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# REVIEW: FORMATION AND METABOLIC FUNCTION OF CORAL RUBBLE BIOFILMS IN THE REEF ECOSYSTEM

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**ABSTRACT:** When coral dies, their calcareous skeletons constitute coral rubble in conjunction with the cementing activity of coralline algae and bacteria, creating a secondary reef structure which takes from years to decades to form. Healthy coral reefs differ from coral–rubble dominated reefs in microbial taxonomic composition and metabolic functional roles. The metabolisms of healthy reefs are dominated by autotrophic pathways, where carbon and nitrogen fixation dominate, while the metabolism of rubble–dominated reefs predominate in degradation of organic matter. Nitrogen fixation is 3 orders of magnitude lower in rubble–dominated reefs than in healthy reefs. Coral–rubble harbors a vast diversity of microbes that can precipitate carbonate through coupling several metabolic processes including photosynthesis, ureolysis, ammonification, denitrification, sulfate reduction, methane oxidation, and anaerobic sulfide oxidation. All these metabolic processes were found in rubble microbial communities, but ammonification and sulfate reduction were most prevalent. Anthropogenic and non–anthropogenic perturbations of healthy coral reefs in the past decades have led to the prevalence of rubble–dominated reefs in areas of the Caribbean where the ecological and functional shifts of the community still need further study.

**KEY WORDS:** Coral reef, Mexican Caribbean, Microbial communities, Metabolic process, Nutrient cycles

## INTRODUCTION

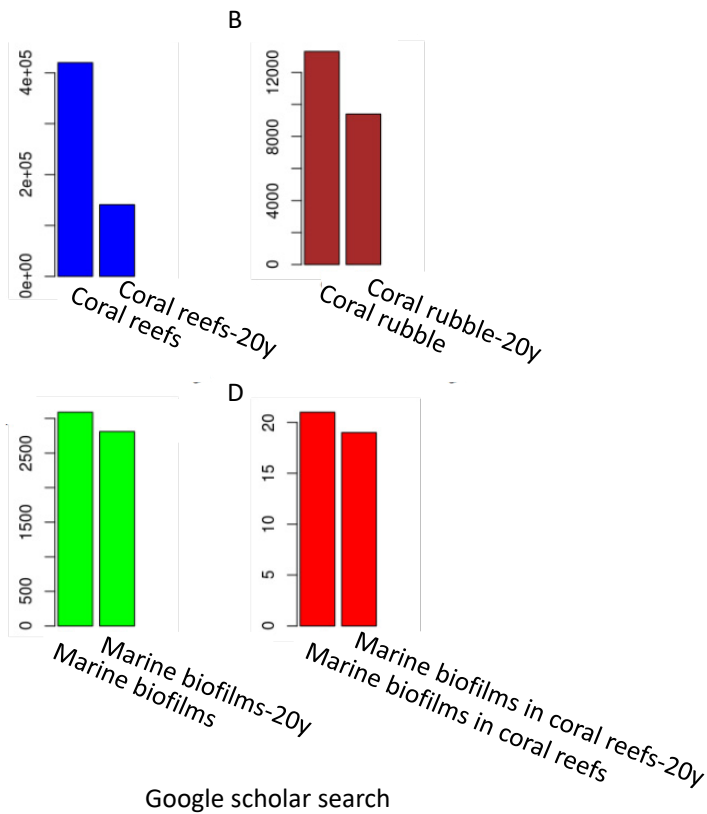
Microbialization (changes in ecosystem trophic structure by higher microbial biomass and energy use) leads to coral diseases and coral bleaching. Several causes such as overfishing and eutrophication facilitate fleshy and turf algae to grow on living reefs, promoting competition with corals and coralline algae for the benthos (Haas et al. 2016). In addition, *Sargassum* blooms have also impacted these environments in the past decade (Rodríguez–Martínez et al. 2010, Alvarez–Filip et al. 2019, Oviatt et al. 2019). These shifts in the coral reef environment culminate in coral death and rubble formation (Hoegh–Guldberg 1999, Hoegh–Guldberg et al. 2007, Harborne et al. 2017). A scenario where all these factors are present and exponentially increasing causes a change in the homeostasis of the coral colonies, making them vulnerable to disease (Hoegh–Guldberg 1990, Hoegh–Guldberg et al. 2007, Canadell et al. 2007). For example, the microbial composition of healthy coral mucus shifts into a pathogenic community, which induces disease in coral holobionts (Bourne et al. 2009, Bourne and Webster, 2012, Krediet et al. 2013). When coral's health deteriorates, the loss of their endosymbionts provokes the whitening and sometimes the death of the cnidarian (Hoegh–Guldberg et al. 2007, Shinzato et al. 2014, Hawkins et al. 2016). The reduction in coral benthos coverage directly impacts the function and structure of the reef (*Acropora* Biological Review Team 2005, Mayor et al. 2006, Alvarez–Filip et al. 2009).

When branching, finger, or leafy corals die, their calcareous skeletons form coral rubble in conjunction with the cementing activity of coralline algae and bacteria (Beltrán et al. 2016, Sanchez–Quinto and Falcón, 2019). These calcareous structures provide complex microenvironments, which sustain a wide microbial and macrofaunal diversity, and constitute a secondary reef structure (Beltrán et al. 2016, González–Gó-

mez et al. 2018, Sanchez–Quinto and Falcón, 2019, Li, 2019). The colonization of the dead coral with microbial biofilms begins to create a new reef structure that increases in extent according to the deterioration of corals (Hughes et al. 2017, Perry and Alvarez–Filip 2019). Weber et al. (2019) revealed that bacteria associated with corals differ from those found in the surrounding water. Beltrán et al. (2016) suggests that bacteria found in coral rubble are different to those in healthy corals, and they are different from those in sediments and microbial mats found in the same reef, suggesting that coral rubble is constituted by a specific microbiome.

There is a general lack of knowledge regarding the metabolism of bacteria in corals and coral reefs. However, it is a reality that the functional role of microbes in coral reefs is becoming a new research topic, since microorganisms play a fundamental role in the cycle of nutrients and energy in our planet (Paerl and Pinckey 1996, Arrigo 2005, Hawley et al. 2017, Weber et al. 2019, Sanchez–Quinto and Falcón 2019). In coral rubble, the processes of colonization and succession of organisms in addition to their implications in climate change are almost completely unknown. However, it is thought that bacteria and other microorganisms are the first to colonize coral rubble surfaces (Dang and Lovell 2016). After microbial colonization and biofilm formation (see below), coralline algae may colonize and provide a favorable calcareous substrate for the settlement of corals or other invertebrates (Harrington et al. 2004, Negri et al. 2004). This successional process is dependent upon water quality and other environmental factors (Blanchon et al. 2010, Rodríguez–Martínez et al. 2010, Pérez–Cervantes et al. 2017).

Although there is ample scientific literature on coral reefs, we have just started addressing questions regarding the formation and composition of coral rubble. Google Scholar searches



**FIGURE 1.** Results of Google Scholar literature searches. A. Results obtained when searching for “coral reefs” in 2020 (left) and the same search from 2000-2020 (right). B. Results when searching for “coral rubble” in 2020 (left), and the same search from 2000-2020 (right). C. Results obtained when searching for “marine biofilms” in 2020 (left), and the same search from 2000-2020 (right). D. Results obtained when searching for “marine biofilms in coral reefs” in 2020 (left), and the same search from 2000-2020 (right).

showed that 30% of the literature pertaining to “coral reefs” has been published from 2000–2020 (Figure 1A), yet 70% of studies pertaining to coral rubble have been published during this same time span (Figure 1B). However, most coral rubble research is mainly associated with geological reports; information about the colonizing diversity of these structures is scarce. The majority of research on marine biofilms (90%) has occurred within the past 20 years (Figure 1C). Literature pertaining to marine biofilms in coral reefs is uncommon, and the majority of these papers (90%) were also published in the past 20 years (Figure 1D). Finally, only one published report on

coral rubble biofilms was found in the past 20 years, suggesting this is an area of fruitful research.

In this Review, we synthesize the current knowledge on coral rubble, the mechanisms in which bacteria can colonize the rubble, and the metabolisms associated with these structures. Finally, we discuss the implications to coral reef ecosystems of loss of coral cover and increase in rubble-dominated communities based on knowledge generated in the Puerto Morelos reef in the Mexican Caribbean.

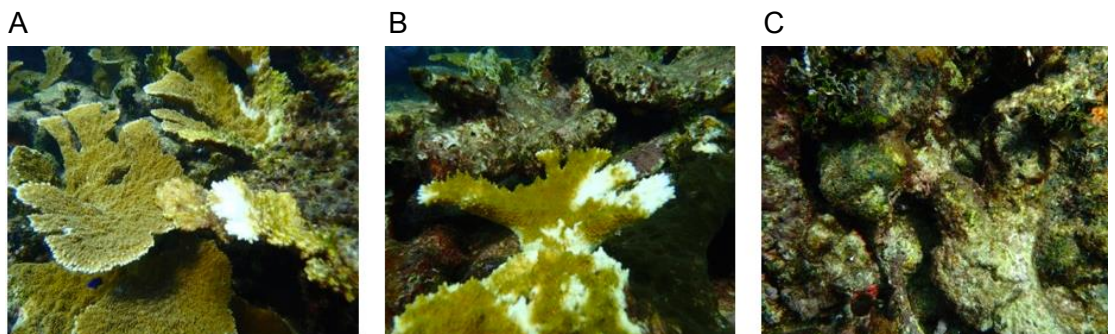
### Rubble Formation and Ecological Succession

Throughout the literature, there are different names that have been used to define rubble. Some of the names used as synonyms are biogenic mounds, lithified crusts, bioclastic sediments or biological framework. The composition varies but corals, stromatoporoids, calcareous sponges, bryozoans, foraminifera (coscinophragmatids), calcareous algae, annelids and stromatolitic/skeletal elements are frequent in geological samples (Arias et al. 1995). According to Rasser and Riegl (2002), a reef rubble by definition is a chemically or mechanically abraded part of reef rocks or frame-builders larger than sand fraction with the capability of binding the coral rubble fragments.

There are mainly 2 different ways in which rubble can form: natural and anthropogenic events. Water movement associated with waves, earthquakes, bioerosion, storms, and hurricanes can be considered natural events. Anthropogenic events include ship groundings, dredging, careless scuba diving activities, and dynamite fisheries (Gardner et al. 2005, Hoegh-Guldberg 2014, Hughes et al. 2017, Perry and Alvarez-Filip 2019). Other indirect factors that could increase the potential amount of rubble in a reef are a combination of natural and anthropogenic events such as diseases, changes in dissolved nutrient concentrations (eutrophication), blooms, and temperature increase (Bourne et al. 2009, Blanchon et al. 2010, Hoegh-Guldberg 2014, Haas et al. 2016, Hughes et al. 2017; Figure 2). All these events can create rubble directly or indirectly, transforming the entire structure or parts of the reef framework into loose pieces (Rasser and Riegl 2002, Reed 2002).

As the coral weakens, the calcareous structure breaks down and some of these fragments are deposited on the seabed where they disintegrate due to friction with sand and bioerosion, causing an increased loss of the reefs (Edwards 2010, Glynn and Maanzello 2015). Coral-rubble consists of these

**FIGURE 2.** Gradient of the deterioration of a coral reef. A. Healthy *Acropora palmata*. B. A diseased *A. palmata*. C. Calcareous rubble colonized by diverse algae and microbial biofilms. Photo by A. Sánchez-Quinto.



dead coral fragments. Further, branching corals such as *Acropora* are more fragile than more robust, slow growing corals such as encrusting *Montipora* and massive *Porites* and *Favites* (Great Barrier Reef Marine Park Authority 2011) and break easily during hurricanes. Although coral rubble is exposed to physical abrasion, they also contribute to secondary reef structure formation (Rasser and Riegl 2002, Reed 2002, Birkeland 2015). The formation of rubble also originates from early diagenesis, which has been active at different levels and at different geological periods. The early calcification of the microbial mats forming secondary stromatolitic frameworks are some of the first reported reef rubble worldwide (Arias et al. 1995, Reitner et al. 2000, Dupraz and Visscher 2005). The primary mineralogy of the corresponding substrates were mainly aragonitic with calcite also present in the fossil record within reefs (Arias et al. 1995, Reitner et al. 2000).

#### *Acropora palmata* in the Mexican Caribbean

In the western Atlantic, a few species of framework-building corals have dominated coral reef habitats throughout the region since the late Pleistocene (Jackson 1992, Budd and Johnson 1999, Precht and Miller 2007, Le Roy et al. 2014). *Acropora* has been one of the historical reef-building corals over the geological record on shallow-water coral reefs (Jackson 1992). The Acroporids have a main role in the function and structure of the reefs of the Mexican Caribbean (Figure 3) since no other reef-building species combines branching morphology and high rates of calcification (Alvarez-Filip et al. 2009, Young et al. 2012).

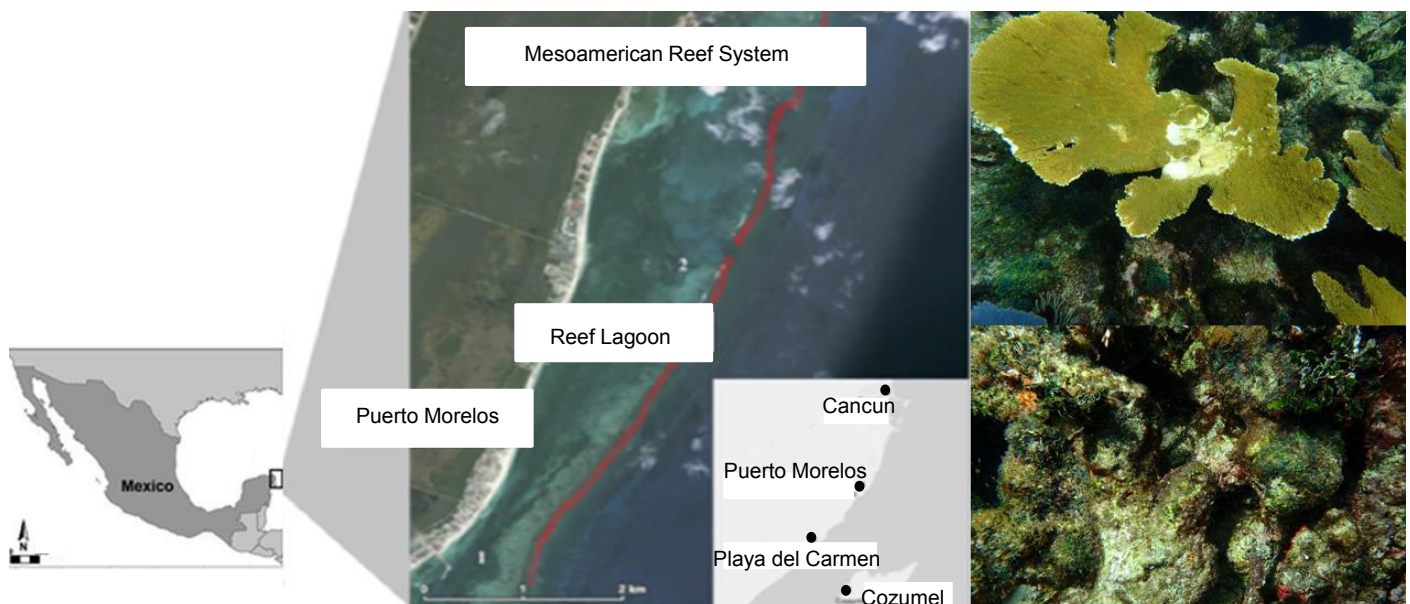
*Acropora* spp. have reflected a decline in population and the deterioration of their habitat in the Mexican Caribbean. Between the 1970's and 1980's the decline in *Acropora* populations was massive. Today, few signs of recovery have been reported in Mexican reefs (*Acropora* Biological Review Team 2005, Mayor et al. 2006, Estrada-Saldivar et al. 2019). This

situation coincides with the persistence and higher incidence of emerging diseases (e.g white syndrome; Anthony et al. 2008, Alvarez-Filip et al. 2019). The massive mortality of Acroporids in the Caribbean throughout the Mesoamerican Reef System generates patches of coral rubble (Jordán-Dahlgren and Rodríguez-Martínez 2003) which can be later colonized by macro and microorganisms.

#### Microbial Biofilms and Coral Rubble Colonization

Bacteria are main drivers of biogeochemical cycles and are distributed in many marine environments which are characterized by fluctuating and challenging conditions (Paerl and Pinckney 1996, Arrigo 2005, Bijlsma and Loeschcke 2005, Hawley et al. 2017, Kelly et al. 2018). The phenotypic plasticity of bacteria enables them to grow and thrive under these conditions (Bijlsma and Loeschcke 2005, Brooks et al. 2011). One example of this plasticity is the adhesion of bacterial cells to surfaces such as coral rubble and the formation of biofilms (Costerton et al. 1978, Flemming and Wingender 2010, Sanli et al. 2015, Beltrán et al. 2016, De Carvalho 2018). Biofilms are defined as consortiums of microorganisms that grow embedded in an extracellular adhesive-protective matrix. This conglomerate is composed of different biopolymers (e.g. proteins, nucleic acids, and lipids, among others) known as extracellular polymeric substances (EPS; Costerton et al. 1995, Flemming and Wingender 2001, Donlan 2002, Decho and Gutierrez 2017).

Biofilms can contribute to metabolic cooperation, genetic exchanges, and quorum sensing (microbial communication) in the community (Flemming 2016, Steinberg and Kolodkin-Gal 2015, Krupke et al. 2016, Dang and Lovell 2016, Decho and Gutierrez 2017). The ecophysiological activities of biofilms differ from those of free-living (e.g., planktonic) microbial communities in marine environments. These biofilm-associated microbial communities can survive, grow and maintain



**FIGURE 3.** Geographic location of the reef in Puerto Morelos, Quintana Roo, Mexico. *Acropora* spp. are important in the structure and function of these reefs.

activity in certain conditions, while other free-living individual organisms are not capable of doing so. The establishment, signaling, sensing of surface, and adaptive responses of the associated microbiota in a biofilm promotes diversification, niche specialization, and higher-level microbial community organization (Dang and Lovell 2016, De Carvalho 2018).

Microbial adhesion initiates by altering gene expression with consequent changes in cell surface chemistry, physiology, and behavior (Donlan 2002, Flemming 2016, Dang and Lovell 2016). Then, the microbes start with diffusive or active movement and EPS may facilitate the attachment of different species of bacteria (Flemming 2016, Flemming and Wingender 2001, 2010). Microorganisms are able to sense and respond to surface environmental signals (specific ligand-receptor interactions) and different surface components (Dang and Lovell 2016, De Carvalho 2018). The production of a biofilm matrix provides several benefits to the microbial community, such as protection from predators, viruses, antibiotics, other chemical toxins, and deleterious environmental pressures (Azam and Malfatti 2007, Matz et al. 2008, Krupke et al. 2016). The EPS in marine bacteria are characterized by high levels of uronic acids (e.g. D-glucuronic and D-galacturonic acid) which react to other chemical species (Kennedy and Sutherland 1987). The functional activity is reflected in the diversity of bacterial genera, although the composition of the EPS will depend not only on the species but also on the physiological stage of the biofilm (Grossart and Simon 2002, Banat et al. 2011). Hence, each type of EPS will provide different physical properties according to the polymer concentrations, composition, steric availability of functional groups on polymers, and types and abundances of ions (Chew et al. 2014, Decho and Gutierrez 2017).

The colonization of microbial consortia in the coral rubble is of great relevance to the ecological processes within the ecosystem, although we are only starting to understand their composition and associated metabolisms (Dupraz et al. 2009, Ainsworth et al. 2010, Sánchez-Quinto and Falcón 2019). Some studies reveal that Gammaproteobacteria, Alphaproteobacteria (*Roseobacter*), and Bacteroidetes predominate in the formation of EPS in marine environments, although yeasts and various types of algae have also been reported (Donlan 2002, Flemming and Wingender 2010, Witt et al. 2012, Dang and Lovell 2016, Li 2019). The formation of biofilms can persist if the appropriate environmental conditions exist (Donlan 2002, Flemming and Wingender 2010, Uthicke et al. 2012). Interestingly, the properties of EPS can change post-secretion due to photochemical, geochemical, or enzymatic processes or by trapped or absorbed molecules (Decho and Gutierrez 2017). Thus, EPS composition is continually changing according to environmental modifications, which will impact the functionality and structure of communities. Therefore, these conglomerates in coral rubbles support critical ecological and biogeochemical shifts in coral reef ecosystems (Dang and Lovell 2016).

### Coral Rubble Biofilm Diversity

Microbial diversity from healthy and diseased corals has been well studied (Cook 2009, Wegley et al. 2007, Ainsworth

et al 2010, Sunagawa et al. 2010, Bourne et al. 2016, and many more). Additionally, some studies are starting to characterize microbial biofilms from different coral rubble reefs around the Mexican Caribbean (Sánchez-Quinto et al. unpublished data). Sunagawa et al. (2010) identified differences between species and morphologies of coral species, in which corals that form massive, mound-shaped colonies (e.g., *Montastraea* spp., *Diploria strigosa*, and *Porites astreoides*) have higher microbial diversity than branch-forming Acroporid species (*Acropora* spp.). Frias-Lopez et al. (2002) and Beltrán et al. (2016) showed that the microbial composition associated with healthy *A. palmata* is less diverse and different from the microbial composition of the biofilm that colonizes the coral rubble. According to results based on a metagenomic analysis of coral rubble by Sánchez-Quinto and Falcón (2019), Gammaproteobacteria and Alphaproteobacteria were the groups of organisms with a greater abundance in the coral rubble structures, followed by Actinobacteria, Deltaproteobacteria and Betaproteobacteria. In contrast, in healthy *A. palmata* and other corals, Bacteroidetes, Proteobacteria, and other groups such as Firmicutes, Planctomycetes, Cyanobacteria and Actinobacteria were the most abundant (Rohwer et al. 2001, Wegley et al. 2007, Birkeland 2015, Beltrán et al. 2016, Li 2019). Furthermore, Fungi, Demospongiae, green and rhodophilic algae were also found in the coral rubble, and Thaumarchaeota was the most abundant Archaea (Sánchez-Quinto and Falcón 2019). According to Wegley et al. (2007) similar archaeal species may be found on different healthy coral species where Crenarchaeota and Euryarchaeota are the most abundant. Interestingly, a similar diversity of viruses has been reported in healthy corals and coral rubble in which bacteriophages predominate (Wegley et al. 2007, Sánchez-Quinto and Falcón 2019).

Data published to date suggests that coral rubble and the microbial diversity within these structures can change from a healthy high-coverage reef to a low coverage and mainly rubble-dominated reef. On the other hand, the composition of the microorganisms that colonize this rubble are not affected under scenarios of pH decrease or temperature increase, suggesting that these microbial biofilms will continue to colonize coral rubble under conditions of climate change (Beltrán et al. 2016). The bacteria associated with corals and coral rubble have not been considered for predictions about the future responses to climate change scenarios (Ainsworth et al. 2010). Therefore, the bacterial diversity and the functionality associated with these ecosystems and their interactions in cementation processes is fundamental.

### Metabolism of Coral Rubble Dominated Reefs

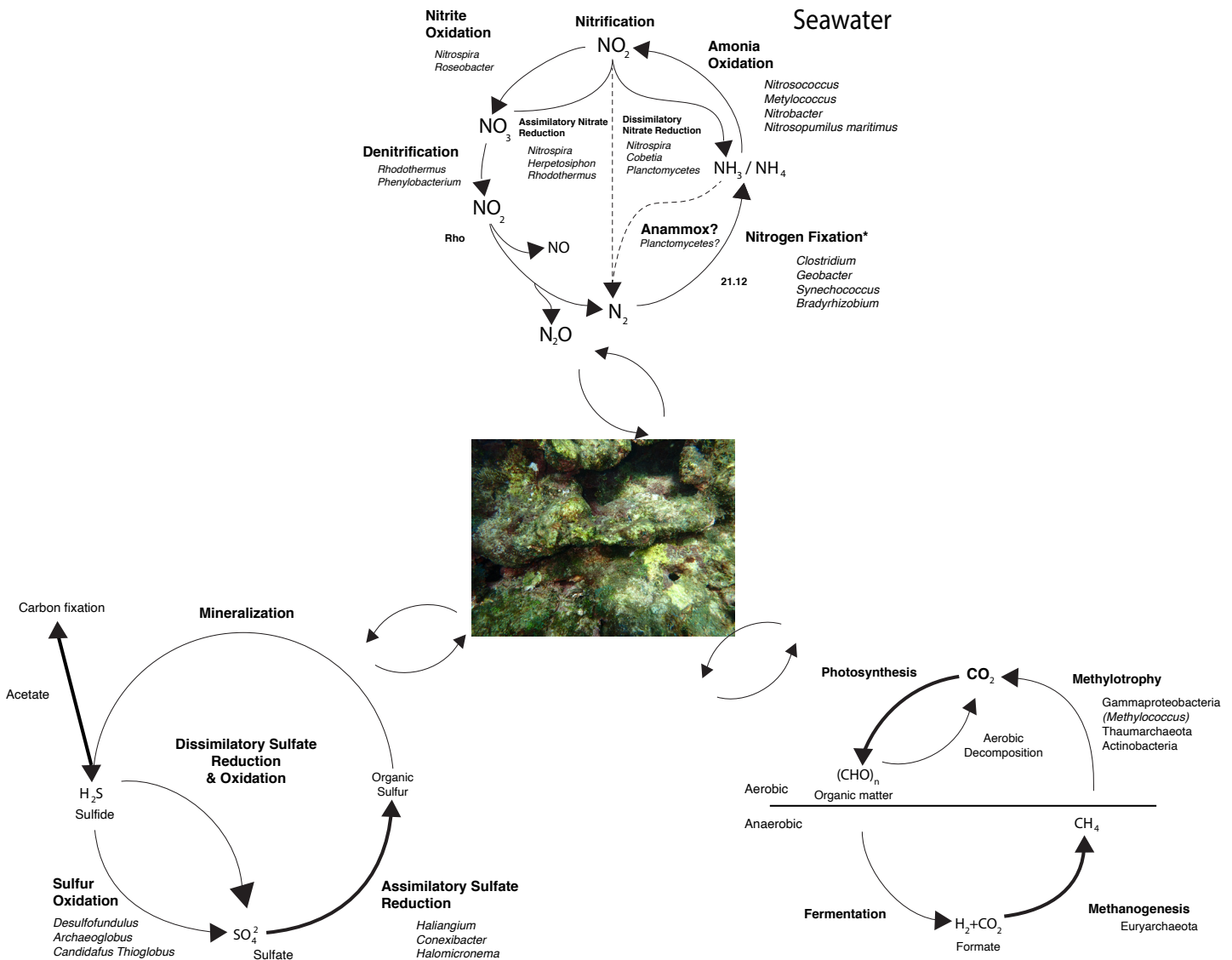
Microbes have important roles in numerous marine processes such as organic matter remineralization, nutrient regeneration and element cycling (Dang and Lovell 2016, Haas et al. 2016, Hawley et al. 2017). They can concentrate pollutants (e.g., heavy metals) and transfer energy in food webs (Azam et al. 1983, Decho 1990, Bu-Olayan et al. 2005, De Carvalho and Caramujo 2012). They also have an important role in deleterious effects such as biofouling, biocorrosion, and the persistence

and transmission of harmful or pathogenic microorganisms and their genetic determinants (Rohwer et al. 2001, Reopanichkul et al. 2009, Bourne et al. 2009, Flemming and Wingender 2010, Bourne and Webster 2012). In coral reefs, there is evidence that microbes contribute to the induction of benthic invertebrate larval settlement and xenobiotic compound biodegradation (Donlan 2002, Negri et al. 2004, Dang and Lovell 2016).

Sanchez–Quinto and Falcón (2019) identified the metabolic processes within coral rubble structures of Acroporid remains in Puerto Morelos reefs using a metagenomic approach. In contrast to healthy reefs, which are characterized as autotrophic ecosystems and where carbon or nitrogen fixation predominate (Kelly et al. 2018, Weber et al. 2019), the predominant metabolism in coral rubble is associated with the degradation of organic matter. Therefore, a possible functional change in ecosystems could be the succession from an ecosystem where autotrophic metabolism predominates to a

heterotrophic one (Haas et al. 2016, Dang and Lovell 2016, Sanchez–Quinto and Falcón 2019). Coral rubble also has an important role in the nitrogen cycle primarily through denitrification as well as assimilatory and non–assimilatory reduction of nitrate. Further, in coral rubble, nitrogen fixation is 3 orders of magnitude lower than in healthy corals (Lesser et al. 2007, Sanchez–Quinto and Falcón 2019), although there is a great diversity of nitrogenase–associated Alphaproteobacteria, suggesting the role of heterotrophic diazotrophs in coral rubble (Figure 4).

Coral reefs are likely to play an important role in the biogeochemical sulfur cycle (Arrigo 2005, Raina et al. 2010, Hawley et al. 2017), since sulfur is found in seawater and sedimentary rocks, including calcium and magnesium carbonates (Raina et al. 2010). In the coral rubble, assimilatory sulfate reduction is the predominant pathway for the S cycle (Sanchez–Quinto and Falcón 2019). This suggests that most of the sulfur is metabolized into organic compounds. In addition, Actinobacteria



**FIGURE 4.** Coral rubble structures originating from the death of *A. palmata* colonies. Model of the potential functional role of bacteria in coral rubble, indicating biogeochemical pathways associated with the nitrogen, sulfur and methane cycles. Modified from Sanchez–Quinto and Falcón (2019).

in coral rubble can have a key role in sulfate assimilation, and in the dissimilation of nitrate and methane (Sanchez–Quinto and Falcón 2019, Li 2019). The coral rubble is also potentially important in the carbon cycle. Archaea such as Euryarchaeota could play a key role for methanogenesis and the presence of methanotrophs such as Gammaproteobacteria suggests multiple methane transformation strategies within the rubble community.

### Cemented Coral Rubble Biofilms and Their Role in Carbonate Precipitation

The role of coral rubble cementation in reef development (processes that may take from years to decades) not only contributes a significant amount of carbonate to the primary reef structure, but it also aids in stabilization (binding) of the reef framework (Hughes and Connell 1999, Barott et al. 2011, Sweet et al. 2013, Beltrán et al. 2016, Sheppard et al. 2017). Lithification by either biological or physical cement stabilizes the secondary reef structure and is involved in the composition and preservation of the rubble (Rasser and Riegl 2002). Other authors have reported that non–cemented structures have been deteriorating for the past 90–100 years (Holmes et al. 2000, Birkeland et al. 2013). According to Birkeland (2015), the recovery of coral communities on the reef crest and outer reef flat is significantly higher than those behind the reef crest, where the substratum is mainly loose rubble. Birkeland (2015) suggested that the coral recovery depends on the resistance and resilience of each reef rather than perturbations. In reefs where loose rubble predominates, the recovery will take decades until the substratum lithifies or until the corals re–aggregate (Birkeland et al. 2013). Victor (2008) determined that there was no significant difference in larval recruitment between unstable rubble and lithified substrata, but the survival of recruits was significantly higher on lithified substrata.

Reef ecosystems are relevant in terms of their biological diversity and ability to produce carbonate. There are reports of the relationship between microorganisms and carbonate precipitation. These reports provide an understanding of the fundamental role of microorganisms (mainly prokaryotes) for the precipitation or dissolution of carbonates (Paerl 2001, Zhu and Dittrich 2016, Sanchez–Quinto and Falcón 2019). James (1974) reported that *A. palmata* precipitates aragonite. However, carbonate mineralization induced by microbial activity and certain calcareous algae (CCA) in the coral rubble is associated with magnesium–rich calcite (Camoin et al. 1999, Riding 2006, Beltrán et al. 2016).

The function of these carbonates is fundamental for the development of the reef and the organisms that inhabit it since they provide support, shelter, structural stabilization, surface to colonize, and trap organic matter, among others (Moberg and Folke 1999, Riding 2011, González–Gómez et al. 2018). Microbial biofilms have the ability to trap sediments and elaborate microscale changes in pH. They serve as a crystal core providing zones for the precipitation of calcium carbonate ( $\text{CaCO}_3$ ; Flemming and Wingender 2010, Flemming 2016,

Beltrán et al. 2016, Dang and Lovell 2016, De Carvalho 2018). Microbes can precipitate carbonate through the interaction of different metabolic pathways. Among these metabolisms are photosynthesis, ureolysis, ammonification, denitrification, sulfate reduction, anaerobic sulfide oxidation and methane oxidation (Zhu and Dittrich 2016). All these metabolic pathways were identified in the coral rubble microbial communities, with ammonification and sulfate reduction the most abundant (Sanchez–Quinto and Falcón 2019). Furthermore, in marine systems photosynthetic microorganisms are responsible for triggering calcite precipitation (Arp et al. 2001). There is still much to decipher regarding the role of biofilms in the accretion of coral reefs. Nevertheless, these microbial communities possess the metabolic potential to have an important role in these processes.

### Perspectives

In the future, a metagenomic comparison between healthy corals, coral rubble, and their environment is crucial to understand the diversity and the potential metabolic pathways associated with coral reefs. Moreover, coral rubble from different regions should be analyzed using “omics” to understand if there are patterns in their composition relating to environmental conditions or biogeography. Furthermore, more research is needed in order to reveal the relative contributions of these rubble communities to the ecosystem. Understanding the diversity associated with coral rubble and the interactions in biogeochemical processes is essential to predict the functional change of coral reefs.

The ecophysiology and mechanisms of carbonate mineral precipitation in the colonizing communities of the coral rubble should be also considered in future research. The presence of pathways associated with the generation of methane,  $\text{CO}_2$ , and denitrification indicates that it is important to carry out characterizations with metatranscriptomics and ecophysiology to determine the contribution of greenhouse gases in these emerging ecosystems.

According to Rohwer et al. (2001), microbial wealth increases with deterioration of coral health, which in turn may have a role in the pathogenicity of the holobiont. Hence, more research on coral reefs and their interaction with pathogens should be addressed. Resolving the connection between coral and algal microbiome structure through a metabolomic outcome will be crucial for determining the mechanisms underlying the algal phase shifts. Finally, understanding the diversity and functionality associated between coral reefs and the interactions or shifts in biogeochemical processes is essential to predict functional changes in a future where coral rubble is more likely to be dominant. An interdisciplinary characterization (i.e., using isotopes and PCR/shotgun–sequencing) of coral rubble reefs in the Mexican Caribbean will contribute to understand the role of the biofilms in the biogeochemical cycles and their implications in the formation of coral reefs. Therefore, the study of biofilms in the Mexican Caribbean coral reefs is crucial and still needs further investigations.



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