Chapter 7
The Microbiota of Brazilian Mangroves

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7.1 Introduction

Mangrove sediments are complex systems affected by the interaction among geological, hydrological, physicochemical, and biological factors (Köster and Meyer-Reil 2001) that are intensively colonized by microorganisms such as bacteria, archaeon, fungi, cyanobacteria, algae, virus, and protozoa. These microorganisms play an important role in the cycles of matter and energy in sediments (Danovaro et al. 2000; Moreno et al. 2006).

As in the water column, high metabolism leads to an increase in the biomass of microbial producers, consumers, and decomposers, forming a microbial food chain called "microbial loop" (Azam et al. 1983), responsible for the transfer organic matter and energy to the higher trophic levels and nutrient regeneration, contributing to the formation of humic substances and oxygen, which will be consumed through aerobic metabolism, consequently exerting influence on the carbon transference of the food chain of mangrove sediments (Danovaro et al. 2000).

The microbial contribution to the system depends on the density, diversity, and activity of the present microorganisms, which in turn are influenced by biotic and abiotic factors. Among them, densities and species of prey and predator, sediment composition, organic and inorganic matter concentrations, local hydrodynamics, granulometry, and temperature. On the other hand, microorganisms influence the sediments where they occur through their metabolic activity (Peroni and Rossi 1986; Deming and Baross 1993). The main questions in the microbial ecology of

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mangroves are how the microbiological communities are adapted to the conditions of this environment and what are the main factors controlling the diversity, distribution, and activity of these organisms (Moreno et al. 2006).

The importance of bacterial, cyanobacterial, and fungal species is being widened since the products of their metabolism have been the subject of bioprospecting studies and many species have been isolated from mangrove sediments due to their capacity to biodegrade certain compounds and produce enzymes and molecules of commercial interest (Demain 2007; van Dommelen et al. 2016; Luna and Townsend 2007).

This chapter will cover the knowledge on the Brazilian mangrove microbial loop, including studies on the diversity of bacteria, archea, fungi, and viruses in mangrove sediments.

7.2 Microbial Loop

Microorganisms play a major role in the maintenance of marine ecosystems. Nevertheless, for many years, they have received little attention from researchers. Aquatic bacteria have great importance not only in the decomposition of organic matter and in the remineralization of inorganic nutrients (Pomeroy et al. 2007), but also in adding energy to higher levels. In some ecosystems, such as mangroves, microbial processes greatly contribute to productivity, regenerating nutrients and exporting them to adjacent ecosystems (Hemminga et al. 1994; Alongi 1996; Holguin et al. 2001; Sjöling et al. 2005).

Until the end of the 1970s, researchers believed that the role of microorganisms, in the traditional food web, was only as a food source to planktonic organisms, and discarded them in studies of carbon flux dynamics (Fenchel 2008; Andrade 2015). The idea was of a straight flow, where microorganisms were just the base of the food web, giving no direct input of energy and carbon to the higher levels. But, with the development of new techniques and study methods (e.g., estimate growth rates), and the improvement of the existing ones, the idea of a straight flow became outdated (Pomeroy 1974; Steele 1974; Azam et al. 1983; Azam 1998; Fenchel 2008). Herewith, scientists discovered that the counts of microorganisms were underestimated, corresponding to only about 10% of the actual number of organisms in nature (Krambeck et al. 1981; Azam et al. 1983; Andrade 2015).

However, what is the *Microbial loop*? In the early 1980s, Azam et al. (1983) coined the term to describe the result of several ecological interactions between microorganisms involved and the pathways of nutrients (Fig. 7.1). Figure 7.2 displays examples of microorganisms commonly found in Brazilian mangrove sediments.

Most of the dissolved organic matter (DOM) in the marine environment is controlled by microorganisms, mainly by heterotrophic bacteria, cyanobacteria, and heterotrophic nanoflagellates (Pomeroy 1974; Anderson and Ducklow 2001). The cyanobacteria are a significant portion of the autotrophic phytoplanktonic

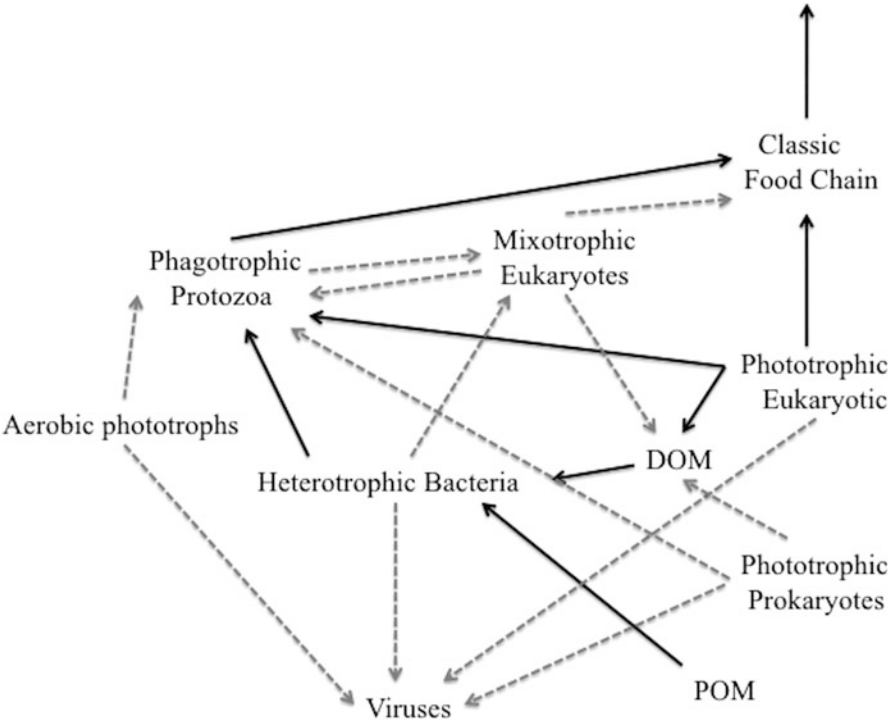

Fig. 7.1 Overview of general microbial loop pathways that also operate in mangrove sediments. Black arrows: Microbial Loop described by Azam et al. (1983). Gray dotted arrows: subsequent additions to the microbial loop. *POM* particulate organic matter. *DOM* dissolved organic matter. (Adapted from Fenchel 2008)

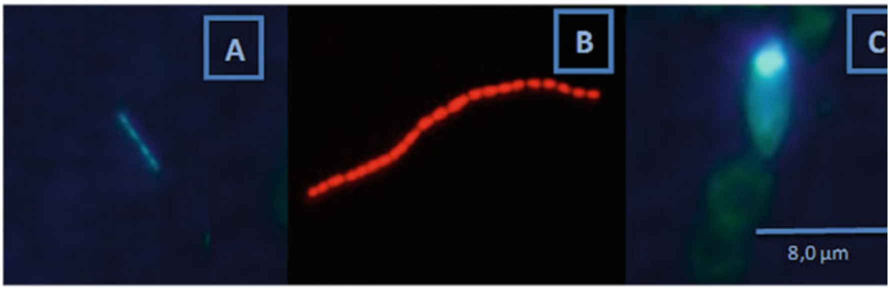

Fig. 7.2 Heterotrophic bacteria, cyanobacteria, and nanoflagellates from Brazilian mangrove sediment samples. (**a**) Heterotrophic bacteria colored with fluorochrome DAPI (4′,6-diamidino-2-phenylindole), (**b**) Self-fluorescence of cyanobacteria chain, and (**c**) Heterotrophic nanoflagellate with DAPI (4′,6-diamidino-2-phenylindole)

biomass, being responsible for a significant part of the primary production in aquatic ecosystems, with densities of about 10^5 cells mL^{-1} (Oliveira 2000; Pomeroy et al. 2007; Pereira 2014). The heterotrophic bacteria are responsible for about 30% of the primary production in coastal waters, with average densities of 10^6 cells mL^{-1} (Pereira 2014). They also have enzymes that develop important activities (e.g., cellulolytic, pectinolytic, amylolytic, and proteolytic), which allow the decomposition of mangrove matter (Matondkar et al. 1981).

Nanoflagellates present average densities of 10^3 cells mL^{-1} and are great predators of autotrophic and heterotrophic picoplankton, developing an essential ecological role in the control of the bacterial community (Caron et al. 1991; González 1993; Fernandes and Mesquita 1999; Oliveira 2000; Pereira 2011; Pereira 2014; Andrade 2015). In the early 1990s, viruses were added to the model of the Microbial Loop, acting in the control of bacterial density (Proctor and Fuhrman 1990; Oliveira 2000). They can change the distribution of particles and other organisms in any trophic level (Proctor and Fuhrman 1990; Bratbak et al. 1992, 1994; Thingstad et al. 1993; Fenchel 2008). According to Bratbak et al. (1994), viral densities vary from 2×10^6 to 50×10^6 Virus Particle-Like (VPL) mL^{-1}, in coastal and estuarine ecosystems, much higher than in offshore and oceanic systems (0.2×10^6–2×10^6 VPL mL^{-1}). Also, the grazing rates of bacteria over viruses are similar to protozoan grazing rates, but since viruses are highly specific, their effects are different and sustain the high diversity of bacteria (Fenchel 2008).

Focusing on the mangrove ecosystem, the mineralization of organic matter in sediments, especially nitrogen fixation, is an important role of microorganisms (Sjöling et al. 2005). The mangrove sediment is rich in organic matter, receiving abundant light and water, resulting in very high biomass production rates (Ghizelini et al. 2012). According to Alongi (2002), the microbial biomass in mangrove sediments is never greater than 1.2% of the total mass of detritus, and 91% of this biomass is composed of bacteria and fungi.

Unfortunately, according to Ghizelini et al. (2012), many Brazilian mangroves are contaminated, which can modify their hydrology, sediment composition, and nutrient dynamics (Lee et al. 2006). There are only a few studies about the microbial loop in Brazil, especially in the sediment of coastal and mangrove areas. Most studies were carried out in the Southeast coast, relating microbial densities to some anthropogenic impacts (e.g., sewage discharge and oil spills), population structure, grazing (e.g., nanoflagellates, viruses), and abiotic factors (Mesquita and Fernandes 1996; Fernandes and Mesquita 1999; Koch and Wolff 2002; Oliveira et al. 2007; Gomes et al. 2010; Souza et al. 2010; Pereira 2011; Moraes et al. 2014; Pereira 2014; Andrade 2015; Quintana et al. 2015; Santana et al. 2021; Tavares et al. 2021; Bezerra et al. 2022).

In recent years, with the development of pyrosequencing and new-generation sequencing techniques, in Brazil, the focus has been on the study of microbial diversity, as can be seen in the next session.

7.3 Microorganisms in Brazilian Mangrove Sediments

Mangroves are known to be rich in microbial diversity, which is fundamental to their homeostasis. According to Alongi (2002), about 91% of the mangrove microbial biomass corresponds to bacteria and fungi involved in nutrient transformation, biogeochemical cycles, and, for some specific groups such as cyanobacteria, in photosynthesis. Besides, they present a high biotechnological potential for being used in bioremediation and the production of certain substances.

These microorganisms not only contribute to high productivity but are also responsible for most of the carbon flow in the sediments, since much of the organic matter retained there undergoes degradation or chemical modification by the microorganisms (Kristensen et al. 1998).

Thus, due to the great importance of microorganisms mangrove ecosystems, knowing their diversity and the processes they carry out can contribute to the advancement of knowledge about the functioning of ecosystems, as well as to the development of protection measures and more effective public policies. In the next sections, we will explore a little more about the diversity of bacteria, archaea, fungi, and viruses in the Brazilian mangroves.

7.3.1 Bacterial and Archea Diversity in Brazilian Mangrove Sediments

Heterotrophic bacteria are 1–2-μm-sized species in the domain Bacteria and live by assimilating dissolved organic compounds from water or by degrading nonliving detrital organic matter (Fig. 7.3). Species in the domain Archaea are also widely present in both sea and freshwater habitats (Sherr and Sherr 2009); however, Archaea studies in Brazilian mangroves are rare.

Bacteria in mangrove sediments, including cyanobacteria, play an important role in the biogeochemical cycles of these coastal ecosystems. These organisms are directly involved in the transformation of nutrients, photosynthesis, nitrogen fixation, methanogenesis, phosphate solubility, sulfate reduction, and production of other substances, including antibiotics and enzymes (Santos et al. 2010). The analysis of prokaryotic communities is crucial to understand ecosystem functioning (Fernandes et al. 2010).

However, for many years, the development of knowledge about microbial diversity has been linked and limited to cultivation methods. The development of molecular techniques capable of identifying noncultivable organisms has considerably increased knowledge of biodiversity in general.

Investigations on marine sediment diversity based on molecular methods began in 1996 (Gray and Herwig 1996), followed by several studies in this field (Urakawa et al. 1999; Shao et al. 2004; Mussmann et al. 2005). Nevertheless, studies on mangrove sediments started with Liang et al. (2006), investigating bacterial diversity

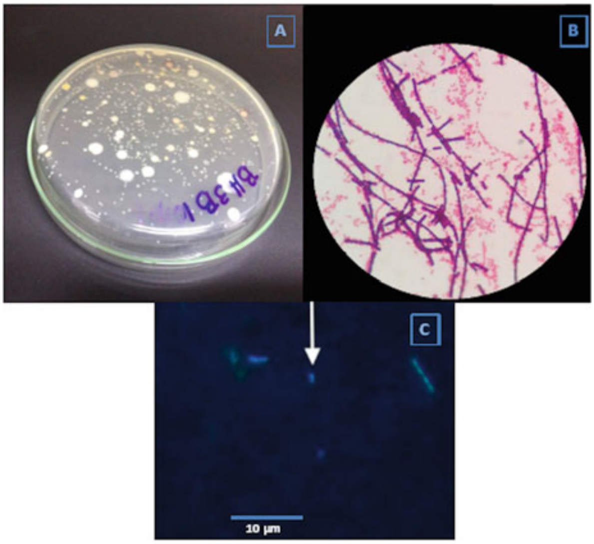

Fig. 7.3 Heterotrophic bacteria isolated from Brazilian mangrove sediments. (**a**) culture media; (**b**) gram; (**c**) epifluorescence microscopy

in subtropical mangroves showing the presence of many gene sequences derived from unknown taxa.

Numerous studies have demonstrated the uniqueness of coastal sediments concerning the composition of their microbiota (Gray and Herwig 1996; Bano et al. 1997; Ravenschlag et al. 1999; Urakawa et al. 1999; Todorov et al. 2000; Polymenakou et al. 2005; Gomes et al. 2010; Santos et al. 2011). However, there is still a gap in the knowledge of microbial biodiversity in mangrove sediments. In Brazil, the studies focus on hydrocarbon-contaminated environments and are mostly conducted in Southeast Brazil.

Dias et al. (2010) conducted a study on pristine mangrove sediments and demonstrated the predominance of the classes Alphaproteobacteria, Gammaproteobacteria, and Acidobacteria. Through molecular techniques (DGGE – Denaturing Gradient Gel Electrophoresis), the authors were able to recover a great diversity of microorganisms as well as to correlate this diversity with environmental factors.

Gomes et al. (2008) conducted a study on urban mangroves under strong anthropogenic pressure and demonstrated the dominance of Alteromonadales, Burkhholderiales, Pseudomonadales, Rhodobacteriales, and Rodocyclales. Members of these groups are involved in hydrocarbon degradation, thus justifying their predominance in human-impacted environments. Gomes et al. (2010) also demonstrated a limited diversity of Betaproteobacteria and Actinobacteria in mangrove sediments from impacted areas in Rio de Janeiro state.

Peixoto et al. (2011) demonstrated that the composition of the microbial community of mangrove sediments reflects the spatial variation of the present pollutants and that the microbial communities are heterogeneously distributed. In this study, Total Petroleum Hydrocarbon (TPH) levels were significantly associated with the presence of bacteria Betaproteobacteria, whereas anthracene and Polycyclic Aromatic Hydrocarbons (PAHs) levels were strongly associated with the presence of Actinobacteria.

Rocha et al. (2016), in a study conducted in the mangroves of Barra Grande, Ceará State, showed a high diversity of Gammaproteobacteria besides the record of three distinct community structures, which evidences the presence of different microhabitats within the same mangrove. Differences in the structure of microbial communities may be associated with the specificity of each site since mangroves are influenced by two distinct environments (marine and terrestrial).

The table below shows studies carried out in different Brazilian mangroves to investigate bacterial diversity in mangroves and estuarine systems using culture-independent methods (Table 7.1).

Brazil still needs many studies that cover all the mangroves in the different regions of the country, in order to fill the gaps in knowledge about the diversity of the microbiota in this ecosystem. Despite the scarcity of studies, some studies have already documented regions with highly diverse bacterial populations and with a very specific microbiome (Rocha et al. 2016; Zampieri et al. 2020). However, we still need to understand how the different types of contaminants influence the diversity and composition of the community, which groups resist these adverse conditions, and which groups have their population reduced.

7.3.2 *Fungi Diversity in Brazilian Mangrove Sediments*

Fungi are nonmotile eukaryotes, whose cell walls are usually made of polysaccharide chitin presented as microfibrillar bundles, for example, cellulose. Other glycans such as mannan, galactosan, and chitosan may replace chitin in some fungal cell walls (Madigan et al. 2008). These organisms are absorptive heterotrophs, and secrete exoenzymes into the environment, later absorbing the digested nutrients. Most are saprophytes that decompose dead organic matter, but some are parasites of plants and animals.

Fungi are informally divided into unicellular yeasts and filamentous molds based on their overall appearance. Dimorphic fungi have both mold and yeast life cycle stages (Fig. 7.4). Fungal life cycles are usually complex, involving both sexual and asexual forms of reproduction. They occur in diverse habitats; some are aquatic, but most inhabit terrestrial habitats, in soil, or dead plant matter, playing a crucial role in the mineralization of organic carbon.

Mangrove forests are among the most productive ecosystems in the world and are characterized by intense carbon processing (Kristensen et al. 1998). Fungi are thought to play an important role in organic matter decomposition pathways in this ecosystem (Jones 2000). Their diversity has been widely studied, especially on mangrove trees and decomposing litter (Ananda and Sridhar 2004).

Mangrove trees are interesting study objects for mycologists, because the bases of their trunks and the aerating roots are permanently or intermittently submerged, whereas the upper parts of roots and trunks are rarely reached by the saltwater. Thus,

Table 7.1 List of studies using culture-independent methods to access bacteria diversity in mangroves and estuarine systems

Study area	State	Method	Sample	References
Mangrove	RJ	Sequencing of 16S rRNA gene and T-RFLP	Sediment	Brito et al. (2006)
Mangrove	CE	PCR analysis of 16S rRNA gene and DGGE	Water	Sousa et al. (2006)
Estuary of Guanabara Bay	RJ	16S rRNA PCR, DGGE, and clones library	Water	Vieira et al. (2007)
Mangrove at Guanabara Bay	RJ	16S rRNA PCR, DGGE and clones library	Sediment	Gomes et al. (2008)
Mangrove at Guanabara Bay	RJ	16S rRNA PCR, DGGE and clones library	Sediment	Gomes et al. (2010)
Mangrove of Cardoso Island	SP	Denaturing gradient gel electrophoresis (DGGE) and analysis of 166 sequences from a clone library	Sediment	Dias et al. (2010)
Mangrove of Todos os Santos Bay	BA	Denaturing gradient gel electrophoresis (DGGE)	Sediment	Peixoto et al. (2011)
Mangrove of Cananéia and Bertioga	SP	Pyrosequencing of 16S rRNA gene	Sediment	Andreote et al. (2012)
São Sebastião Channel and Búzios Island	SP, RJ	16S library and pyrosequencing	Water and sediment	Carlos et al. (2013)
Cardoso Island	SP	T-RFLP and pyrosequencing of 16S rRNA gene	Sediment	Mendes and Tsai (2014)
Barra Grande mangrove	CE	T-RFLP	Sediment	Rocha et al. (2016)
Camamu Bay	BA	MiSeq sequencing	Water	Affe et al. (2018)
São Sebastião Channel and Santos Bay	SP	MiSeq sequencing	Sediment	Zampieri et al. (2020)

Modified from Bruce et al. (2012). Brazilian states: Ceará (CE), Bahia (BA), Rio de Janeiro (RJ), São Paulo (SP). See Chap. 3, Maps 5, 11, 13, and 14, respectively

terrestrial fungi and lichens occupy the upper half of the trees and marine species occupy the lower. At the interface, there is an overlap between marine and terrestrial fungi (Kohlmeyer 1969).

According to Sridhar (2013), the first monograph on marine mycology "A Treatise on Fungi in Oceans and Estuaries" was published by Johnson and Sparrow in 1961. In 1975, Hughes summarized the studies on marine mycology up to that year. Kohlmeyer and Kohlmeyer (1979) listed 209 filamentous fungi in their taxonomic and ecological monograph (Marine Mycology: The Higher Fungi), subsequently elevating them to 321 species (Kohlmeyer and Volkmann-Kohlmeyer

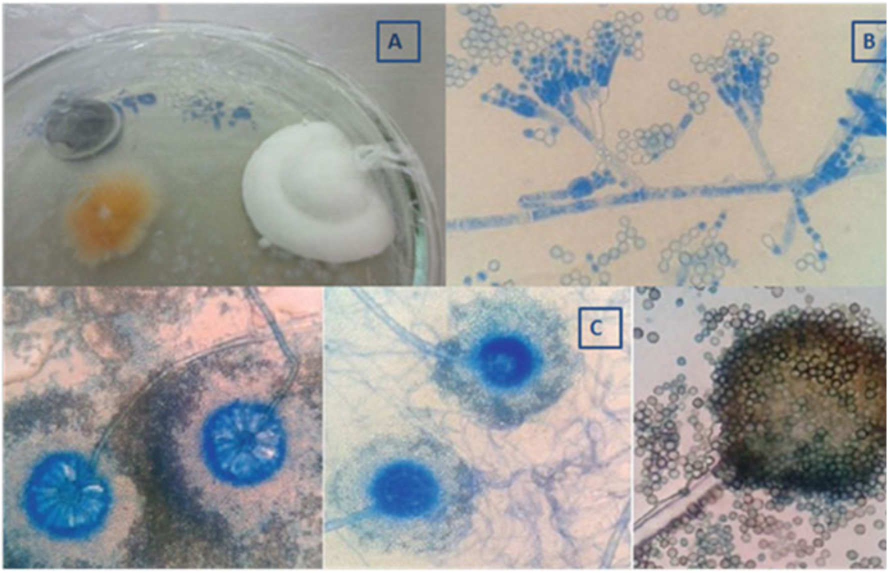

Fig. 7.4 Fungi isolated from Brazilian mangrove sediments. (**a**) Culture showing colonies of *Aspergillus* (gray and orange) and *Penicillum* (white); (**b**) *Penicilum* conidia; and (**c**) *Aspergillus* conidia

1991), until Hyde and Pointing (2000) reached the mark of 444 species. The literature review by Schmit and Shearer (2003) reveals the occurrence of 625 fungal species from different mangrove habitats. About 200 species have been considered as obligate marine fungi, whereas 131 species that occur in mangrove sediment or peat are not restricted to the marine environment.

In Brazil, there is little knowledge of mangrove fungi in comparison to what is known about bacteria. The molecular/culture-independent methods that have been widely used to study bacteria have not yet been reported on the same scale for fungi. Some studies, like Soares et al. (1997), found ascomycetes, basidiomycetes, zygomycetes, and mitosporic in the mangroves. More often, studies try to find a biotechnological application to fungi, focusing on species such as *Cyclothyrium* spp., *Penicillium* spp., and *Psilocybe* spp., isolated from the Santos' estuarine sediment and showing the ability to degrade phenanthrene and pyrene. A study by Gomes et al. (2011) isolated and identified filamentous fungi from mangrove sediments of Pernambuco, in Northeast Brazil. They found *Penicillium* and *Aspergillus* as the dominant genera, followed by *Trichoderma*, *Fusarium*, *Phoma*, *Talaromyces*, *Cladosporium*, *Eupenicillium*, *Gongronella*, *Microsphaeropsis*, *Mucor*, *Stibella*, and *Thielavia*.

Sebastianes et al. (2013) showed through molecular identification that the fungal community associated with some mangroves in São Paulo State is composed of at least 34 different genera, the most frequent being *Diaporthe, Colletotrichum,* *Fusarium*, *Trichoderma*, and *Xylaria*. The results indicated that the mangrove fungal community possesses a vast diversity and richness of endophytic fungi. The data also revealed a large reservoir of fungal genetic diversity inhabiting these Brazilian mangrove forests and highlighted substantial differences between the fungal communities associated with distinct plant tissues, plant species, level of human impact, and seasonality.

A few Brazilian studies have recently focused on endophytic fungi (Costa et al. 2012; Sebastianes et al. 2013). These are microorganisms that invade the tissues of plants during their life cycle without causing disease symptoms, and many show biotechnological purposes, producing a high diversity of substances with potential medical, agricultural, and industrial applications. All the above-mentioned studies revealed a large reservoir of fungal genetic diversity inhabiting these Brazilian mangrove forests.

Ghizelini et al. (2012) emphasized the existence of few publications about fungal communities in mangrove sediments. There are many reasons for this, including the fact that short fragments of ribosomal DNA, which are frequently used to describe bacterial diversity, are not suitable to adequately describe fungal diversity. This fact shows that there is a real need to refine and establish specific molecular markers for fungal taxonomy. This is the reason why even today there is a certain difficulty in accessing fungal communities in mangroves, despite the progress that has already been made. In addition to that, the diversity of environments in which Brazilian mangroves can be found hinders generalization. Each of them possesses specificities and different degrees of conservation. This way, much effort is still needed to better characterize fungal diversity in this unique and extensive area, such as the study by Ghizelini et al. (2019) on the effects of a massive oil spill that affected most of the northeastern Brazilian coast on mangrove sediment fungal diversity.

7.3.3 Virus Diversity in Brazilian Mangrove Sediments

A virus is a small parasite that cannot reproduce by itself. Once it infects a susceptible cell, however, a virus can adjust the cell machinery to produce more viruses. Most viruses have either RNA or DNA as genetic material. The nucleic acid may be single- or double-stranded. The entire infectious virus particle, called a virion, consists of nucleic acid and an outer protein shell. The simplest viruses contain only enough RNA or DNA to encode four protein types. The most complex can encode 100–200 proteins (Lodish et al. 2000).

Viruses infect numerous microorganisms including, predominantly, bacteria (bacteriophages or phages) but also archaea, protists, and fungi. They are the most abundant and ubiquitous biological entities on Earth and are important drivers of ecosystem functioning. Little is known, however, about the vast majority of these viruses that live off microorganisms (Allen and Abedon 2014). Studies show that viruses present incredible abundance. The estimated overall abundance of marine viruses in the world's oceans is on the order of 10^{30} (Suttle 2005, 2007), a value that exceeds by ten times the abundance of prokaryotes (Suttle 2005).

Viruses are no longer viewed as static but instead as dynamic players within the microbial ecology of the oceans. Through cell lysis, viruses return photosynthesis-derived carbon to the ocean. Some studies show that viruses may be responsible for 50% of all bacterial mortality (Fuhrman and Noble 1995). The particles also have a function in the control of bacterial blooms and in altering the genetic composition of their host. More research is required to fully understand the processes occurring in the microbial loop. However, it is clear that viruses play a central role in this loop, and that many questions remain to be answered.

According to Weitz and Wilhelm (2012), the study of viruses in the oceans has been key to many discoveries, like the finding that viruses have evolved novel lineages of key photosynthetic genes, as seen in cyanophages infecting *Synechococcus* and *Prochlorococcus* (Mann et al. 2003). Considering so much new information about viruses, the identification of many novel viral families defies much of the conventional knowledge about the viral life history, for example, the discovery of "giant" algal-infecting viruses (Derelle et al. 2008), and the discovery of viruses that exploit other viruses (La Scola et al. 2008).

Although no specific studies show the role of viruses in mangroves areas, especially in Brazil, one can infer that the same findings for the marine environment would take place in the mangrove environment. Thus, there are still gaps in the knowledge on virus diversity in mangroves all over the world.

7.4 Final Remarks

The field of marine microbial ecology is just at the beginning of its specific technological evolution. Such advances in technologies include direct-imaging methods, sequencing technologies, and bioinformatics that have revealed a previously unknown world of viral diversity in natural environments. However, microbial activities in the mangrove ecosystem are highly complex, especially the microbial loop itself. For this reason, there is a need for more studies about the structure of microbial communities, their function and impact on productivity, potentially changing paradigms in the management and conservation strategies of mangroves in the country.

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