Dynamics of the Coral Microbiome and Its Link to Climate Change

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Abstract

Coral reefs are one of the most diverse ecosystems in the world. Due to climate change and several anthropogenic activities such as overfishing, coral mining, waste disposal, marine pollution, etc., corals have been greatly affected. Corals are sessile animals that are in multipartite symbiosis with various microbes, forming the basic framework for the reef ecosystem. Microbes are considered a crucial part of the marine ecosystem as they play a key role in ecological functions, primary productivity, nutrient cycling, and producing chemical defense to protect hosts from invading microbes, etc. Coral microbiome

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investigations are gaining focus in recent years by incorporating various conventional and high-throughput sequencing technologies for determining the diversity of bacteria present in corals concerning their genera, location, health status, etc., as their diversity tends to be both static as well as dynamic in nature.

Keywords

Coral ecosystem · Holobiont · Climate change · Response · Coral reef management

5.1 Introduction

Oceans are one of the most under studied environments. They have the central importance in detecting changes in structural habitat, food web, and biodiversity. There is a limited scope for sampling in the ocean environment (Smith et al. 2015). The influence of the pollutants, eutrophication, and rapid change in temperature, along with the hypoxic conditions, affect the ocean health and the microbiota living in it (Gruber 2011). Due to the increase in climatic variations, the ecosystem in all parts of the world is affected (IPCC 2014). The most biodiverse ecosystem on the planet Earth is the coral reefs (Muller-Parker et al. 2015). Due to human activities in the late eighteenth century, there has been a tremendous change in the Earth's atmosphere which leads to rise in the Earth's temperature rapidly (Trenberth et al. 2007). Most of the coral reef ecosystems are located in the vulnerable part of the Earth's atmosphere where climate change takes place very frequently (Hughes et al. 2003; Hoegh-Guldberg et al. 2007).

The coral reef ecosystem has a greater role in the persistence of Anthropocene, the species that are present in the corals are sensitive to various changes (anthropogenic disturbances) like extreme fishing, ocean pollution, coastal development, and ocean acidification. The acidification of the ocean has a direct impact on the ocean calcifiers (corals); acidification inhibits growth and limits calcification (Doney et al. 2009). It also reduces the reef's structural integrity and in turn increases the bioerosion process which leads to the destruction during severe weather like storms and cyclones (Andersson and Gledhill 2013). In 1998, >45% of the coral cover has been lost across the Indian ocean due to climate change (Hoegh-Guldberg et al. 2007). The coral community has associated microorganisms and also comprises metaorganism which is together known as coral holobiont (Rohwer et al. 2002). These bacterial communities help in the nitrogen fixation, sulfur cycling, and protection against pathogenic attacks (Glasl et al. 2016; Lema et al. 2012; Lesser et al. 2004; Raina et al. 2009; Ritchie 2006). These microbial associations with corals change with the variation in the depth allowing the corals to obtain a wide range of nutrients from the surroundings (Hernandez-Agreda et al. 2016). Heatwaves in the oceans disrupt the symbiotic relationship between the coral and its associated microbes leading to the loss in physiological function and its nature (Glynn 1984; Eakin et al. 2016; Berkelmans et al. 2004). The increase in climatic change disrupts the natural microbiome of the coral reef leading to the destabilization and emergence of pathogenic taxa ultimately leading to host mortality (Littman et al. 2011; van Oppen and Blackall 2019). It is clear that the change in climatic conditions directly affects the coral microbiome, and it can be considered an early warning signal (Bourne et al. 2008; Glasl et al. 2017; Lee et al. 2016).

In this review, we discuss the diversity of the coral microbiome and its beneficial effects on the reef system and survival mechanism, how these beneficial microbes act and change during various stress conditions like bleaching, high temperature, carbon dioxide, lower pH, etc., and the possible ways to mitigate these conditions.

5.2 Significant Terminologies

5.2.1 Holobiont

A eukaryotic host with all its associated microbial partners. This multispecies assemblage includes viruses, phages, eubacteria, archaea, fungi, and protozoa.

5.2.2 Hologenome

Genetic information is encoded in the eukaryotic host and all of its associated partners. This collective genome forms the theoretical genetic repertoire of a holobiont (definition by Deines et al. 2017).

5.2.3 Metaorganism

In order for a holobiont to function properly, it must have a stable hologenome, which is dependent on the hologenome's associated partners, their activity, abundance, and the transcriptionally active regions of their genomes all in balance. This results in host-microbe and microbe-microbe interactions that must be maintained in homeostasis to keep the holobiont stable. To underline this extremely dynamic functional condition (capacity) of a holobiont, we will in the following use the term "metaorganism" (Deines et al. 2017).

Microbiome refers to an "ecological community of commensal, symbiotic, and pathogenic microorganisms within a given host" (Lederberg and McCray 2001).

5.3 Coral Ecosystem

5.3.1 Coral Habitats

Corals are the richest marine ecosystem on the planet Earth. These are threatened due to pollution and rapid climatic changes (Hoegh-Guldberg et al. 2007; Graham et al. 2014; Mora et al. 2016; Casey et al. 2014). They have a diverse range of bacterial associates (Brown and Bythell 2005), and some of them are species-specific (Ritchie and Smith 1997; Rohwer et al. 2002). Fossil records show that the existence of reef-building corals dates back >400 million years in which the reef-building corals are thought to emerge at the end of 250 million years (Stolarski et al. 2011). Coral-associated microbes have some important physiological and ecological roles in the coral reef ecosystem. The nitrogen fixation process of microbes present in the coral reef was first proposed in 1987 (Williams et al. 1987). When the oxygen concentration is low intracellularly, the endosymbiotic eukaryotic dinoflagellate photosynthesis takes place (Lesser et al. 2004; Kvennefors and Roff 2009). Some of the coral-associated microbes can protect the host from predation by producing antibiotics (Ritchie 2006). It is found that 30% of the coral-associated bacteria have antibiotic capabilities (Castillo et al. 2001). Coral metaorganism is a collection of bacteria, fungi, and viruses (Knowlton and Rohwer 2003; Bang et al. 2018), and they also have a symbiotic association with the algal family Symbiodiniaceae (LaJeunesse et al. 2018). For the development of the three-dimensional structure of the massive calcium carbonate skeleton system of the host coral, more than 95% of the energy is obtained by exporting photosynthates from micro-algal endosymbionts (Jones et al. 1994). The bacterial community of the coral is highly sensitive to environmental changes (Reshef et al. 2006; Santos et al. 2014, 2015, 2016; Thompson et al. 2015).

5.3.2 Coral Complexity

Generally, the coral microbiome comprises living organisms like prokaryotes, microeukaryotes, viruses, and coral polyps (Hernandez-Agreda et al. 2017; Marcelino and Verbruggen 2016). The coral prokaryotic distributions are found to be too high in the coral skeletal system by the use of metabarcoding studies. The prokaryotic and eukaryotic organisms of the coral skeleton structure altogether are called endoliths (Marcelino and Verbruggen 2016; Marcelino et al. 2018). Some of the eukaryotes can create boreholes on the limestone of the coral skeleton (Marcelino and Verbruggen 2016; Yang et al. 2016; Wegley et al. 2007; Le Campion-Alsumard et al. 1995a). Among the microbiome, the endolithic algae play an important ecological role as a microbial agent for reef erosion (Tribollet 2008). Among them is the genus *Ostreobium* (*Ulvophyceae, Chlorophyta*) which is considered to be the most abundant of all (Vroom and Smith 2001). Mostly the balancing role of these algae is unknown. The microbial community changes with the change within the coral colony and also within the coral reef environment. Studies show that the community of the coral colony and reef exhibits distinct nature (Rohwer et al.

2002). The endosymbiotic dinoflagellates present on the coral polyp secretes mucus which contains the polymer of sulphated glycoprotein (mucocytes) (Brown and Bythell 2005). These mucous were made up of amino acids like serine, threonine, aspartate, glutamate, and glycine (Meikle et al. 1987, 1988). They also contain a small number of monosaccharides like arabinose and xylose which were believed to be produced during photosynthesis (Molchanova et al. 1985).

5.3.3 Coral Fungi

Several fungal species have been found in every marine habitat (Gao et al. 2010). The depth gradients and climatic conditions show variations in these types of microbes (Giovannoni and Stingl 2005; DeLong et al. 2006; Zinger et al. 2011; Barberán and Casamayor 2010). Mostly the geographical scales are limited to 100 s of km within the Pacific Gyre of North (Gao et al. 2010). Further studies showed that wood-inhabiting fungal composition is favored by temperature and salinity (Booth and Kenkel 1986). The first isolation and culturing of ascomycetes and basidiomycetes fungus were from the skeletons of hermatypic corals belonging to the Atlantic and Pacific oceans (Kendrick et al. 1982). By RNA analysis, it is found that there is a link between physiochemical properties and the active fungal composition of that particular area (Orsi et al. 2013). Endolithic coral fungi can develop resistance to environmental stress; some of them are symbiotic which helps in the nitrogen fixation to benefit the associated coral species (Wegley et al. 2007). Some of the coral-associated fungal species produce mycosporine-like amino acids which in turn prevent the corals from UV damage (Dunlap and Shick 1998). Like other marine microbes, marine fungi also has some similar qualitative biogeographic patterns even if there is a change in environment and dispersal mechanism (Duarte et al. 2016). It has been reported that the presence of various factors like temperature, and pH, helps in the strong structural development of hyphomycete morphospecies at the regional scale. Fungi can live symbiotically without harming the host coral along with associated coral microbiome.

5.3.4 Coral Algae

The skeleton of live coral contains high amount of eukaryotic green algae which is 16 times higher than that of the *Symbiodiniaceae* that is present in the coral tissue (Odum and Odum 1955). Among them are the green algae *Ostreobium* found to be present in most of the stony coral reefs (Marcelino and Verbruggen 2016). Most of the algae are found at >100 m below sea level and are also found in deep caves underwater (Odum and Odum 1955; Gonzalez-Zapata et al. 2018; Hoeksema 2012). Algae Dinoflagellate survives within the coral cells and provides the host with the energy they needed to perform most of their metabolic tasks (Muscatine 1990). Dinoflagellates belonging to the genus *Symbiodinum* commonly called zooxanthellae are referred to as reef-building corals (Freudenthal 1962).

Symbiodinums are well developed in balancing the sunlight absorbed in turn converting it into useable energy by the corals through photochemistry; thus, the fixed energy source (carbon) is utilized in the development of coral and calcification process (Goreau 1959; Muscatine 1990). More amount of oxygen is produced during the process is proportional to the calcification rate in the coral (Colombo-Pallotta et al. 2010). Fluctuations in the temperature and light condition lead to the destruction of the coral-algal symbiosis; this process is termed coral bleaching (Lesser 2011). Thus, the bleached corals are very difficult to regenerate even if they are prepopulated with the desired host *Symbiodinum* spp. (Jokiel and Coles 1977; Goreau and Macfarlane 1990; Meesters and Bak 1993; Ward et al. 2002). Records show that reef-building coral was found in the photic zone at about 165 m (Maragos and Jokiel 1986).

5.3.5 Coral Virus

The amount of virus present per milliliter of seawater is 10^6–10^8 which is higher than that of the other microbial cells present per milliliter (Wigington et al. 2016; Wommack and Colwell 2000; Fuhrman 2009). By the use of transmission electron microscopy, the virus that is present inside the cnidarian tissue was found to be 60 nm in diameter which is icosahedral in shape (Wilson and Chapman 2001). The sea anemones (stony corals) which are close relatives to the coelenterate are the first to show virus-like particles (VLP) (Wilson and Chapman 2001). Later, these viruses particles were characterized by comparing stressed and non-stressed coral animals where the normal non-stressed coral showed virus particles ranging from 30–40 to 50–60 nm in diameter, whereas stressed coral animal shows 40–50 and 60–80 nm in diameter along with more abundant viral particles (Wilson et al. 2005). Among 60 virus families, 58 of them live in corals around the world with 7 orders, 104 families, and 410 genera of viruses and were found to be recognized by the International Committee on the Taxonomy of the Virus (ICTV) (King et al. 2011). With recent advancements in data collection methods like metagenomics and transcriptomics, it is evident that all coral samples have the order *Caudovirales* with double-stranded DNA with particular three families *Siphoviridae, Podoviridae,* and *Myoviridae* (Lawrence et al. 2014). A recent investigation shows that the 24 coral reefs which were infected by the virus are mostly by temperate virus where the microbial densities are found in higher concentrations (Knowles et al. 2016). By using RNA-dependent RNA polymerase and shotgun sequencing methods, it is found that the vast majority of the ssRNA virus belongs to the family Picornaviridae, a virus that is known to affect marine protists (Culley and Steward 2007). The metagenomic analysis helps in the identification of the double-stranded DNA virus as a potential lysogen in the tropical coastal waters (McDaniel et al. 2014; Knowles et al. 2016). This virus also plays a very important role in the microbial evolution process called transduction (horizontal gene transfer method) (Rohwer and Thurber 2009; Paul and Sullivan 2005).

5.4 Coral Endoliths

5.4.1 Endolithic Algae

In the coral reef environment, endolithic microbes form the major component of the food chain (Hutchings 1986; Radtke et al. 1996). The first visible band appearance on the coral reef by an endolithic microbe was characterized in 1902 (Duerden 1902). More than 50–60% of the nitrogen available to the host coral was provided by the endolithic microbes says Ferrer and Szmant (1988). During the process of thermal bleaching, the process of translocating the photosynthetic carbon to the nearby host coral takes place (Fine and Loya 2002). Endolithic microbes are highly capable of nitrogen fixation and regeneration of nutrients to the coral reefs (Shashar et al. 1994; Cardini et al. 2014). Endolithic microbes that are associated with the coral skeleton systems include algae, fungi, bacteria, archaea, and viruses (Rosenberg et al. 2007; Schönberg and Wisshak 2012). Underneath the corals, there is a noticeable green band appearance formed by the green algae *Ostreobium* spp. (*Siphonales, Chlorophyta*) which were considered a coral symbiont (Kornmann and Sahling 1980; Del Campo et al. 2017). These are also found in the aragonite skeletons belonging to the coral reefs of the Caribbean, South Pacific, and Atlantic oceans which mainly include certain species like *Pocillopora* spp., *Stylophora* spp., *Acropora* spp., *Favia* spp., *Montastrea* spp., *Porites* spp., and *Goniastrea* spp., these organisms can penetrate dead as well as live carbonate coral substrates (Le Campion-Alsumard et al. 1995b; Zubia and Peyrot-Clausade 2001; Godinot et al. 2012; Halldal 1968). The green sulfur bacteria like *Prosthecochloris* are dominantly seen in *Isopora polifra* (coral spp.); some of the green sulfur bacteria were found in the tissue and mucus of the corals (Yang et al. 2016; Koren and Rosenberg 2006; Reis et al. 2009; Kimes et al. 2013; Li et al. 2015; Cai et al. 2017). By using the latest molecular techniques, it is found that these endolithic microalgae have varied diversity with 80 taxonomic units (Marcelino and Verbruggen 2016; Marcelino et al. 2017, 2018).

5.4.2 Endolithic Fungi

The endolithic fungi have the advantage of coral penetration and ultimately interacting with the *Ostreobium* cells; among these, the primarily isolated endolithic fungi that belong to *Ascomycota* and *Basidiomycota* are from the Caribbean and South Pacific (Le Campion-Alsumard et al. 1995b; Kendrick et al. 1982). The certain fungus will penetrate the polyp zone of the coral *Porites lobata* which in turn activates the defense mechanism resulting in the heavy deposition of the carbonate material giving a pearl-like appearance (Le Campion-Alsumard et al. 1995b). There are more than 10,000 species in the phylum Cnidaria which was studied for its abundance in fungal association (Zhang 2011). There is a threefold increase in the fungal sequence in the bleaching sample of the *A. millepora* by the metagenomic analysis method, yet the proper role of this fungi is unclear (Littman et al. 2010). When the spatial distribution is disturbed in *A. formosa*, the fungi present in the healthy tissue develop into a new skeletal cavity (Yarden et al. 2007). Endolithic fungi exhibit a parasitic association rather than that of the saprophytic way of association with the corresponding coral by activating the defensive mechanism (Le Campion-Alsumard et al. 1995b; Golubic et al. 2005). The *Aspergillosis* of sea fans was believed to be caused by the dust-borne propagules that were introduced from the Sahara (Garrison et al. 2003). Along with the aspergillosis, it is believed that other opportunistic fungal infections of the sea fan are caused by the combination of more than one fungal species (Barrero-Canosa et al. 2013).

5.4.3 Endolithic Prokaryotes

The endolithic microbiome (prokaryotic and eukaryotic) performs various functions like providing nutrition to the coral, bioerosion, cycling of the nitrogen, etc. (Schlichter et al. 1995; Tribollet 2008; Miller et al. 2011). Based on the green band appearance on the coral skeleton and mussel shells, some of the first described marine *Cyanobacteria* are *Plectonema terebrans, Mastigocoleus testarum*, and *Halomicronema excentricum* (Le Campion-Alsumard et al. 1995b; Yamazaki et al. 2008). *Cyanobacteria* and other non-oxygenic phototrophic bacteria were present in higher abundance which can be seen by the appearance of the deeper darker green bands that were caused by the bacteriochlorophyll 2 pigments (Ralph et al. 2007; Magnusson et al. 2007). Targeted amplicon sequencing on 16SrRNA has identified more than 90 non-classified cyanobacterial operational taxonomic unit (OTUs) in 132 coral fragments (Marcelino and Verbruggen 2016). In coral *Isopora palifera*, the green sulfur bacteria *Prosthecochloris* was found to be in higher abundance (Yang et al. 2016). The distance decay relationship (DDR) measures beta diversity and heterogenicity habitat and was used to understand the decrease in the community similarity inside the skeletons of the corals (Nekola and White 1999; Anderson et al. 2011; Martiny et al. 2011).

5.5 Climatic Impact on Coral Reef

5.5.1 Effects of Climatic Change on Coral Ecosystem

There is an enormous change in the ocean temperature over the past 15 years also resulting in the disappearance of the arctic ice covers; it is also recorded that the precipitation is more variable with heavy rainfall, intense hurricanes, and early occurrence of the spring season (Johnson et al. 2011; Wernberg et al. 2011; Solomon et al. 2007). Most of these changes occur due to rapid climatic changes (Hoegh-Guldberg and Bruno 2010).

5.5.2 Bleaching-Associated Changes

The dinoflagellate symbionts zooxanthellae help the host by providing them with photosynthates along with coral calcification, due to extreme environmental conditions like radiation and high-temperature damage; this machinery leads to the overproduction of oxygen radicals leaving the symbionts to cellular damage and pigment degradation; this process is referred to as "bleaching" (Muscatine and Porter 1977; Lesser 2006). Heat stress damages the biological property of a coral holobiont (Littman et al. 2011). Once the symbionts were lost, more amount of solar radiation and the CO_2 enters the coral skeleton and helps the photosynthesis of endolithic algae which results in the harmful algal blooming during these bleaching periods (Fine and Loya 2002; Shashar and Stambler 1992; Diaz-Pulido and McCook 2002; Fine et al. 2006). The primary bleaching of the coral results in secondary bleaching of the nearby *Symbiodiniaceae* of the adjacent coral such a mechanism is called an optical feedback loop (Swain et al. 2018; Wangpraseurt et al. 2017). During these high temperatures caused by the irradiation, the lipid composition of the thylakoid membrane of the symbiont gets deteriorated; this compromises the photosystem II, paying the way for the increased production of nitric acid synthase which also tends to increase the bleaching of the coral reef (Tchernov et al. 2004; Trapido-Rosenthal et al. 2005). Metagenomic of the bleached coral microbiome shows increase in the carbohydrate utilization and processing along with the rapid increase in the virulence-associated gene (Littman et al. 2011; Thurber et al. 2009). If there is an increase in the wavelength of visible light (400–700 nm) and ultraviolet light (290–400 nm) it has also been linked to coral bleaching (Hoegh-Guldberg and Smith 1989; Brown et al. 1994; Fitt and Warner 1995).

5.5.3 Response to Climatic Disturbances

When the coral microbiome is exposed to ocean acidification or higher temperature, there is a shift from beneficial bacteria to more pathogenic ones like *Endozoicomonas* to *Alteromonadaceae* and *Vibrionaceae* (Bourne et al. 2016; Littman et al. 2011). Thus the variation in the species dominance and evenness disturbances shows the coral has undergone a stress response (van der Voort et al. 2016). It is found that not only stressor like climate or temperature changes the microbiome of the coral, but coming in close contact with macroalgal spp. tend to shift the microbiome to a macroalgal microbiome. This was well studied in *A. millepora* and *Seriatopora hystrix* microbiomes that they maintained stability even under lower pH and higher temperature, whereas the *S. hystrix*'s microbiome showed a considerable change when compared with similar taxa like *Foraminifera* and crustose coralline algae; this sudden shift leads to diseases like black band disease, yellow band disease, dark spot syndrome, etc., especially when the corals were exposed to multiple stressors (Zaneveld et al. 2016). During high temperatures, the nitrogen fixation process continues to increase, dramatically changing the nutrient balance in the coral holobiont, leading to an induced phosphate starvation state in the *Symbiodiniaceae*; this ultimately leads to the poor translocation of photosynthates to the host coral also termed as selfish symbiont (Baker et al. 2018; Morris et al. 2019). When there is a dimension of corals at a specific reef due to bleaching, it signals a positive feedback loop which increases algal dominance (Rädecker et al. 2015). There will be increase in dissolved organic carbon (**DOC**) which interacts with temperature and accelerates the bleaching by inducing the proliferation of diazotrophs, thus increasing DOC leads to a further decline in the coral mortality by forming **hypoxic zones** (Pogoreutz et al. 2017; Rädecker et al. 2015; Silveira et al. 2017).

Changing climate results in a destabilized microbiome, dysbiosis, etc. which ultimately leads to the development of a more stable state characterized by increased mortality, bleaching events, and disease (Egan and Gardiner 2016; van Oppen and Blackall 2019). Certain corals show little resistance to stressors like lower pH and higher temperature (Meron et al. 2012; Epstein et al. 2019). Certain corals can revert to their original state once the stressor is gone, whereas some change irreversibly which can be either beneficial or detrimental to the holobiont (Bourne et al. 2008; Tracy et al. 2015). The effects of coral bleaching have been increased due to climatic change and various stress factors which tend to decrease reef framework and depress reef accumulation rates.

5.6 Coral Reef Management

5.6.1 Reef Microbiome Recovery and Restoration

Most of the coral degradation signs will show up once the coral reef has reached its advanced stage of decline; hence, it releases certain stress markers (Glasl et al. 2017). In the early decades, microbes act as an indicator system for various responses to environmental disturbances (total coliform count in drinking water (Faust et al. 2015; Glasl et al. 2019; Tallon et al. 2005). Coral reef conservation and restoration were primarily formed to prevent water quality and to handle massive coral depletion due to climate change in efforts to restore it (Hughes et al. 2017; Silveira et al. 2017). Most of the restoration practices were done by coral aquaculture gardening or by fragment transplantation onto the specific reef (Rinkevich 2008). Microorganism plays an important role in the maintenance of the coral animal and the proper functioning of the ecosystem; thus, it is important in preserving the threatened species (West et al. 2019). The recovery and loss of coral reefs from eastern pacific sites have been recorded for 10–28 years showing both 100% elimination to 100% total recovery (Wellington and Glynn 2007), whereas in costa Rica, live corals have been increased by 4–23% from 1987 to 2002 with other similar species in which is found in the pre-disturbance community utilizing sexual regeneration. In Panama, asexual regeneration has been observed in *Pocillopora elegans* and *Pavona clavus*, whereas *Acropora* which is found in the Arabian gulf regenerates sexually (Riegl 2002). Transplanting asexually regenerating colony tissue or replacing a sexually developing larva in the disturbed place tends to increase live coral cover (Harrison and Wallace 1990; Richmond 1997). To support proper regeneration of the coral reef regrowth, it needs stable and firm lighting with relatively sediment-free substrates. Most importantly the substrates should be free from any other taxa (Bellwood et al. 2003).

Developing coral stocks with higher stress tolerance by inducing evolutionary changes to the coral microbiome community is referred to as assisted evolution (Van Oppen et al. 2017). The highly successful recovery rate was seen in *Acropora, Pocillopora,* and branching *Porites*, whereas the *Porites* spp. can survive for longer periods. When these taxa are found in the corals, they can regenerate their coral cover back to normal structure (Rogers et al. 2008). The ecosystem-based management (EBM) approach suggests removing local stressors from the affected area will increase coral health and improves coral health (Marshall and Schuttenberg 2006; Marshall et al. 2006). Certain studies demonstrated that the application of specific phages can act only over the coral pathogen and does not affect the integrity of the resident microbiota (Atad et al. 2012; Cohen et al. 2013; Efrony et al. 2009).

5.6.2 Management and Conservation of Coral Reefs

The change in the climate either has direct changes (like warming, aridity) or indirect effect (elevated carbon dioxide) on the coral microbiomes' diversity, distribution, and functions; one of the major change that occurs were the change in the nutrient cycle (Singh et al. 2010). Thus, if there is a loss in the microbial diversity, it leads to dysfunctionality, low stability, and increases in the unknown consequences (Delgado-Baquerizo et al. 2016). Apart from these changes, the microbes have an indirect effect on the environment by the production of greenhouse gases, even though there is enough evidence showing the link between climate change and the microbes involved the focus-based studies on microbes for climatic change is less studied (Cavicchioli et al. 2019). Beneficial Microorganisms of Corals (BMC) can be incorporated into coral reefs through methods like microencapsulation and nanoparticles to feed adult corals heterotrophically; the use of biodegradable substrates like alginate act as a bio-friendly encapsulation of BMC to deliver it to the respective coral (Martínez Cruz et al. 2012). Human-Assisted Evolution (HAE) helps naturally enhance their stress tolerance including random mutation, acclimatization, and also drastic changes in microbial symbiont communities (van Oppen et al. 2015). Before the field application, it is advisable to test in a controlled experimental system; it is also to be noted that the selected BMC should not be a pathogen to the microbiome (Sweet and Bulling 2017). The variation in the microbial symbiont occurs through switching of the symbiont, shuffling of the symbiont, and also through horizontal gene transfer methods; this helps in the development of the overall population fitness of the coral generations (Torda et al. 2017; Quigley et al. 2019). The proper developmental phase should be made together by marine ecologists and coral reef conservationists to know in-depth about the long-term survival, preservation, and conservation of these diverse environments (Kelly et al. 2018; West et al. 2019).

5.7 The Way Forward

The benefits of the coral holobiont for the healthy survival of the coral reef is suffering due to rapid change in the climate and other anthropogenic disturbances; when stress is high, they lose their natural tendency to benefit the environment (Hughes et al. 2017a). But the microbial response of different spots should be studied separately to get a good insight for proper long-term conservation (Hutchins et al. 2019). Advanced research methodology should be preferred to gain access to microbial diversity of the coral reef, rather than a DNA-based molecular approach; most of the findings were performed and analyzed based on 16S rRNA analysis. Combining metatranscriptomics, with advanced microscopic techniques, should be used to validate and record the response of the microbial holobiont under varying stress situations finally leading to the identification of the fluxes over the ecosystem (Trevathan-Tackett et al. 2019). Recent findings show that there is a chance of increasing the ability to resist climatic stress response by modifying microbial holobiont or by the application of coral-specific probiotics (Trevathan-Tackett et al. 2019). Lastly, the interdisciplinary approach should be preferred for the in-depth understanding of climate-linked coral reef microbiome variations.

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