganisms, such as other protists, archaea, viruses, and fungi, whose roles in the coral holobiont and response to elevated temperatures remain poorly understood (Ainsworth et al., 2017). Here, we review the limited information available on how climate change impacts these underexplored coral–microbe interactions, as well as symbiont–symbiont interactions, and highlight the need to more deeply investigate these members of the coral holobiont.

Archaea

Coral-associated archaea are often overlooked in metabarcoding and metagenomics studies because read numbers are much lower than their bacterial counterparts (Wegley et al., 2007; Littman et al., 2011), and primers used to target the bacterial 16S rRNA gene often do not detect archaeal 16S rRNA sequences (Elloe-Fadrosch et al., 2016). Nonetheless, archaeal symbionts are known to colonize the coral surface mucus layer (Kellogg, 2004; Frade et al., 2016). Archaeal communities are composed primarily of Euryarchaeota, with the phyla Thaumarchaeota and Crenarchaeota also consistently detected (Kellogg, 2004; Wegley et al., 2004; Littman et al., 2011; Wang et al., 2018). Unlike bacterial communities, the taxonomic affiliation of archaeal communities shows larger overlap with seawater communities and is likely more dependent on geographical location than host taxonomy (Kellogg, 2004; Frade et al., 2016; but see O’Brien et al., 2021). Although archaeal functions are still poorly understood, genomic and metagenomic analyses have pointed at a potential for nitrogen cycling, and specifically for ammonium

oxidation in Crenarchaeota (Beman et al., 2007; Siboni et al., 2008, 2012; Robbins et al., 2019). Archaeal genes involved in carbon fixation and vitamin B₁₂ biosynthesis have also been detected in several coral species (Kimes et al., 2010; Robbins et al., 2019), but whether they translocate any of this carbon to the coral host is unknown. Study of carbon translocation genes and isotope labeling of cultured archaea followed by reinoculation in corals may shed light on this aspect.

Few studies have assessed the impact of thermal stress on coral-associated archaeal communities (Fig. 1). The overall relative abundance of archaea was found to decrease in bleached *Acropora millepora* (Littman et al., 2011). Additionally, thermal stress was linked with a decrease in the relative abundance of Euryarchaeota and an increase in Crenarchaeota in both *A. millepora* and *Porites compressa* (Vega Thurber et al., 2009; Littman et al., 2011). The hypothetical role of Crenarchaeota in ammonium oxidation means they may compete for ammonium with Symbiodiniaceae, which are nitrogen-limited *in hospite* and prefer ammonium over nitrate as a nitrogen source (Rädecker et al., 2015). Additionally, environmental mesophilic archaea were shown to exhibit increased metabolic activity under increased temperatures (Smith et al., 2019), which may increase ammonium oxidation rates. An increase in ammonia oxidation by the archaeal community may counteract the ammonia increase from host catabolism observed during early thermal stress (Baker et al., 2018; Rädecker et al., 2021b). This may assist in maintaining Symbiodiniaceae's nitrogen-limited state and control of their proliferation rate and the amount of photosynthate that is transferred to the host. Archaeal abundance in the coral holobiont is relatively low, and their ammonia oxidation rates have not yet been investigated. It is therefore possible that their involvement in nitrogen cycling is negligible compared to the other members of the holobiont. For example, diazotrophs may compensate an increase in nitrogen removal by archaea, as their nitrogen-fixing activity can increase during heat stress (Santos et al., 2014; Cardini et al., 2016; Rädecker et al., 2021a). Hence, the degree to which archaea may impact holobiont nitrogen cycling and in turn Symbiodiniaceae functioning should be investigated further.

Fungi

Corals harbor diverse fungal communities, dominated by Ascomycetes and Basidiomycetes, most of which are thought to be endolithic (Bentis et al., 2000; Gleason et al., 2017; Góes-Neto et al., 2020). Octocorals also harbor complex fungal communities, although culture-independent data are lacking (Van De Water et al.,

2018). Endolithic communities actively penetrate the coral carbonate skeleton by chemical means and are major players in tropical reef bioerosion (Tribollet, 2008). Most emphasis has been placed on fungi as potential pathogens and skeletal borers. For example, *Aspergillus sydowii* is a pathogen of sea fans (Harvell et al., 1999), and corals lay down dense skeletal layers when endolithic fungal hyphae approach living coral tissue (Le Campion-Alsumard et al., 1995; Bentis et al., 2000). Endolithic fungi also play important roles in the global calcium carbonate cycle by participating in the bioerosion of coral skeleton (Gleason et al., 2017). Metagenomic analyses suggest they may also be involved in nitrogen and carbon cycling within coral holobionts (Wegley et al., 2007; Kimes et al., 2010).

Coral-associated fungal communities can be affected by increases in sea surface temperatures (Fig. 1). Phylogenetic diversity was higher in fungal communities associated with *Acropora hyacinthus* sampled from warm reef pools, compared with conspecific colonies from naturally colder, adjacent pools (Amend et al., 2011). Further, total fungal DNA was found to increase in thermally stressed *P. compressa* (Vega Thurber et al., 2009), suggesting an increase in abundance of fungi with elevated temperature. In plant-mycorrhizal associations, elevated temperatures often result in increased fungal extra-radical hyphae size, thereby expanding the surface for fungus-soil exchanges (Bennett and Classen, 2020; Chanda et al., 2020). This may impact fungal metabolic capabilities and lead to improved respiration and carbon distribution in the case of arbuscular mycorrhizal fungi (Chanda et al., 2020). Future investigations should focus on assessing changes in coral-associated fungal community composition and functional roles under thermal stress.

Ostreobium

Along with fungi, coral endolithic communities include filamentous algae (Chlorophytes and Rhodophytes) (Tribollet, 2008; Marcelino and Verbruggen, 2016), and sometimes green sulfur bacteria (Yang et al., 2019). The photosynthetic *Ostreobium* spp. (Chlorophytes) (Iha et al., 2021) often dominate coral endolithic communities, and can form visible green bands in adult coral skeletons (Ricci et al., 2019; Pernice et al., 2020). Primary polyps (7-day-old *Pocillopora damicornis*) can already be colonized by *Ostreobium* (Massé et al., 2018). The recently sequenced genome of *Ostreobium* reveals unique adaptations to the darker and extremely variable endolithic environment. This includes a rich repertoire of light-harvesting complex proteins and genes involved in the oxidative stress response, as well as the absence of

many genes involved in photoprotection and photoreception (Iha et al., 2021). Additionally, *Ostreobium* can translocate photosynthate to coral tissues (Sangsawang et al., 2017).

After coral bleaching, the absence of Symbiodiniaceae in coral tissues results in increased light availability to the skeleton (Enríquez et al., 2005) and *Ostreobium* blooms (Diaz-Pulido and McCook, 2002; Fine et al., 2006; Galindo-Martínez et al., 2022), which may have potential benefits to other members of the coral holobiont (Fig. 1). For example, thermally bleached *Orbicella falveolata* colonies with *Ostreobium* blooms were able to recover, while colonies without *Ostreobium* blooms did not (Galindo-Martínez et al., 2022). First, this increased abundance of *Ostreobium* in the coral skeleton may reduce skeletal light scattering and limit light stress for the remaining Symbiodiniaceae (Enríquez et al., 2005; Yamazaki et al., 2008; Galindo-Martínez et al., 2022). Second, photosynthate translocated by *Ostreobium* may provide an alternate source of energy for bleached corals, thereby partly compensating the loss of photosynthate translocation from Symbiodiniaceae (Fine and Loya, 2002; Sangsawang et al., 2017). In *Oculina patagonica*, *Ostreobium* showed increased carbon translocation rates in bleached corals, compared to healthy corals (Fine and Loya, 2002), and may thereby limit starvation and promote coral recovery.

Other protists

Many other protists beside Symbiodiniaceae and *Ostreobium* are known to associate with corals, including alveolates (Clerissi et al., 2018), such as chromerids and corallicolids. Corallicolids were formally described only recently as part of the mostly parasitic taxon Apicomplexa (Kwong et al., 2019, 2021), although they had been detected in previous amplicon studies (Toller et al., 2002; Clerissi et al., 2018). They are located intracellularly within the coral's mesenterial filaments (Kwong et al., 2019), although whether they are mutualistic or parasitic remains unknown. Corallicolids have maintained some of the cellular machinery to synthesize chlorophyll, although their plastid genome lacks photosystem genes, suggesting that they are unlikely able to photosynthesize and that their plastid could be an apicoplast—a vestigial, non-photosynthetic plastid (Kwong et al., 2019). Corallicolids were detected in corals at depths as great as 1400 m (Vohsen et al., 2020), suggesting they might be mixotrophic or non-photosynthetic at all. However, the function of chlorophyll synthesis related genes in corallicolids remains unknown. Having been discovered very recently, the effects of environmental stressors, including high

temperatures, on corallicolids and coral–corallicolid interactions have not yet been examined.

Chromerids were first described more than 10 years ago after being isolated from the temperate coral *Plesiastrea versipora* (Moore et al., 2008), and can colonize various other tropical corals (Cumbo et al., 2013). Chromerids possess a chloroplast and are capable of photosynthesis (Moore et al., 2008; Oborník et al., 2012; Chakravarti et al., 2019), and may therefore be beneficial for corals, in a similar way to Symbiodiniaceae. One study has assessed the effect of elevated temperatures on the health and performance of chromerids, both in culture and *in hospite* (Fig. 1) (Chakravarti et al., 2019). Cultured chromerids of two species showed higher photochemical health above 30°C, when compared with the Symbiodiniaceae *Cladocopium* C1^{acro} (formerly known as *Cladocopium goreau* (Beltrán et al., 2021)). While uptake of chromerids by larvae of two *Acropora* species was minimal compared to *Cladocopium* C1^{acro}, larvae colonized by *Chromera velia* exhibited higher survival rates to thermal stress (Chakravarti et al., 2019). We hypothesize that, like *Ostreobium* algae, chromerids may act as alternative carbon sources in thermally stressed and bleached corals, although their typically low *in hospite* density may limit their nutritional impact.

Viruses

Viruses are present in relatively large abundances in the water column, outnumbering bacteria by an order of magnitude (Bergh et al., 1989). They have a high diversity in hard and soft corals (Weynberg et al., 2015; Gudenkauf and Hewson, 2016) and can target every member of the holobiont as a potential host (Vega Thurber et al., 2017), i.e., eukaryotic viruses interact with corals and eukaryotic microbes as hosts, while bacteriophages and archaeal viruses infect bacteria and archaea, respectively. Viruses are believed to have versatile roles during their interactions with the different members of the coral holobiont and can be drivers of disease (Buerger and van Oppen, 2018). For example, lysogenic bacteriophages that integrate into the genome of infected bacteria may increase bacterial virulence and alter their functionality, as suggested for the virulence of *Vibrio coralliilyticus* related to the coral disease white syndrome (Weynberg et al., 2015). Other coral diseases have been directly linked to viral activities, such as yellow band/blotch disease (Cervino et al., 2004) and white plague disease (Soffer et al., 2013). However, bacteriophages can also prevent diseases and control bacterial populations (Buerger et al., 2016). For example, when bacteriophages infect some pathogenic bacteria and take over the cell machinery for propagation, lysis

of the infected bacteria may reduce the impact of a bacterial disease (Bull and Gill, 2014; Vega Thurber et al., 2017). As such, bacteriophages used in phage therapy have successfully prevented white plague disease in *Favia fava* when administered at the same time as the pathogen and limited coral-coral transmission (Efrony et al., 2009).

Increased seawater temperature can affect the activity and dynamics of these host–virus interactions (Fig. 1) (Vega Thurber et al., 2017). Several studies have shown an increase in viral reads during thermal stress (Marhaver et al., 2008; Vega Thurber et al., 2009; Nguyen-Kim et al., 2015; Correa et al., 2016; Messyasz et al., 2020). Coral heat resilience may also be affected by viral activity, since heat stress in corals can trigger an increase in activity or abundance of DNA- and RNA-viruses that infect Symbiodiniaceae (Levin et al., 2016; Grupstra et al., 2021), which may result in increased Symbiodiniaceae lysis. However, while increased seawater temperatures may provide more optimal conditions for some virus-host dynamics and an increase in viral production, for others it may result in reduced optimal conditions for virus propagation and activity (Danovaro et al., 2011). It is therefore difficult to predict a directional shift for the overall coral–virus interactions and dynamics.

Symbiodiniaceae–bacteria interactions

While coral interactions with Symbiodiniaceae and bacteria are often at the forefront of research, Symbiodiniaceae–bacteria associations remain largely understudied (Matthews et al., 2020). Indeed, cultured Symbiodiniaceae have been shown to associate with diverse communities of bacteria (Frommlet et al., 2015; Lawson et al., 2018; Nitschke et al., 2020; Maire et al., 2021b), and intracellular bacteria were observed in cultured and *in hospite* Symbiodiniaceae (Maire et al., 2021b). While the functions of such bacterial symbionts remain elusive, co-cultivation of bacterial consortia with microalgae other than Symbiodiniaceae improved microalgal carbon conversion efficiency and significantly enhanced biomass yields (Vasseur et al., 2012; Bell et al., 2016). The growth enhancing role of symbiotic bacteria is mainly attributed to the release of growth promoting factors such as indole acetic acid (De-Bashan et al., 2008) and vitamin B₁₂ (Croft et al., 2005). As Symbiodiniaceae are also auxotrophic for vitamin B₁₂ (Agostini et al., 2009), it is expected that the metabolic associations between Symbiodiniaceae and symbiotic bacteria partly resemble other microalgal systems. Co-cultivation of *Chlamydomonas reinhardtii* with vitamin B₁₂-producing bacteria enhanced its thermal tolerance (Xie et al., 2013), suggesting live

bacteria and bacterial metabolites might confer thermal tolerance to microalgae, including Symbiodiniaceae. In line with this, addition of an algal phycosphere-associated bacterium belonging to the *Muricauda* genus to an antibiotic-treated Symbiodiniaceae culture (*Durusdinium* sp.) was recently shown to restore the algal heat tolerance (Motone et al., 2020). It is important to understand how Symbiodiniaceae–bacteria interactions may influence Symbiodiniaceae and coral holobiont thermal tolerance, and how increased temperatures will impact Symbiodiniaceae-associated bacteria. To date, only one study monitored Symbiodiniaceae-associated bacteria during a heat stress experiment. Increased temperatures resulted in increased bacterial numbers and changes in the bacterial community composition in cultured Symbiodiniaceae (Camp et al., 2020). Bacterial communities were more stable in association with *Durusdinium trenchii*, which is more thermally tolerant than the other cultures from this study (Camp et al., 2020). Whether bacterial community stability is a cause or a consequence of enhanced thermal tolerance remains unknown (Camp et al., 2020).

Conclusions

Elevated sea surface temperatures are a major threat to marine ecosystems, including coral reefs. Not only does climate change drive coral bleaching (the loss of Symbiodiniaceae), but temperature anomalies also affect other coral-associated microorganisms with changes in microorganism community composition and function likely impacting coral health and thermal resistance. While these symbiotic imbalances are clear in the case of Symbiodiniaceae, additional work is needed to understand the extent of thermal stress on other coral-associated microbes (Ainsworth et al., 2017).

The relatively low number of studies for these underexplored microbes is partly due to technical challenges, such as their low abundance, and the inability to specifically sequence their genomic material (e.g., 18S rRNA coral or Symbiodiniaceae sequences would far outweigh similar sequences from other micro-eukaryotes, making the latter harder to characterize). However, techniques such as fluorescence-activated cell-sorting, or laser capture-microdissection for the bigger symbionts, can be used to stain and sort different cell populations and enrich targeted symbionts (Rosental et al., 2017; Maire et al., 2021a). These populations can subsequently be used for meta-omics experiments, while minimizing host or Symbiodiniaceae contamination. Spatial approaches, such as metabolite distribution mapping with matrix-assisted laser desorption/ionization (MALDI-MSI), or

spatial genomics and proteomics through NanoString technologies may also assist in obtaining functional information on specific symbionts. Higher resolution techniques, such as nanoscale secondary ion mass spectrometry (NanoSIMS) or elemental analysis coupled with electron microscopy, may be needed for smaller symbionts like viruses and archaea. As it is also very challenging to culture most of these symbionts, functional data rely on culture-independent techniques such as meta-omics and advanced visualization studies. Genome data can inform on the requirements for culturing, thereby providing a potential path to *in vitro* functional characterization.

Microbiome manipulation has been proposed as a tool to enhance certain coral traits, such as thermal bleaching tolerance. Bacterial microbiome transplantation and probiotics (Doering et al., 2021; Santoro et al., 2021) and the introduction of experimentally evolved Symbiodiniaceae into coral (Chakravarti et al., 2017; Buerger et al., 2020) are showing promising results in enhancing coral thermal resistance. While most of the proposed approaches currently focus on Symbiodiniaceae and bacteria (van Oppen and Blackall, 2019; Chan et al., 2021; Peixoto et al., 2021; Maire and van Oppen, 2022), the symbionts and interactions highlighted in this review may represent a yet untapped resource for microbial-mediated conservation approaches. Some methods, like phage therapy, have already been trialed and show promising results (Efrony et al., 2009). However, the lack of fundamental data on these understudied symbionts (e.g., whether corallicolids and chromerids are mutualistic or parasitic) is hampering the development of such approaches. Understanding which symbionts are mutualistic and may provide benefits, and how their interactions with other coral holobiont members are affected by thermal stress will be key in expanding our microbial arsenal for coral bleaching mitigation.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

No new data were generated or analyzed in support of this research.

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