

Review

Untangling Structural and Functional Diversity of Prokaryotic Microbial Assemblage on Mangrove Pneumatophores

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Abstract: Mangroves are important coastal wetlands along tropical and subtropical regions. Pneumatophore, a kind of aerial root, is among the prominent components of a mangrove ecosystem, which provides microhabitats for a range of prokaryotic (bacteria and cyanobacteria) microbial assemblages, whose role in the maintenance of mangrove ecology often remains neglected. Very few studies are available on pneumatophore-associated prokaryotic microorganisms (PAPMs). The majority of them are related to the microscopic identification of cyanobacteria, with very limited research on the bacterial population, even though they demand more attention. Also, very scarce information is available on biotic and abiotic factors shaping the PAPMs. The objective of this review is to highlight the structural and functional importance of prokaryotic organisms associated with pneumatophores. This review begins with a brief introduction of what mangrove pneumatophores are, then focuses on the PAPMs, accentuating the breadth and depth of information gained from previous research. We further discuss how a combination of a traditional cultivable approach and a newly developed omics approach can be efficaciously employed to untangle PAPMs. This review provides updated information on PAPMs, which will intensify the visibility and necessity of pneumatophore-associated microbial community research.

Keywords: pneumatophores; prokaryotic community; biotic and abiotic factors; omics approach; mangrove



Citation: Bohra, V.; Tam, N.F.-Y.; Chen, L.; Lai, K.K.-Y.; Lam, W.; Xu, S.J.-L.; Zhou, H.-C.; Lang, T.; Lee, C.-L.; Lee, F.W.-F. Untangling Structural and Functional Diversity of Prokaryotic Microbial Assemblage on Mangrove Pneumatophores. *J. Mar. Sci. Eng.* **2024**, *12*, 802. <https://doi.org/10.3390/jmse12050802>

Academic Editor: Jun Gong

Received: 5 April 2024

Revised: 2 May 2024

Accepted: 9 May 2024

Published: 11 May 2024



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1. Introduction

1.1. Mangroves

Mangroves are unique, productive ecosystems present at the interface of marine and terrestrial environments. These ecosystems consist of woody plants, herbaceous halophytes, bacteria, algae, fungi, and other associated organisms, all dwelling in the same tidally influenced region [1,2]. Mangroves are sensitive to temperature and cannot tolerate temperatures less than 4 °C [3], limiting their distribution to tropical and subtropical regions around the equator (between 30° N and 30° S latitudes) [4]. Mangrove vegetation accounts for around 0.4% of global forests and around 1% of the world's tropical forests, covering an area of around 152,000 km² [5,6]. Geographically, mangroves are dispersed across America, Asia, Africa, and Oceania [7]. Despite their varied distribution in 123 different countries and territories, more than two-thirds of mangroves are confined to just 12 countries. Southeast

Asia is home to 33.5% of the world's mangrove forests [8]. Mangroves occur in a range of geomorphic settings, such as lagoons, deltas, and estuaries in dry or wet climates, with varying species diversity, material cycles, and energy flow [9]. Although they comprise only 0.4% of the global forest area, mangroves are vital for maintaining healthy coastal environments. Mangroves deliver various ecosystem services, including carbon storage and nutrient cycling of inorganic and organic materials to related biotopes and coastal waters [7,9,10]. They also help in preserving rich coastal biodiversity by providing physical habitats for various economically and ecologically important species [11,12]. The mangrove environment in general is often nutrient-deficient, particularly in terms of nitrogen and phosphorus [13,14]. Despite limited nutrients, mangroves are one of the most productive ecosystems on the planet and are extremely prolific, at about 50% more productive than other tropical forests [15,16]. Their net primary production of about $9.3 \text{ t ha}^{-1} \text{ year}^{-1}$ [17] indicates a very effective nutrient recycling system in mangrove ecosystems. New nutrients are regenerated and scarce essential nutrients are retained through microbes that play crucial roles in major nutrient transformations [14,18]. Several studies have been undertaken in the past to investigate the roles of diverse microbes in different components of the mangrove ecosystem; however, the majority of the research remains restricted to the assessment of the microbial community associated with mangrove sediment and adjacent coastal water [19–21]. The microbes associated with other prominent components, particularly pneumatophores, have seldom been explored.

1.2. *Pneumatophores*

Mangrove plants are the most evident and basic constituents of mangrove ecosystems. Mangrove forests, in contrast to other tropical forests, contain comparatively low numbers of tree and shrub species [22]. There are around 110 mangrove plant species worldwide, with only 54 species belonging to 20 genera and 16 families being described as true mangroves [23]. *Avicennia* is the only mangrove genus found all over the world and forms the dominant plant group in mangrove forests and mangrove research [24]. Mangrove plants inhabit waterlogged soils or areas frequently inundated with seawater, making it difficult to fulfill the plant's oxygen demand using roots alone [25,26]. To overcome oxygen scarcity, plants develop various morphological adaptations that enable sufficient oxygen (O_2) supply to the submerged roots, and pneumatophores are among them [1,27]. A pneumatophore is a negatively geotropic structure that protrudes from the cable root to aerate underground parts of the plant, which are otherwise surrounded by an anaerobic environment [1,28]. Pneumatophores spread horizontally in the soil and are around 1–20 cm or more in length [29]. Approximately 10,000 pneumatophores are produced by a single tree of 2–3 m in height [25]. Pneumatophores have numerous minute pores on their surface, called pneumatophores or lenticels, which are connected to the aerenchyma tissues of the near-surface roots, resulting in a dense root system in mangrove trees [28]. Such biogenic structures allow the diffusion of oxygen-rich air from the pneumatophore surface to the underground root system, thus creating an oxic micro-niche surrounding the root surface and escape of carbon dioxide from the interior of the root [30]. A high density of pneumatophores at a specific site could also significantly reduce the water current and turbulence, increasing the sedimentation rate and the formation of a sediment layer on the surface of the pneumatophore [25]. This sediment layer serves as a complex habitat and supports the colonization of ecologically important marine organisms, including the prokaryotic (bacteria and cyanobacteria) microbial diversity [31,32]. The contribution of pneumatophore-associated prokaryotic microorganisms (PAPMs), particularly their impact on the mangrove ecosystem, is still under scanner. Based on the abstract and citation database Scopus (<https://www.scopus.com>) accessed on 8 May 2024, around 1.2% of the total research on “mangrove” between 1974 to 2023 targeted pneumatophores. From 1975 to 2023, around 40 research articles on pneumatophore prokaryotic diversity have been published, mainly targeting the taxonomic diversity of cyanobacteria. Studies on pneumatophore-associated bacteria are very rare, and only ten research articles are

currently available (Figure 1, Table S1). It has been found that blue-green algal mats colonized on pneumatophores play a significant role in nitrogen fixation in the mangrove ecosystem [33–36]. Mann and Steinke [37] showed that about 24.3% of the annual nitrogen requirements within mangrove environments are contributed by the cyanobacteria associated with *Avicennia* pneumatophores. The same study also emphasized the role of the diazotrophic bacteria found within the periderm of pneumatophores in augmenting the nitrogen nutrition of their host. A mutualistic relationship between pneumatophore epiphytes and mangroves has been suggested, whereby pneumatophores could obtain the benefits from the metabolism of carbon and nitrogen performed by the epiphytes, while pneumatophores provide habitats for the epiphytes. However, knowledge of microbial colonization and the functional role of the microorganisms on the pneumatophore surface is limited. So far, the available literature information is restricted to knowledge of the macro-algal and cyanobacterial community structures. The taxonomic and functional diversity of the PAPMs are still poorly understood.

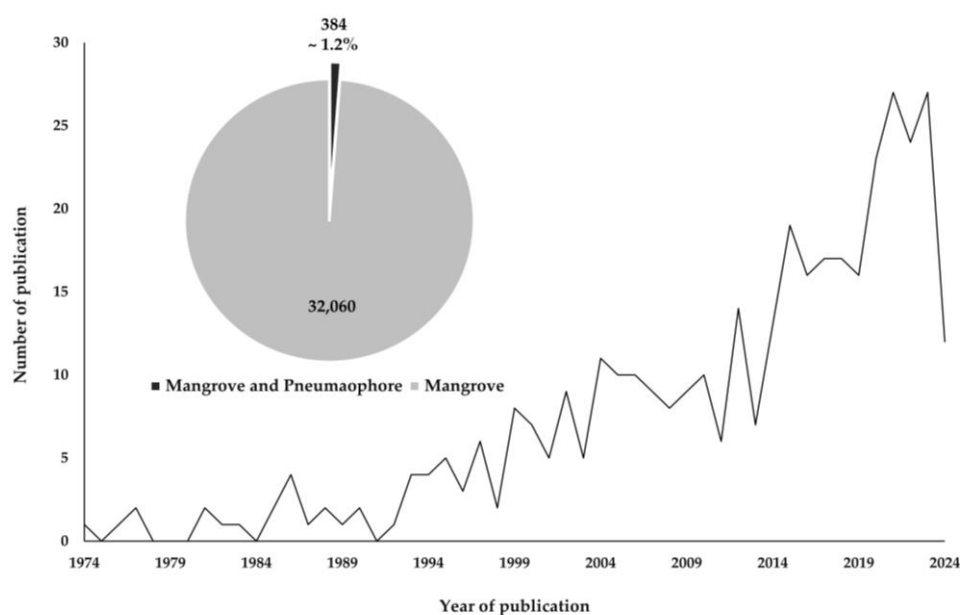


Figure 1. Historic mangrove and pneumatophore publications. The line graph shows pneumatophore-related publications over time. The pie chart depicts the share of pneumatophore publications out of the total number of mangrove publications (total number of papers on mangroves from 1846 to 9 May 2024 was 32,060, while the number on mangroves and pneumatophores from 1974 to 9 May 2024 was 384).

2. Community Composition and Function of the Prokaryotic Microbial Community Associated with Pneumatophores

2.1. Participation of Pneumatophore-Associated Prokaryotic Communities in Nutrient Cycling

Mangroves are mostly flourishing in areas with almost no nutrient input from the surrounding environment, except those receiving sewage discharge from adjacent human activities. The high rates of biomass production by mangrove plants demand high nutrient input to support their growth. Therefore, efficient nutrient recycling becomes essential for maintaining the density and health of mangrove forests. Microbes play a crucial role in photosynthesis, decomposition, nutrient cycling (transformations of major nutrients, including carbon, nitrogen, sulfur, and phosphorous), and the production of metabolites (antibiotics, exopolysaccharides, enzymes, etc.) [11,14,38]. Microorganisms isolated from mangrove ecosystems have biotechnological significance due to the presence of enzymes, proteins, antibiotics, and salt-tolerant genes [39]. Mangrove ecosystems support rich microbial diversity, where 98% of the total microbial biomass is constituted by bacteria, cyanobacteria, microalgae, and fungi [40]. These microorganisms colonize microhabitats such as the surface of roots (prop root, cable root, and pneumatophores), silt or mud, water,

etc. [19,41]. Among different kinds of roots, pneumatophores offer an ideal habitat for the colonization of diverse epibionts, and a significant fraction of microbes form symbiotic associations with them [34,42].

The earliest accessible information regarding pneumatophore-associated cyanobacteria pertained to Sinai mangroves [43]. The biological function, such as diazotrophic activity, was first described in pneumatophore-associated sediment in the 1970s [44,45] and pneumatophores in the 1980s [46] throughout the world, but rarely with any reference to the particular species of microorganisms, which varies from site to site. Past studies have specifically reported the active role of PAPMs in nitrogen cycling, whereas their role in other metabolic processes by far remains unexplored. Researchers found that the nitrogenase activity on mangrove pneumatophores is equivalent to or substantially elevated when compared to adjacent sediments, suggesting the presence of unexplored, uncharacterized functional microbial diversity, particularly bacteria and microalgae, which contributes to nitrogen availability in mangrove ecosystems. For instance, Hicks and Silvester [46] reported higher nitrogenase activity (100 to 500 nmol of C_2H_4 pneumatophore⁻¹ h⁻¹) associated with *A. marina* pneumatophores than adjacent sediment (1.23 nmol C_2H_4 cm⁻² h⁻¹) in New Zealand mangroves, attributed to the higher abundance of the cyanobacteria *Calothrix* on the pneumatophore surface. Similar observations were reported at mangroves around Zanzibar and the high nitrogenase activity on pneumatophores was correlated with the possible presence of *Rivularia*, *Aphanocapsa*, and *Scytonema* sp., the potential cyanobacteria known to inhabit mangrove pneumatophores [47]. On the other hand, Zuberer and Silvester [45] found that the nitrogenase activity in pneumatophore-associated sediment was the same as that in adjacent sediment. There was also no significant difference in the nitrogenase activity on *A. germinans* pneumatophores as compared to adjacent sediments in South Florida, USA, probably due to the absence of nitrogen-fixing bacteria on *A. germinans* pneumatophores [48]. Some studies contradictorily reported lower nitrogenase activity on pneumatophore surfaces as compared to surrounding habitats. Mann and Steinke [33] found that the nitrogenase activity in the wet and dry mat habitat of the Beachwood Mangroves Nature Reserve, South Africa, was 1.5- to 25-fold higher than that on the pneumatophore, and the maximal difference was observed under submerged conditions, while the difference was the least in the presence of sucrose and organic carbon. Similar results were observed in a year-round study in the same mangrove by Mann and Steinke [37], where nearly four- to seven-fold lower nitrogenase activities were observed in the pneumatophore habitat than in the adjacent mat. Microbial nitrogenase activity on pneumatophores also varied with season, with higher activity recorded in the summer season as compared to the winter season [46]. Variations of the nitrogenase activity on pneumatophores and in adjacent sediments from different habitats in different geographical regions are summarized in Table 1.

Table 1. Nitrogenase activity (ARA) on pneumatophores and in adjacent sediments in mangroves at different geographical regions.

Geographical Region	Mangrove Plant	Major Microbial Community on Pneumatophores	Habitat	Nitrogenase Activity (Nmmole C_2H_4 Reduced)	In Situ/ Ex Situ	Reference
Zanzibar Island, Indian Ocean	<i>Sonneratia alba</i> and few <i>Avicennia marina</i>	<i>Rivularia</i> sp.	Mangrove pneumatophores without <i>Rivularia</i> sp.	27–118.5 *	In situ	[47]
			Mangrove pneumatophores with <i>Rivularia</i> sp.	6–25.9 *		
			Mangrove sediments with cyanobacterial-dominated microbial mats	6–16.8 *		
			Bare sediment	1.3–3.8 *		
Shark River Estuary, Southwest Florida, USA	<i>Avicennia germinans</i> (L.) Stern	Not mentioned	Mangrove pneumatophores	0 to 4.8 #	Ex situ	[48]
			Bare sediment	0 to 31.3 #		

Table 1. Cont.

Geographical Region	Mangrove Plant	Major Microbial Community on Pneumatophores	Habitat	Nitrogenase Activity (Nmole C ₂ H ₄ Reduced)	In Situ/Ex Situ	Reference
Beachwood Mangrove, Mgeni Estuary, South Africa	<i>Avicennia marina</i> (Forssk.) Vierh.	<i>Lyngbya</i> sp.	Pneumatophores	15–90 *	Ex situ	[37]
		<i>Oscillatoria</i> sp.	Wet sediment	100–700 *		
		<i>Microcoleus</i> sp.	Dry sediment	100–350 *		
Beachwood Mangrove, Mgeni Estuary, South Africa	<i>Avicennia marina</i> (Forssk.) Vierh.	Not mentioned	Pneumatophores	450 *	Ex situ	[33]
			Wet mat habitat	3300 *		
			Dry mat habitat	3000 *		
New Zealand Mangrove	<i>Avicennia marina</i> (Forssk.) Vierh. var. <i>resinifera</i> (Forst. f.) Bakh.	<i>Caothrix</i> sp.	Sediment beneath mangrove tree	1.23 *	Ex situ	[46]
			Sediment (dark)	0.62 *		
			Sediment (light)	0.61 *		
			Sediment (summer)	1.35 *		
			Sediment (winter)	0.2 *		
			Mangrove pneumatophores (5 to 12 mm diameter) (dark)	18 ^		
			Mangrove pneumatophores (5 to 12 mm diameter) (light)	94 ^		
			Mangrove pneumatophores (5 to 12 mm diameter) (summer)	100–500 ^		
			Mangrove pneumatophores (5 to 12 mm diameter) (winter)	less than in summer (data not reported)		

* cm^{−2} h^{−1}; # g dry wt^{−1} h^{−1}, ^ pneumatophore^{−1} h^{−1}.

Inconsistency observed in the literature may be due to different impacts of biotic factors, such as the composition of diazotrophic organisms and/or abiotic factors, including light regime, temperature, and inorganic nutrients on nitrogenase activity in mangroves distributed in different regions. Further research is required to verify these variations and estimate the share of nitrogen input by PAPMs in mangrove ecosystems.

2.2. Diversity of Prokaryotic Community Associated with Mangrove Pneumatophores

Pneumatophores are indispensable structures of the mangrove ecosystem and are subject to colonization by diverse marine microorganisms [49]. Profuse growth of algae and bacteria epiphytes on *A. marina* pneumatophores [50], principally N₂-fixing and non-N₂-fixing cyanobacteria, has been recorded [42,51]. Many studies in the past have documented the diversity of macroalgal species on pneumatophores [52–56]. However, research on pneumatophore-associated microorganisms is still limited throughout the world [35]. The least explored area is the pneumatophore-associated bacteria even though they are generally the most abundant biota associated with pneumatophores, which hampers our understanding of PAPM diversity and its functional importance. This section covers all the information available on PAPM diversity and function.

2.2.1. Cyanobacteria

Cyanobacteria are a group of photosynthetic prokaryotes that form the dominant component of the microbiota colonizing mangrove pneumatophores, as they can survive under extreme environmental conditions [46,57,58]. Cyanobacteria, via photosynthesis and nitrogen fixation, contribute substantially to the primary productivity of mangrove habitats [1,59,60], produce plant growth-promoting and anti-pathogenic compounds, and act as phosphorous reservoirs [61,62]. The occurrence of the cyanobacterial community in various habitats of mangrove ecosystems has been investigated throughout the world, but only a few studies are on pneumatophore-associated cyanobacteria diversity, with a limited number of species being reported [63–66]. Also, the researchers only focused on the nitrogen fixation abilities of pneumatophore-associated cyanobacteria, with no

available literature discussing their potential role in other metabolic processes like primary production and nutrient cycling.

Por and Dor [43] reported the presence of *Lyngbya*, *Symploca*, *Rivularia*, *Calothrix*, *Brachytrichia*, *Scytonema*, and *Cyanohydnum* species on *A. marina* pneumatophores in mangroves of the Sinai Peninsula. Other studies also reported the presence of the same genera in Sinai mangroves, except *Scytonema* [51,67]. *Calothrix* sp. was found associated with *A. marina* pneumatophores in New Zealand mangroves [46].

In South Africa, the richest cyanobacterial diversity (20 taxa) was supported by pneumatophores of *A. marina* compared to mud and rock, with *Coleofasciculus chthonoplastes* (formerly *Microcoleus chthonoplastes*) being the most common species on most of the substrata [68]. The four-year study on algal populations at the St Lucia estuary in South Africa detected the presence of *Xenotholos kernerii* (formerly *Xenococcus kernerii*), *Dermocarpa acervata* (formerly *X. acervatus*), *Phormidium baculum* (formerly *Lyngbya baculum*), *L. confervoides*, *Coleofasciculus chthonoplastes* (formerly *Microcoleus chthonoplastes*), *Oscillatoria subbrevis*, and *Phormidium nigroviride* (formerly *O. nigroviridis*) epiphytes on *A. marina* pneumatophores [50]. Another year-round survey of epiphytic algal populations on *A. marina* pneumatophores carried out in the Kosi system in South Africa revealed that cyanobacteria were the most numerous groups of microalgae, which consisted of 17 taxa and made up 50% of the total algal species, especially at sites where pneumatophores remained submerged for longer periods [55]. A study on the horizontal zonation pattern of algae epiphytes on *A. marina* pneumatophores at Beachwood Mangroves, South Africa, reported nine cyanobacterial taxa, with *C. chthonoplastes* and *L. confervoides* being the most abundant and dispersed cyanobacteria species across the mangrove reserve, whose frequency declined with distance from the creek [69].

A year-round survey on the colonization of cyanobacteria epiphytes was carried out on *A. germinans* pneumatophores in Balandra lagoon, Baja California Sur, Mexico, and the most distinguished feature in this region was the microbial colonization of the entire pneumatophore by cyanobacteria, dominated by morphotypes resembling *Lyngbya*, *Oscillatoria*, and *Microcoleus* species, and a few bacteria throughout the year [70]. Twenty-nine distinct algal species, of which twenty-one were identified as cyanobacteria, either directly epiphytic on pneumatophores or associated with red algae or other cyanobacteria growing on the pneumatophores, were detected on the east coast of the Baja California Peninsula based on a year-round survey of cyanobacterial and macro-algal assemblages on *A. germinans* pneumatophores [71]. The cyanobacterial association with red algae was an adaptive strategy that helped them escape desiccation in the arid climate of the Baja California Peninsula [34].

Gab-Alla [72] compared the spatial variability in cyanobacterial diversity on *A. marina* pneumatophores at four different sites along the Egyptian coast of the Red Sea and found the presence of *Calothrix* sp., *Lyngbya* sp., *Oscillatoria* sp., and *Rivularia polyotis* in all four sites. Another study investigating cyanobacteria diversity on microbial mats associated with pneumatophores in different mangrove swamps in the Red Sea observed twelve different cyanobacteria taxa, and eight cyanobacteria species (*Chroococcus turgidus*, *Lyngbya majuscula*, *Leptolyngbya tenuis*, *Oscillatoria tenuis*, *Pseudanabaena catenata*, *Spirulina subsalsa*, *Calothrix breviarticulata*, and *Oxynema acuminatum*, formerly *Oscillatoria acuminata*) were successfully isolated and tested for toxicity against *Artemia salina* [73]. This study further showed that three species, *Leptolyngbya tenuis*, *Oscillatoria tenuis*, and *Calothrix breviarticulata*, produced microcystins, and three species, *Lyngbya majuscula*, *Leptolyngbya tenuis*, and *Oxynema acuminatum*, released saxitoxins. The occurrence of toxicity-producing cyanobacteria in mangroves is of significant concern, as such toxicity may accumulate in the aquatic food chain and potentially transfer to higher trophic levels.

In another study, a total of thirteen taxa belonging to eleven epiphytic genera of cyanobacteria were found on *A. marina* pneumatophores in mangroves at Inhaca Island, Mozambique, with eight cyanobacterial genera exclusively present on the pneumatophore surface, while five were associated with several red algae species, including *Catenella*, *Gelid-*

ium, *Murrayella*, and *Bostrychia* in the so-called “Bostrychietum” on pneumatophores [74]. Moreover, Huisman and Kendrick [75] recorded seven species (*Calothrix aeruginea*, *Coleofasciculus chthonoplastes*, *Dichothrix utahensis*, *Lyngbya semiplena*, *Myxohyella papuana*, *Rivularia atra*, and *Heteroscytonema crispum*, formerly *Scytonema crispum*) of cyanobacteria associated with the pneumatophores of *A. marina* in Shark Bay, Western Australia. Nine different cyanobacteria genera (*Chroococcus*, *Aphanothece*, *Aphanocapsa*, *Myxosarcina*, *Oscillatoria*, *Microcoleus*, *Lyngbya*, *Phormidium*, and *Calothrix*) were found on the pneumatophores of *A. marina* [76]. *Oscillatoria ornata* was isolated from the pneumatophores of *A. officinalis* at Kadalundi, India [77]. Novel chlorophyll (Chl) d-containing cyanobacteria, *Acaryochloris* sp. MPGRS1 and *Acaryochloris marina* mangrove1, were isolated from the red algae colonizing the pneumatophores of *A. marina* in Australia [78,79]. The presence of Chl d-containing cyanobacteria on the pneumatophore surface indicated that the mangroves could extend the range of photosynthetic light to the near-infrared (~750 nm) in habitats where the availability of visible light (400–700 nm) is limited [78].

The details of cyanobacteria isolated from pneumatophores of mangrove plants at different locations are listed in Table S2.

The literature information reveals there are common cyanobacterial species across different mangrove ecosystems, with the species *Microcoleus*, *Lyngbya*, *Oscillatoria*, and *Calothrix* seeming to be the universal colonizers. It is clear that the pneumatophore surfaces of mangrove plants harbor a rich diversity of cyanobacteria. However, the identification and classification of cyanobacteria discovered in most of the previous studies were exclusively based on morphology-based methods, with a few based on molecular techniques. The role of the microorganisms on the pneumatophores had hardly been investigated.

2.2.2. Bacteria

Diverse bacterial populations constantly interact with pneumatophores; their main function is to facilitate the recycling and retention of essential nutrients that promote plant growth [80,81]. Pneumatophore-associated bacteria colonized on the root surface (outside of the root tissue) are classified as epiphytes, while those present inside root tissues are endophytes. Naidoo et al. [82], using transmission electron microscopy and culture study, for the first time reported the presence of diazotrophic bacterial endophytes in the pneumatophores of *A. marina* collected from the Beachwood Mangroves Nature Reserve, South Africa. Endophytic bacteria isolated from the surface of sterilized pneumatophores of *A. marina* at the Vellar estuary, India, identified as *Bacillus* sp., *Enterobacter* sp., *Sporosarcina aquimarina*, and *Bacillus cereus*, were shown to have differentially expressed phosphate-solubilizing, nitrogen-fixing, and sulfur-reducing abilities, and some could produce plant growth-promoting compounds like indole acetic acid and siderophore [80,81]. Abhijith et al. [83] isolated phosphorus-solubilizing *Bacillus* strains from sediments on *A. marina* pneumatophores in the mangrove forests of Mumbai, India and proposed their potential usage as phosphatic bio-fertilizers to enhance agriculture, aquaculture, and mangrove productivity. Another batch of epiphytic bacterial species on the pneumatophores was isolated from the Ayiramthengu mangrove ecosystem in India, predominated by phosphatase-solubilizing bacterial strains (78% of the total bacterial isolates), and these isolates could also produce extracellular enzymes lipase (75%), cellulase (71%), and amylase (52%) [84]. Bibi et al. [85] isolated and identified three different endophytic bacterial strains, *Nocardioide aromaticivorans*, *Streptomyces spectabilis*, and *Nocardioide albus*, on the pneumatophores of *A. marina* collected from the western coastal area of Jeddah, Saudi Arabia, and all had antipathogenic activity against plant pathogens *Phytophthora capsici* and *Pythium ultimum*. Other than these, no information is available on other functional attributes of pneumatophore bacteria. The information on all the bacterial species isolated from pneumatophores are listed in Table 2. The functions of cyanobacteria and bacteria isolated from the pneumatophore are summarized in Table 3.

Table 2. List of bacteria reported on pneumatophores of mangroves at different locations.

Bacteria	Methodology	Habitat	Country and Location	Reference
<i>Pseudomonas</i> , <i>Acinetobacter</i> , <i>Moraxella</i> , <i>Streptococcus</i> , <i>Deinococcus</i> , <i>Micrococcus</i> , <i>Paenibacillus</i> , and <i>Staphylococcus</i> species	Isolation and microscopic identification	Epiphytic on pneumatophores	Ayiramthengu mangrove ecosystem, Kerala, India	[84]
<i>Pseudomonas alcaligenes</i> PMB1, <i>Aeromonas taiwanensis</i> PMB4, <i>Aeromonas taiwanensis</i> PMB3, and Bacterial strain PMB2	Isolation and 16s rDNA identification	Endophytic on <i>A. officinalis</i> pneumatophores	Poovar, South Kerala, India	[86]
<i>Nocardioides aromaticivorans</i> EA83, <i>Streptomyces spectabilis</i> EA85, and <i>Nocardioides albus</i> EA87	Isolation and 16s rDNA identification	Endophytic on <i>A. marina</i> pneumatophores	Western coastal area of Jeddah, Saudi Arabia	[85]
<i>Bacillus atrophaeus</i> strain F2 and <i>Bacillus</i> sp. D04-1	Isolation and 16s rDNA identification	Sediment on <i>A. marina</i> pneumatophores	Mangrove forests of Mumbai, India	[83]
<i>Bacillus</i> sp. SjAM16101, <i>Enterobacter</i> sp. SjAM16102, <i>Sporosarcina aquimarina</i> SjAM16103, and <i>Bacillus cereus</i> SjAM16104	Isolation and 16s rDNA identification	Endophytic on <i>A. marina</i> pneumatophores	Vellar estuary, southeast coast of India.	[80]
Diazotrophic bacterial strains	Isolation	Endophytic on <i>A. marina</i> (Forssk.) Vierh. pneumatophores	Beachwood Mangroves Nature Reserve, South Africa	[82]

Table 3. Identified functions of cyanobacteria and bacteria isolates from the pneumatophores.

Microbial Isolate	Feature of Interest	Assay Method	Reference
<i>Chroococcus turgidus</i> , <i>Spirulina subsalsa</i> , <i>Oxynema acuminatum</i> (formerly <i>Oscillatoria acuminata</i>), <i>Oscillatoria sancta</i> , <i>Leptolyngbya tenuis</i> , <i>Lyngbya majuscula</i> , <i>Pseudanabaena catenata</i> , and <i>Calothrix breviararticulata</i>	Toxic against <i>Artemia salina</i>	Artemia assay, ELISA, HPLC, and LC-MS/MS	[73]
<i>Acaryochloris</i> sp. Mangrove1	Presence of chlorophyll D	Not available	[79]
<i>Acaryochloris</i> sp. MPGRS1	Presence of chlorophyll D	(HPLC)-based pigment analysis and by confocal imaging of cultured cells	[78]
<i>Rivularia</i> , <i>Aphanocapsa</i> , and <i>Scytonema</i> species	Nitrogen fixation	Acetylene reduction assay	[36]
<i>Microcoleus</i> and <i>Anabaena</i> species	Nitrogen fixation	Acetylene reduction assay	[42]
<i>Nocardioides aromaticivorans</i> EA83 (Actinomycetota), <i>Streptomyces spectabilis</i> EA85 (Actinomycetota), and <i>Nocardioides albus</i> EA87 (Actinomycetota)	Antifungal activity against fungal pathogens, <i>Phytophthora capsici</i> and <i>Pythium ultimum</i>	Cross streak method and LC-MS analysis of bacterial culture	[85]
<i>Bacillus atrophaeus</i> strain F2 and <i>Bacillus</i> sp. D04-1	Phosphate solubilization	Plate zymography and broth assay	[83]
<i>Bacillus</i> sp. SjAM16101 and <i>Enterobacter</i> sp. SjAM16102	Selective PGP activity: IAA production, phosphate solubilization, nitrogen fixation, sulfur reduction	Plate zymography and biochemical assay	[80]
<i>Bacillus cereus</i> SjAM16104 and <i>Sporosarcina aquimarina</i> SjAM16103	Selective PGP activity: IAA production, phosphate solubilization, nitrogen fixation, siderophore production, sulfur reduction	Plate zymography, biochemical assay, and in vitro inoculation of plants with bacterium	[80,81]

2.3. Interaction between Pneumatophore-Associated Microorganisms and Mangrove Plants

Interactions between rhizosphere microorganisms and plants have been reported to have beneficial impacts on plant growth via various mechanisms, including carbon fixation, nitrogen fixation, phosphate solubilization, sulfur reduction, and indole acetic acid production [87–89]. Various microbial entities, particularly bacteria and cyanobacteria, are always associated with the pneumatophore of mangrove plants [42,90]. However, the nature of these associations (beneficial or not) is not known, and it remains unclear whether these microbes contribute to the growth of mangrove plants or not. Some laboratory inoculations and field experiments with strains isolated from pneumatophores have documented the interactions between mangrove plants and the pneumatophore-associated microbes [70,91,92]. Relatively high nitrogenase activity and total nitrogen concentration were found in seedlings inoculated with *Microcoleus* sp. isolated from pneumatophores under in vitro conditions, and these nursery-reared seedlings had a 76.5% survival rate without any apparent negative effects when transplanted into a disturbed site in Balandra lagoon [70,91]. Furthermore, Bashan et al. [92], employing ^{15}N assimilation tests, showed that the total nitrogen content of inoculated plants increased by 5–114%, and the nitrogen fixed by *M. chthonoplastes* was primarily assimilated in plant leaves and other plant tissues. Similarly, artificial inoculation experiments also revealed that the isolates from *A. marina* pneumatophores, *Bacillus cereus*, and *Sporosarcina aquimarina* promoted plant growth by enhancing early root development with a substantial increase in the length and number of roots along with increased shoot length in the inoculated *Bacopa monnieri* (a perennial, creeping wetland herb) compared to the non-inoculated explants [81]. Table 4 summarizes previous studies on the microbial inoculation of explants for plant growth promotion, suggesting the possibility of using prokaryotic isolates from pneumatophores as bioinoculants to promote the growth of mangrove plant species. Nevertheless, the exact interactions between PAPsd and mangrove plants and any resulting mutual benefits are yet to be established because of the relatively limited number of studies.

Table 4. Microbial inoculation of explants for plant growth promotion.

Microbial Isolate	Source	Method of Study	Experimental Plant	Observation	Reference
<i>Sporosarcina aquimarina</i> SjAM16103	Endophytic bacteria from pneumatophores of <i>Avicennia marina</i>	In vitro	<i>Bacopa monnieri</i> , <i>Eupatorium triplinerve</i> , <i>Excoecaria agallocha</i> , and <i>Avicennia marina</i>	Bacterial inoculation significantly increased growth (in terms of root length, shoot length, number of roots). Root hairs and early root development were observed in inoculated explants.	[81]
<i>Bacillus cereus</i> SjAM16104	Endophytic bacteria from pneumatophores of <i>Avicennia marina</i>	In vitro	<i>Bacopa monnieri</i>	Growth rates of treated explants (in terms of root length, shoot length, number of roots) were significantly increased compared to the control explants.	[80]
<i>Microcoleus chthonoplastes</i> strains B1	BGA epiphytic on <i>Avicennia germinans</i> pneumatophores	In vitro	Black mangrove propagules	Levels of total N and ^{15}N in inoculated leaves were significantly higher than those in non-inoculated plants.	[92]
<i>Microcoleus</i> sp.	BGA epiphytic on <i>A. germinans</i> pneumatophore	In vitro	Black mangrove propagules <i>Avicennia germinans</i> (L.) Stem	Post-inoculation, nitrogen fixation gradually increased with time. Nitrogen fixation in the presence of plant was significantly higher than the amount of nitrogen fixed by a similar quantity of cyanobacteria on a N-free growth medium.	[70]

3. Biotic and Abiotic Factors Affecting Composition, Diversity, and Function of Microorganisms Associated with Pneumatophores

Biotic and abiotic factors are known to play crucial roles in defining the microbial community structure and function of diverse ecosystems [34]. Mangroves flourish in extremely harsh environmental conditions with ever-changing surrounding factors, particularly varying tidal regimes, which may have huge impacts on the microbial community associated with pneumatophores. Although awareness about PAPMs and their significance within the

ecosystem is increasing [71,84], little knowledge is available on the factors affecting their colonization pattern.

3.1. Factors Affecting Microbial Composition and Diversity

Dor [49] reported that the abundance of cyanobacterial communities on the surface of pneumatophores exposed to sunlight was higher than that on the shaded pneumatophores nearer the tree trunk, which usually lack algal cover. Not only light but nutrients like phosphorus and nitrogen also influence microbial composition. An exclusive nitrogen-fixing community of Rivulariaceae epiphytes was found on pneumatophores exposed to nutrient-limited Gulf waters in the Sinai mangroves [51]. With the increased availability of nutrients, the pneumatophore community structure changed, and the typical *Rivulariaceae* community was replaced by *Oscillatoria* sp. [67]. Moreover, Phillips et al. [34,69] reported that the zonation of algae epiphytes on pneumatophores in the Mgeni Estuary was regulated mainly by tidal phenomena such as tidal inundation and wetting frequency, desiccation, and salinity. The algal distribution on the pneumatophores was found to decline with salinity, while a higher abundance of Cyanophyceae relative to other algal groups on pneumatophores was recorded under a longer immersed period [55,67]. These studies suggest that microbial colonization on pneumatophores is primarily regulated by exposure to sunlight, desiccation, salinity, and wetting frequency, while increased nutrient availability may also partially explain some of the microbial colonization patterns.

3.2. Tidal Inundation Influence on Pneumatophore-Associated Microbial Community and Vertical Zonation

The epiphytes on pneumatophores show a vertical zonation pattern from their apex to basal regions, which reflects the impact of the tidal regime. In most situations, a pneumatophore can be marked into three zones: supralittoral (the upper zone), littoral (the middle zone), and sublittoral (the lower zone). Several studies on the vertical zonation of species along the pneumatophores have previously been undertaken, and a stable vertical zonation of cyanobacterial colonization on mangrove pneumatophores has been observed (Table 5). *Scytonema* usually inhabits the supralittoral region, the upper 5–8 cm of the pneumatophore that undergoes the longest exposure period, because the short and large “muffs” of this alga have high porosity, store water during high tide, and hold it for the next few hours to avoid desiccation, thus enabling it to outcompete other algae at the upper end of the pneumatophore [51,67]. The occurrence of many heterocystous blue-green algae, *Microcoleus*, *Rivularia*, *Calothrix*, and *Brachytrichia* species, on the exposed middle section of the pneumatophores indicates their involvement in nitrogen fixation, while the lower submerged communities of non-heterocystous algal species *Lyngbya*, *Oscillatoria*, and *Symploca* do not fix atmospheric nitrogen and utilize dissolved nitrate instead [93,94]. The observed vertical zonation is a reflection of changes in environmental conditions, particularly the tidal ebb and the increased exposure to sunlight, temperature, evaporation, and salinities, all of which explain microbial positions in relation to the diurnal ebb and flow of water down and up the aerial roots. However, some studies have reported the uniform distribution of cyanobacterial species across the lengths of pneumatophores, suggesting the wide tolerance of various cyanobacteria against varying environmental conditions [34,72,76].

Table 5. Vertical zonation of cyanobacteria species associated with pneumatophores.

Mangrove Plant	Location	No. of Zones	Species Identified in Bottom Zone	Species Identified in Middle Zone	Species Identified in Upper Zone	Sediment/Sublittoral Oncolites *	Reference
<i>Avicennia marina</i>	Station I, Cagar Alam Pulau Dua (CAPD) Serang, Banten	3	<i>Aphanothece</i> , <i>Oscillatoria</i>	<i>Aphanothece</i> , <i>Myxosarcina</i> , <i>Oscillatoria</i> , <i>Microcoleus</i> , <i>Lyngbya</i> , <i>Phormidium</i>	<i>Chroococcus</i> , <i>Aphanothece</i> , <i>Myxosarcina</i> , <i>Oscillatoria</i> , <i>Lyngbya</i> , <i>Phormidium</i>	-	[76]

Table 5. Cont.

Mangrove Plant	Location	No. of Zones	Species Identified in Bottom Zone	Species Identified in Middle Zone	Species Identified in Upper Zone	Sediment/Sublittoral Oncolites *	Reference
<i>Avicennia marina</i>	Station II, CAPD Serang, Banten	3	<i>Chroococcus</i> , <i>Aphanocapsa</i> , <i>Myxosarcina</i> , <i>Oscillatoria</i> , <i>Lyngbya</i> , <i>Calothrix</i>	<i>Myxosarcina</i> , <i>Oscillatoria</i> , <i>Lyngbya</i> , <i>Calothrix</i>	<i>Oscillatoria</i> , <i>Calothrix</i>	-	[76]
<i>Avicennia marina</i> (Forssk.) Vierh.	Egyptian Red Sea coast	3	<i>Calothrix</i> , <i>Lyngbya</i> , <i>Oscillatoria</i> , <i>Rivularia</i>	<i>Calothrix</i> , <i>Lyngbya</i> , <i>Oscillatoria</i> , <i>Rivularia</i>	<i>Calothrix</i> , <i>Lyngbya</i> , <i>Oscillatoria</i> , <i>Rivularia</i>	-	[72]
<i>Avicennia germinans</i> (L.) Stern	Balandra lagoon, Baja California Sur, Mexico	3	<i>Lyngbya</i> , <i>Oscillatoria</i>	<i>Microcoleus</i>	<i>Aphanothece</i>	<i>Anabaena</i>	[42]
<i>Avicennia</i>	Ras Muhammad, mangroves of Sinai Peninsula	1	<i>Rivularia</i>	-	-	<i>Microcoleus</i>	[67]
<i>Avicennia</i>	Shura el Manqata, Gulf of Elat, Sinai Peninsula	3	<i>Kyrtuthrix</i> , <i>Rivularia</i>	<i>Calothrix</i>	<i>Scytonema</i>	<i>Lyngbya</i> , <i>Gloeotheca</i> , <i>Lyngbya aestillarii</i> , <i>Microcoleus chthonoplasles</i> , <i>Hydrocoleliin</i> , <i>Schizothrix</i>	[67]
<i>Avicennia marina</i> (Forst.) Vierh.	Shura el Manqata, mangroves of Sinai Peninsula	3	<i>Rivularia</i> , <i>Kyrtuthrix</i>	<i>Calothrix</i>	<i>Scytonema</i>	<i>Phormidium</i>	[51]
<i>Avicennia marina</i> (Forst.) Vierh.	Ras Muhammad, mangroves of Sinai Peninsula	2	<i>Rivularia</i> , <i>Kyrtuthrix</i>	<i>Calothri</i>	-	<i>Phormidium</i>	[51]
<i>Avicennia marina</i>	Mangrove forests of Sinai	3	<i>Lyngbya</i> , <i>Symploca</i>	<i>Rivularia</i> , <i>Calothrix</i> , <i>Brachytrichia</i>	<i>Scytonema</i>	<i>Phormidium</i> , <i>Aphanocapsa</i>	[95]

* Oncolite refers to the hard structures composed of oncoids, which are layered structures formed by cyanobacterial growth at a small sediment region around the base of the pneumatophore; -: not specified or not mentioned.

4. Approaches for Untangling Prokaryotic Microbial Diversity: Culture-Independent, Culture-Dependent, and Their Integration

In recent years, many new beneficial microbes and their bioactive compounds have been extracted from various components of the mangrove ecosystem, but PAPMs are yet to be systematically studied. Two groups of methodologies are usually employed to explore microbial diversity: traditional culture-dependent and culture-independent/molecular biology methods. In the past few years, molecular biology methods have transformed our understanding of the microbial community. Metagenomics, metatranscriptomics, proteomics, and metabolomics, facilitated by recent advances in bioinformatics and sequencing technologies, have provided much clearer pictures of the taxonomic and functional diversity in different ecosystems. While molecular methods have opened the door to hitherto unknown microbial diversity, the challenge of expanding the culture-dependent method is still ongoing. To harness the power of microbial processes, functionally important microbes need to be isolated under laboratory conditions, but this depends on successfully mimicking their natural environment.

4.1. Culture-Dependent Assessment of Microbial Diversity

Traditional culture-dependent approaches are employed to cultivate microorganisms and study their functional roles under laboratory conditions. For many years, the application of culture-dependent microbiological techniques has remained an extremely proficient and robust tool for the assessment of the taxonomic and functional diversity of microbes in various ecosystems. To date, most of the studies assessing the functions of mangrove microbial isolates, in particular pneumatophore-associated microbes, have relied on the isolation of microbial species in specific growth media and investigated plant growth-promoting traits, the production of antimicrobial enzymes, and secondary metabolites [42,76,85]. However, it is well accepted that only a few microorganisms can be cultured in a laboratory, as

very little is known about the organism's natural environment, making it difficult to fully replicate it. The microbes that cannot be cultured under laboratory conditions are likely to be ignored.

4.2. Culture-Independent Assessment of Microbial Diversity

4.2.1. Metagenomics

An era of microbial ecology has been revolutionized with the commencement of "metagenomics". Metagenomics refers to the high-throughput sequencing of a collection of genes or genomes directly isolated from environmental samples without targeting a specific region. The approach does not rely on cultivation or prior knowledge of the microbial communities [96,97]. The technique allows the evaluation of the total structural and functional potential of the microbial community and thereby provides an opportunity for the simultaneous exploration of two different attributes of a microbial community: what is there, and what are they capable of doing? However, this approach fails to account for which component is responsible for which action [96]. Metagenomic datasets are highly intricate, which poses challenges to data analysis, especially in microbial communities with high microbial diversity. Advancements in next-generation sequencing (NGS) technologies within the past few years have brought about a revolution in the metagenomic world [98,99]. NGS has brought down the cost of sequencing and yielded an in-depth understanding of the so-far underexplored microbial communities. For the past decade, several environmental ecology studies have employed these techniques to explore the microbial diversity of different environmental niches [96]. The advent of metagenomics can help massively in exploring the functional and genomic potential of untapped pneumatophore-associated microbiota. An initial study on seasonal changes in the prokaryotic diversity of below-ground pneumatophore-associated soil using amplicon metagenomics reported that the highest bacterial diversity and richness occurred during summer, with Proteobacteria being the most dominant, followed by Acidobacteria, while Archaea dominated the monsoon season with the most abundant phylum Thaumarchaeota, followed by Crenarchaeota and Euryarchaeota [32]. Another such study reported the presence of a core microbiome in mangrove sediment and pneumatophore samples. Despite sharing a core of 81 taxa, pneumatophores and sediment samples hosted a significantly different bacterial community [100].

4.2.2. Metatranscriptomics

While metagenomics targets DNA to provide holistic information about the entire microbial community, metatranscriptomics targets RNA to examine the active microbial community and their gene expression profile. Consequently, metatranscriptomics provides a more befitting approximation of ecologically significant microbial processes than metagenomics. However, the handling of RNA samples demands specific precautions when it comes to sample collection and storage, owing to their very short life span, from minutes to days, depending on the environmental conditions. Immediate sample preservation is of the utmost importance in order to obtain precise information on gene expression at the time of sampling. Metatranscriptomic has been successfully employed in the past to characterize the microbial community of mangrove sediments [101,102]. Though it offers an excellent platform to study active microbial populations, by far no study has employed this approach to explore MAPM communities.

4.2.3. Metaproteomics and Metabolomics

With recent developments in analytical techniques, the omics toolbox is no longer restricted to studies based on the sequencing and assessment of nucleic acids. Advanced chemical analytical techniques, such as chromatography (liquid or gas) and high-resolution mass spectrometry (gas chromatography–mass spectrometry and liquid chromatography–mass spectrometry), have allowed the detailed characterization of proteins and metabolites [103,104]. Metaproteomics and metabolomics rely on these analytical techniques to

identify and quantify all the expressed proteins and small metabolites, respectively, in various biological samples. Unlike other omics-based approaches, which generate data representing one aspect of cellular function, metaproteomics and metabolic profiling yield immediate insight into the biological processes occurring inside the cell or tissue at the molecular level. Although analytical organic chemistry has enabled us to identify the structures of thousands of different compounds in a composite sample [105,106], a large fraction of the compounds remain unknown. Our understanding of the diversity of enzymes and metabolites remains very limited, which poses challenges related to the annotation of identified compounds for reconstructing metabolic pathways and assessing microbial processes. So far, only one study has employed metabolomics to detect the presence of various active metabolites, including allopurinol, diazepam, dimetridazole, gemfibrozil, ibuprofen, metronidazole-oh, nalidixic acid, oxibendazole, sulfamonomethoxine, sulfadiazin, sulfacetamide, and sulfaethoxypyridazine, in culture extracts of bacterial isolates from pneumatophores of *A. marina* collected from the western coastal area of Jeddah, Saudi Arabia [85]. The application of metaproteomics to study biological processes occurring within the PAPM community is yet to be explored.

The combination of the traditional cultivation approach with modern omics approaches provides a powerful strategy for the thorough assessment of a microbial community and the processes it drives [96,107]. Past studies have employed cultivation and modern omics techniques in combination to gather novel insights into the structure and functional aspects of various ecosystems, including mangrove sediments [96,107–109]. These techniques, when employed in combination, can help to unfold the structure, function, and significance of PAPMs in mangrove ecosystems.

5. Concluding Remarks and Prospects

The well-being of mangrove ecosystems depends on the efficient recycling of nutrients by microorganisms dwelling in different components of the system. Despite numerous studies on mangroves that have been undertaken, very little information is available on the diversity and functional role of PAPMs. Limited research has provided some information on the diversity of pneumatophore-associated cyanobacteria, but the data pertaining to the bacterial community on mangrove pneumatophores is scarce. Most of these studies are descriptive and lack hypothesis-driven research. More importantly, the available information on the presence of distinct and diverse microbial communities on pneumatophores is mostly based on microscopic observation and identification of the cultured microorganisms, but such an approach is often restricted to cultivable microbes. The culture-independent omics-based analyses will expand our understanding of the distribution and ecological importance of PAPMs in mangrove ecosystems and demand more emphasis in the near future. The combination of traditional cultivation and omics-based approaches is important in comprehensively evaluating the diversity and function of pneumatophore-associated microbes and better understanding their contribution to the productive well-being and the overall ecosystem services of mangrove ecosystems. Some studies suggest that various biotic and abiotic factors, in particular tidal inundation, have significant impacts on the structure and functioning of pneumatophore-associated microbial diversity. However, horizontal variations in the pneumatophore microbial community across the intertidal range, as well as the influential factors, have rarely been inspected, even though this kind of research will improve our understanding of which microbial players can most effectively adapt to stress. The natural complexity of mangrove ecosystems, along with the environmental stresses that epiphytic microbes on pneumatophores are subjected to, suggests that microbes may carry a collection of novel compounds and pathways that enable them to thrive in these habitats. This implies pneumatophores comprise yet-uncultured microorganisms of immense biotechnological potential. Further research is needed to elucidate the intricacies of pneumatophore microbial activities and their impacts on the productivity of the mangrove ecosystem.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse12050802/s1>, Table S1: List of studies on pneumatophores and the associated prokaryotic community (1975–2022); Table S2: List of cyanobacteria reported on pneumatophores of mangroves at different locations.

Author Contributions: Conceptualization, V.B., F.W.-F.L. and N.F.-Y.T.; methodology, V.B., N.F.-Y.T., K.K.-Y.L. and W.L.; validation, K.K.-Y.L., W.L., S.J.-L.X. and N.F.-Y.T.; formal analysis, V.B. and F.W.-F.L.; investigation, V.B., F.W.-F.L. and N.F.-Y.T.; resources, F.W.-F.L.; data curation, V.B.; writing—original draft preparation, V.B. and F.W.-F.L.; writing—review and editing, N.F.-Y.T., L.C., K.K.-Y.L., W.L., S.J.-L.X., H.-C.Z., T.L. and C.-L.L.; visualization, V.B. and N.F.-Y.T.; supervision, F.W.-F.L.; project administration, F.W.-F.L. and N.F.-Y.T.; funding acquisition, F.W.-F.L. All authors have read and agreed to the published version of the manuscript.

Funding: The work described in this paper was supported by grants from the Research Grants Council of the Hong Kong Special Administrative Region, China (UGC/FDS16/M02/21) and (UGC/IDS(R)16/19).

Conflicts of Interest: The authors declare no conflicts of interest.

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