



A Systematic Review of the Physicochemical and Microbial Diversity of Well-Preserved, Restored, and Disturbed Mangrove Forests: What Is Known and What Is the Way Forward?

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Abstract: Mangrove forests are salt-tolerant intertidal vegetation in tropical and subtropical areas. Mangrove ecosystems provide commercial products, valuable fisheries, and aquaculture resources, protect and stabilize coastlines, and are important carbon sinks. However, they are threatened globally by human activities such as deforestation, pollution, and development causing fragmentation between the well-preserved, restored, and disturbed mangrove forests. Despite this, mangroves can adapt and strive well and are notable well associated with microbial diversity. Here, we investigate the diversity of microbes in different environmental settings using preferred reporting items for systematic and meta-analyses (PRISMA) analysis for publications from Scopus and the Web of Science databases. We report publications since 1987, and observed an exponential increase in publications beginning in the year 2000, which may be associated with the development of molecular and sequencing technologies. Differences in bacterial diversity was observed across the well-preserved, restored, and disturbed mangrove environments. Disturbed mangrove forests had a higher diversity (70 unique taxon orders reported) compared to well-preserved (33 unique taxon orders reported) and restored forests (38 unique taxon orders reported). Based on our analysis, we found that the microbial community plays an important role in the survival and adaptability of mangroves under varying environmental conditions. Thus, there is a need and a lot of potential for research in the area of mangrove microbiology with reference to ecology, biogeochemistry, and geomorphology.

Keywords: mangrove; sediment microbiome; bacterial diversity; systematic analysis

1. Introduction

Mangrove forests are salt-tolerant intertidal vegetation along coastal margins and brackish water of coastal estuaries, bordering the land and the sea in tropical and subtropical areas [1,2]. Adapted to harsh coastal conditions, they serve as a barrier for coastal protection and stabilization, play important roles in carbon fixation, and facilitate the reduction of terrestrial nutrient loading from upstream inputs [3]. Mangrove forests occupy approximately eight million ha of coasts worldwide [4] and the highest proportion is found in Asia with about 42% of the global coverage [5]. Mangroves are very dynamic and highly productive ecosystems [6].

Mangrove ecosystems provide valuable services to coastal communities and industries. As an important resource for human sustainability and livelihood, mangroves are exploited for food, timber, fuel, and medicine [7]. Mangrove forests act as carbon sinks that absorb CO_2 and sequester carbon as above-ground and below-ground biomass [8]. Mangrove sediment is deposited below soaked and anoxic environments which impedes the degradation of organic matter resulting in undisturbed carbon that will last for centuries [9–11]. Therefore, dubbed the blue carbon ecosystem, mangroves can facilitate reducing global carbon emissions which helps mitigate climate change [12–14].



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). The unique zonation of mangroves; according to the substrate condition, tidal regime, and topographic ground elevation [15–17] promotes diversity in flora [18] and fauna. Though the diversity of mangrove species is typically low compared to other forest environments, they provide shelter and food for organisms such as crustaceans, mollusks, amphibians, reptiles, small mammals [19], and migratory birds [20]. Mangrove ecosystems are also important for the maintenance of the local coastal fishery industry [21]. The terrestrial nutrients from upstream nourish and nurture the coastal waters by supplementing downstream minerals. These forests provide food and shelter for marine organisms, and a nutrient source exchange for the coastal fishery environment [22,23]. The ecosystem services of mangroves are shown in Figure 1.



Figure 1. Ecosystem services of mangrove forests.

Despite their multiple ecosystem services as shown in Figure 1, mangrove ecosystems have undergone serious alterations largely induced by anthropogenic activities [6,24,25], monsoons, and tidal effects. The reduction of mangrove forests has been estimated at 1%–2% per year globally and accumulate to about 35% since the year 2000 [7]. Human and natural impacts have left us with well-preserved, regenerated, and disturbed mangrove ecosystems. Well-preserved (pristine) mangroves are naturally regenerated, healthy mangrove forests with less human disturbance and low pollution. Restored (also termed regenerated, reforested, or rehabilitated) mangroves include both naturally and anthropogenically planted mangrove trees as conservation. The latter are mainly monospecies plantations used to curb soil erosion and serve as a reintroduction of vegetation in coastal areas. Disturbed mangrove forests are degraded or deforested mangroves which are subjected to contaminants such as hydrocarbons, human wastewater, sewage, microplastics, invasive species, and others. This group of mangrove forests have high artificially introduced nutrients which alter the mangrove ecosystem equilibrium of the microbial community and its mangrove host.

The current mangrove species distribution and composition are subject to geochronology changes [26] and the distribution of mangrove coverage around the world is uneven and cannot be explained by a single influencing factor [27]. A higher concentration of mangroves and a high mangrove species diversity is found in the tropics between longitude 60° E and 170° E with the largest amount of mangrove coverage in Southeast Asia [4,28]. The adaptation and succession of mangroves are speculated to be closely related to the diversity of microbes in the sediments [29]. In fact, the microbial community and the mangrove microbiome, including bacteria, archaea, fungi, and protists is vital in maintaining primary productivity, providing nutrient transformations, and aiding in the conservation of vegetation, to an extent that their presence cannot be ignored. In essence, degradation activities are associated with the microbial community by breaking down organics into inorganics, and vice versa, to be absorbed into the ecosystem and the food web [30]. Mangrove microbial communities are active participants in the biogeochemical cycles such as the carbon cycle and nitrogen cycle which supply nutrients to plants and animals. Limiting nutrients such as phosphorus and nitrogen in sediments, and tidal flooding near the rhizo-sphere, forces microbes to be involved in special roles such as nitrogen fixation, phosphate solubilization, assimilation of photosynthesis, sulfate reduction, enzyme production, and hydrocarbon degradation [31]. Microbial species distribution is known to have a close relation to their corresponding plant hosts. Their community is highly dependent on mangrove species for species selection [32,33] and is driven by the environment's physiochemical properties and other factors.

To date, the diversity and composition of the microbial community in the mangroves it still not entirely known. Without this information, the potential roles of microbes and their functions in mangrove ecosystems are still poorly understood [32–34]. The various environmental factors, zonation [16,35], and spatial–temporal settings [36–38] in mangrove forests affect microbial compositions and the roles each taxon plays in the mangroves [16,35]. The different mangrove forest types, well-preserved, restored, and disturbed, are expected to host a unique set of microbiotas influenced by their surroundings and any external contributing factors such as development and pollution. With technological developments in bioinformatics, we are one step closer to studying species, and communities while paving the way to new fields of ecology with respect to mangrove forests. Every year, more scientific research is conducted and the number of publications that are readily available is on the rise. Figure 2 shows the frequency of publications related to mangrove sediment microbial diversity globally.



Map of Mangrove Sediment Microbial Diversity Publication Counts

Figure 2. Map of mangrove sediment microbial diversity publication counts. The country polygon fill gradient indicates the number of publication counts while the polygon outline represents the top 50 mangrove coverage in km² according to the continuous mangrove forest cover for the 21st century (CGMFC-21) created by Hamilton et al. [4]. The green plots are the sampling plots of each publication. The figure was generated using the ggplot2 package [39] in R [40] using the Mercator projection.

With the advancement of biochemical taxonomy and molecular biotechniques, the identification, classification, and nomenclature of microbes especially bacteria are everchanging with time. Responses to the call to unify and standardize taxonomy prompt databases

such as The National Center for Biotechnology Information (NCBI) Taxonomy [41,42] and The Genome Taxonomy Database Toolkit (GTDB-Tk) [43,44]. Both databases provide a phylogenetically diverse set of taxonomic assignments for microbial diversity study. Here, we retain all nomenclature of microbes from our reviewed articles concerning the original articles and their taxon alignment of respective databases, we found that most published articles aligned their results with the NCBI Taxonomy for its widespread usage. In response to the changes in taxonomic order nomenclature, the comparison of both the NCBI taxonomy and GTDB-Tk databases of the top 20 bacterial taxonomic orders found in the three different mangrove conditions are listed in Table S1.

Since the health of mangrove forests is very much associated with mangrove–microbial interactions, understanding this relationship will be vital for the successful conservation and rehabilitation of mangrove ecosystems. To our knowledge, at present, no study or review has investigated microbial diversity across these three mangrove forest types namely well-preserved, restored, and disturbed. Therefore, in this article we systematically reviewed the diversity of the microbial community in well-preserved, restored, and disturbed mangrove forest ecosystems to determine: (1) whether varying mangrove types host a unique pattern of microbiota; (2) the dominant microbial taxa in each forest type; (3) what the research trend of mangrove sediment microbial studies is; (4) if environmental physio parameters alter the mangrove sediment microbial diversity.

2. Materials and Methods

2.1. Construction of Database

Database establishments of published studies on microbial diversity of different mangrove conditions were performed by using the topic search term: topic = (microb* OR bacteria* OR fung* OR prokaryot*) AND (diversity OR structure OR assemblage) AND mangrove AND (regenerat* OR pristine OR disturb* OR restor* OR degradat*) in Web of Science (WoS) on 12th of June 2022. The document types ranged from articles, review papers, meetings, and others, yielding a total of 653 publications. The earliest publication captured within the search parameters was in 1987.

To encourage a more robust and thorough review, Scopus-indexed databases were searched using TITLE-ABS-KEY ((microb* OR bacteria* OR fung* OR prokaryot* OR diversity OR structure OR assemblage) AND mangrove AND (regenerat* OR pristine OR disturb* OR restor* OR degradat*)) generating a total of 1,815 publications on 14th of June 2022. Combinations of keyword search terms in those databases to acquire relevant kinds of literature are listed in Table 1.

Table 1. Searched terms used for database review.

Search Terms
microb* OR bacteria* OR fung* OR prokaryot* diversity OR structure OR assemblage
mangrove regenerat* OR pristine OR disturb* OR restor* OR degradat*

After combining results from both databases, a total of 2468 published papers were identified. The title, abstract, year of publication, authors, and digital object identifier (DOI) of each paper, were manually screened using R 4.1.3 [40], metagear package [45], preferred reporting items for systematic and meta-analyses (PRISMA) flow chart were used to form a more comprehensive and ideal meta-analysis using the R PRISMA2020 flow diagram package [46] provided in Figure 3.



Figure 3. Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow diagram, generated using searches on the Web of Science (WoS) and Scopus databases. The figure was drawn using PRISMA2020 flow diagram R package [46].

Data extraction was performed manually and categorized into three groups of the surrounding mangrove conditions, namely well-preserved, restored, and disturbed. For a better environmental condition comparison, all articles that mentioned samples collection from pristine and well-preserved mangrove areas were grouped into well-preserved; regenerated, reintroduced, and planted mangroves were regarded as restored; while all articles with microplastic, hydrocarbon incubation, anthropogenic influenced, and waste-water contaminations were classified as disturbed. We reviewed a total of 94 articles associated with mangrove environments profiling the microbial community structures using a variety of sequencing approaches. The majority of the articles were focused on several locations in China, India, and Brazil, while the rest can be traced to Columbia, the USA, Saudi Arabia, Australia, Malaysia, Honduras, and Singapore.

2.2. Trends in Scientific Publication

In this review, we compiled a total of 2428 articles from the years 1987 to 2022. Our analysis revealed that the field of mangrove microbiology exhibited an upward trend. To illustrate the increment of studies regarding microbial diversity within mangrove sediment, the combined database of WoS and Scopus publications were sorted by year, as shown in Figure 4. Interestingly there was a sudden increment in microbial diversity studies in the early 2000s, probably due to the advancement of metagenomics methods and techniques such as denaturing gradient gel electrophoresis (DGGE) and high-throughput sequencing

(HTS), also known as next generation sequencing (NGS). The popularization of sequencing methods coalescing with molecular biological techniques has driven the capability to take microlevel biodiversity and its ecological structural composition from a given environmental sample to new heights. Hence, using metagenomics, the quantification of a given biocommunity's dynamics and roles are made possible, while parsing the relationship with the corresponding environmental gradients and factors.



Figure 4. Trends and numbers of published articles on mangrove sediment microbial studies in two main databases. Publication counts skyrocketed in early 2000.

Furthermore, we found that most publications concentrated on mangroves with various types of pollution and contaminations. A higher amount of attention on disturbed mangrove environments might be due to mangrove microbial dynamics, environmental, and ecological impacts, and the responses to impacts such as hydrocarbon leakage and alien-invasive species altering microbial structure compositions.

3. Factors Influencing Microbial Community and Diversity

Microbial community composition and activities are very much influenced by environmental conditions and interactions with the biotic components. Environmental parameters often differ by forest type and are dependent on geomorphology, anthropogenic factors such as pollution, development, and tourism activities, and natural factors such as the frequency of flooding, tidal inundation, salinity, and the intertidal gradient, which have a big role in determining the microbial diversity in the mangrove forest [47,48]. The extent to which mangrove microbes are regarded as potential bioindicators of environmental changes, with their quick growth rate and delicate response to the bioavailability of nutrients and environmental properties [49] such as pH, salinity, and temperature is shown in Table 2. Total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), total sulfur (TS), and total carbon (TC) recorded in mangrove forests are listed in Table S1.

Helfer and Hassenruck (2021) [50] highlighted that the microbial community in sediments is determined by soil grain size, pH levels, redox conditions, detrital organic matter, organic carbon, and water content. Leaf age and root type may affect the type of microbes on the host (above-ground), the pH, and the C: N ratio can enable the prediction of fungal to bacterial dominance. In this manuscript we try to investigate the extent that environmental parameters, with a focus on pH, temperature, and salinity, can affect microbial patterns across well-preserved, restored, and disturbed mangrove forests.

3.1. Physicochemical Parameters in Well-Preserved Mangroves

The mixing effect of terrestrial freshwater and tidal marine seawater in mangrove ecosystems creates a physiochemically distinct brackish environment of salinity that varies between <5 ppt and 30 ppt, thus offering an exclusive zone of sediment which houses a large number of microbes with distinct functions and metabolisms. Compared to other physical parameters, it was reported that salinity greatly influences the microbial diversity of mangrove sediment [51–53].

A total of 12 articles are listed in Table 2 (information on sampling coordinates are provided in the Supplementary Materials) showing pH, temperature, and salinity values in well-preserved mangrove soil. The ecosystems are mainly alkaline and the salinity changes according to the geolocation of tidal flat elevations relative to the sea. Salinity affects the changes in vegetation type which is the main driver in mangrove zonation [54] and may influence the diversity and structure of its corresponding microbes. The pH levels within mangrove sediments are relatively uniform with a range reported of 5 to 8.09 depending on the zonation, tidal zones [55–57], and seasons [58,59]. Seasonal precipitations and riverine discharge are the main factors of salinity fluctuation [54,60]. High salinity values (33 to 64 ppt) are found in New Caledonia due to its oceanic mangrove environment. A study by Luis et al. (2019) [60] found that salinity is higher in the environment Avicennia spp. populate compared to *Rhizophora* spp. and the zonation between mangrove tree species might directly and indirectly impact the plant's associated microbial communities. High salinity suppressed and constrained microbial differentiation. Reports show that the diversity and species richness was highest when in intermediate salinity which indicated that the optimum salinity range for coastal sediment ammonia-oxidizing bacteria (AOB) was around 10 to 30 ppt of salinity [61–63].

Meanwhile, an investigation by Feng et al. (2019) [64] on stratified layers of mangrove sediment revealed that pH levels had a positive relationship to depth, where the average pH value increased to around eight as the depth increases, thus becoming more alkaline. Additionally, pH serves as a crucial regulator for the microbial community especially in sediment, limiting the biogeochemical metabolism activities, and it is the second driver of microbial structure after salinity [52].

Sampling Site	pH	Temp. (°C)	Salinity ppt	References		
Well-preserved Mangrove						
Wenlock River, Far North Queensland, Australia	7.1 to 7.5	25.5 to 26.1	21.9 to 23.8	[65]		
Tanjung Piaj Johor Malaysia	5.2 to 7.0	-	7.1 to 8.2	[66]		
Tanjung Tiai, jonor, Walaysia	7.2 to 7.4	-	5.8 to 6.9	[00]		
Kalash Island, Sundarbans, India	7.6 to 7.8	22 to 31	22 to 27	[67]		
Saint Vincent Bay, New Caledonia, Overseas France	6.64 to 7.04	-	44 to 64	[60]		
Santi vincent bay, New Caledonia, Overseas France	6.46 to 6.67	-	48 to 62			
Paranaguá Bay, Brazil	5.3 to 7.6	-	5 to 30	[52]		
Virgin Jungle Forest, Matang, Perak, Malaysia	7.6	28.5	20	[68]		
Ferney, Mauritius	7.90 to 8.09	27.9 to 29.1	32.4 to 35.4	[69]		
Boguaçú River, Guaratuba bay, Paraná, Brazil	6.5 to 6.6	-	-	[70]		
Estuary of Cananéia, São Paulo, Brazil	5.4 to 6.7	12.5 to 13.7	0.2 to 1.3	[71]		
Restinga da Marambaia, Rio de Janeiro, Brazil	-	28 to 33	-	[72]		
Ilha do Cardoso, Sao Paulo, Brazil	5.9 to 6.4	-	-	[73]		
Florida Coastal Everglades, USA	-	-	8.4 to 42.6	[74]		

Table 2. Levels of pH, temperature, and salinity of well-preserved, restored and disturbed mangrove soil.

Table 2. Cont.

Restored Mangrove Quanzhou bay, Fujian, China 6.60 to 7.88 - 9.6 to 33 [75] Leizhou Nature Reserve, China 6.75 to 7.63 - 1.43 to 1.50 [76] Quanzhou bay, Fujian, China 6.76 to 7.28 2.2 to 23 1.28 to 1.71 [77] Hainjang River Estuary, Cuangdong, China 6.5 to 7.8 2.28 to 26.3 3.8 to 11.9 [78] Hailing Island National Mangrove Wetland Park, China 5.99 to 7.72 22.6 to 26.3 3.41 to 13.27 [55] Sungai Haji Dorani, Selangor, Malaysia 6.59 to 7.72 26.9 - [34] Cardoso Island State Park, Brazil 6.33 - - [80] Productive Zone, Matang, Perak, Malaysia 7.6 30 21 [68] National Shankou Nature Reserve, Fujian, China 6.19 to 8.25 - - [81] National Shankou Nature Reserve, Guangxi, China 6.69 to 7.03 - 28.4 [82] National Shankou Nature Reserve, Guangxi, China 4.79 to 6.35 1.27 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand	Sampling Site	рн	Temp. (°C)	Salinity ppt	References		
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Xiatanwei mangrove wetland park, Xiamen, China 6.35 to 7.32 13.7 to 14.6 - [79] Sungai Haji Dorani, Selangor, Malaysia 6.59 to 7.72 26.9 - [34] Cardoso Island State Park, Brazil 6.33 - - [80] Productive Zone, Matang, Perak, Malaysia 7.6 30 21 [68] Disturbed Mangrove Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 - - [81] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.69 to 7.03 - 28.6 to 29.6 [59] Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Cuajira, Colombia 7.47 to 7.56 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.92 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Katadwip, Sundarban, India 7.27 - 11.9 to 27.5 [88] <t< td=""><td>Hailing Island National Mangrove Wetland Park, China</td><td>5.99 to 7.78</td><td>29.03 to 32.28</td><td>3.41 to 13.27</td><td>[55]</td></t<>	Hailing Island National Mangrove Wetland Park, China	5.99 to 7.78	29.03 to 32.28	3.41 to 13.27	[55]		
Sungai Haji Dorani, Selangor, Malaysia 6.59 to 7.72 26.9 - [34] Cardoso Island State Park, Brazil 6.33 - - [80] Productive Zone, Matang, Perak, Malaysia 7.6 30 21 [68] Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 - - [81] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 4 to 6.9 21.2 to 38.1 - [82] National Shankou Natural Reserve, Guangxi, China 6.69 to 7.03 - 28.6 to 29.6 [59] Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakom Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Guanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India 7.25 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Katdwip, Sundarban, India - - - </td <td>Xiatanwei mangrove wetland park, Xiamen, China</td> <td>6.35 to 7.32</td> <td>13.7 to 14.6</td> <td>-</td> <td>[79]</td>	Xiatanwei mangrove wetland park, Xiamen, China	6.35 to 7.32	13.7 to 14.6	-	[79]		
Cardoso Island State Park, Brazil 6.33 - - [80] Productive Zone, Matang, Perak, Malaysia 7.6 30 21 [68] Disturbed Mangrove Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 - - [81] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.69 to 7.03 - 28.6 to 29.6 [59] Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [87] Guanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [87] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 5.82 to 5.89 <t< td=""><td>Sungai Haji Dorani, Selangor, Malaysia</td><td>6.59 to 7.72</td><td>26.9</td><td>-</td><td>[34]</td></t<>	Sungai Haji Dorani, Selangor, Malaysia	6.59 to 7.72	26.9	-	[34]		
Productive Zone, Matang, Perak, Malaysia 7.6 30 21 [68] Disturbed Mangrove Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 - - [81] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 4 to 6.9 21.2 to 38.1 - [82] National Shankou Natural Reserve, Guangxi, China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sehakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 5.82 to 5.89	Cardoso Island State Park, Brazil	6.33	-	-	[80]		
Disturbed Mangrove Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 - - [81] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 4 to 6.9 21.2 to 38.1 - [82] National Shankou Natural Reserve, Guangxi, China 6.69 to 7.03 - 28.6 to 29.6 [59] Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Guanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Quanzhou bay, Fujian, China 6.81 to 6.83 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [87] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Mangalavanam, Jang China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minijang River Estuary, Fujian,	Productive Zone, Matang, Perak, Malaysia	7.6	30	21	[68]		
Haimen Island and Haicang Bay Xiamen, Fujian, China 6.19 to 8.25 [81]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 4 to 6.9 21.2 to 38.1 -[82]National Shankou Natural Reserve, Guangxi, China 6.69 to 7.03 - 28.6 to 29.6 [59]Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83]Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84]Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 [85]Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86]Quanzhou bay, Fujian, China 6.92 to 7.66 [87]Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 [87]Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56]Kakdwip, Sundarban, India11.9 to 27.5 [88]Shanyutan Wetland, Minjiang River Estuary, Fujian, China 7.27 -18[91]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.32 to 8.63 - 24.5 to 55.0 [93]Six Coastal Region Mangroves of China 6.32 to 8.63 - 4.5 to 55.0 [93]Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93]Six Coastal Region Mangroves of China 6.32 to 8.620 - 4 to 7 [95]Bhitar		Disturbed Mangrov	/e				
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National Shankou Natural Reserve, Guangxi, China 6.69 to 7.03 - 28.6 to 29.6 [59] Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [87] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Guastal Zones of China 8.18 to 5	Yunxiao Zhangjiangkou Nature Reserve, Fujian, China	4 to 6.9	21.2 to 38.1	-	[82]		
Seven Coastal Region Mangroves of China 4.79 to 6.35 12.7 to 24.4 18 to 31.95 [83] Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [87] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.83 to 7.34 - 0.5 to 4.17 [94] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China	National Shankou Natural Reserve, Guangxi, China	6.69 to 7.03	-	28.6 to 29.6	[59]		
Sahakorn Canal, Bangkok, Thailand 7.48 to 7.62 32 to 35 31 to 33 [84] Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.32 to 8.63 - 24.5 to 5.50 [93] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 5.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 <	Seven Coastal Region Mangroves of China	4.79 to 6.35	12.7 to 24.4	18 to 31.95	[83]		
Valle de Los Cangrejos, La Guajira, Colombia 7.47 to 7.56 - - [85] Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [87] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 -	Sahakorn Canal, Bangkok, Thailand	7.48 to 7.62	32 to 35	31 to 33	[84]		
Serinhaém Estuary, Brazil 7.45 to 7.80 25.0 to 29.3 13.3 to 15.1 [86] Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 6.32 to 8.63 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20	Valle de Los Cangrejos, La Guajira, Colombia	7.47 to 7.56	-	-	[85]		
Quanzhou bay, Fujian, China 6.92 to 7.66 - - [87] Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27	Serinhaém Estuary, Brazil	7.45 to 7.80	25.0 to 29.3	13.3 to 15.1	[86]		
Futian Mangrove Nature Reserve, Guangdong, China 6.81 to 6.83 - - [37] Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - <t< td=""><td>Quanzhou bay, Fujian, China</td><td>6.92 to 7.66</td><td>-</td><td>-</td><td>[87]</td></t<>	Quanzhou bay, Fujian, China	6.92 to 7.66	-	-	[87]		
Mangalavanam, India 7.2 to 7.4 28.77 to 30.5 22.6 to 25.8 [56] Kakdwip, Sundarban, India - - 11.9 to 27.5 [88] Haikou and Sanya, Hainan, China 7.25 to 8.20 25.4 to 29.5 17.10 to 35.1 [89] Shanyutan Wetland, Minjiang River Estuary, Fujian, China 5.82 to 5.89 - - [90] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 7.27 - 18 [91] Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - - [97] Mai Po Wathard Hong Kong China 6 61 to 7.48 - [98] </td <td>Futian Mangrove Nature Reserve, Guangdong, China</td> <td>6.81 to 6.83</td> <td>-</td> <td>-</td> <td>[37]</td>	Futian Mangrove Nature Reserve, Guangdong, China	6.81 to 6.83	-	-	[37]		
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Haikou and Sanya, Hainan, China7.25 to 8.2025.4 to 29.517.10 to 35.1[89]Shanyutan Wetland, Minjiang River Estuary, Fujian, China5.82 to 5.89[90]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China7.27-18[91]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China7.27-18[91]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China6.83 to 7.34-9.27 to 14.53[92]Six Coastal Region Mangroves of China6.32 to 8.63-24.5 to 55.0[93]Coastal Zones of China8.18 to 5.17-0.5 to 4.17[94]Bhitarkanika mangrove, India5.56 to 7.14-0.33 to 2.46[36]Bertioga, Sao Paulo State, Brazil6.93 to 6.20-4 to 7[95]Restinga da Marambaia, Rio de Janeiro, Brazil6 to 8275 to 20[96]La Guajira, Colombia7.3 to 7.94[97]Mai Po Wathand, Hong Kong, China6.61 to 7.48[97]	Kakdwip, Sundarban, India	-	-	11.9 to 27.5	[88]		
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Yunxiao Zhangjiangkou Nature Reserve, Fujian, China7.27-18[91]Yunxiao Zhangjiangkou Nature Reserve, Fujian, China6.83 to 7.34-9.27 to 14.53[92]Six Coastal Region Mangroves of China6.32 to 8.63-24.5 to 55.0[93]Coastal Zones of China8.18 to 5.17-0.5 to 4.17[94]Bhitarkanika mangrove, India5.56 to 7.14-0.33 to 2.46[36]Bertioga, Sao Paulo State, Brazil6.93 to 6.20-4 to 7[95]Restinga da Marambaia, Rio de Janeiro, Brazil6 to 8275 to 20[96]La Guajira, Colombia7.3 to 7.94[97]Mai Po Wathand, Hong Kong, China6.61 to 7.48-[97]	Shanyutan Wetland, Minjiang River Estuary, Fujian, China	5.82 to 5.89	-	-	[90]		
Yunxiao Zhangjiangkou Nature Reserve, Fujian, China 6.83 to 7.34 - 9.27 to 14.53 [92] Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - - [97]	Yunxiao Zhangjiangkou Nature Reserve, Fujian, China	7.27	-	18	[91]		
Six Coastal Region Mangroves of China 6.32 to 8.63 - 24.5 to 55.0 [93] Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - - [97] Mai Po Wathand Hong Kong, China 6 61 to 7.48 - [98]	Yunxiao Zhangjiangkou Nature Reserve, Fujian, China	6.83 to 7.34	-	9.27 to 14.53	[92]		
Coastal Zones of China 8.18 to 5.17 - 0.5 to 4.17 [94] Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - - [97] Mai Pow Wathand Hong Kong, China 6 61 to 7.48 - [98]	Six Coastal Region Mangroves of China	6.32 to 8.63	-	24.5 to 55.0	[93]		
Bhitarkanika mangrove, India 5.56 to 7.14 - 0.33 to 2.46 [36] Bertioga, Sao Paulo State, Brazil 6.93 to 6.20 - 4 to 7 [95] Restinga da Marambaia, Rio de Janeiro, Brazil 6 to 8 27 5 to 20 [96] La Guajira, Colombia 7.3 to 7.94 - - [97] Mai Po Wathand Hong Kong, China 6 61 to 7.48 - [98]	Coastal Zones of China	8.18 to 5.17	-	0.5 to 4.17	[94]		
Bertioga, Sao Paulo State, Brazil6.93 to 6.20-4 to 7[95]Restinga da Marambaia, Rio de Janeiro, Brazil6 to 8275 to 20[96]La Guajira, Colombia7.3 to 7.94[97]Mai Po Wathand, Hong Kong, China6 61 to 7.48-[98]	Bhitarkanika mangrove, India	5.56 to 7.14	-	0.33 to 2.46	[36]		
Restinga da Marambaia, Rio de Janeiro, Brazil6 to 8275 to 20[96]La Guajira, Colombia7.3 to 7.94[97]Mai Po Watland, Hong Kong, China6 61 to 7.48-[98]	Bertioga, Sao Paulo State, Brazil	6.93 to 6.20	-	4 to 7	[95]		
La Guajira, Colombia 7.3 to 7.94 - [97] Mai Po Watland Hong Kong China 6.61 to 7.48	Restinga da Marambaia, Rio de Janeiro, Brazil	6 to 8	27	5 to 20	[96]		
Mai Po Watland Hong Kong China 661 to 748	La Guajira, Colombia	7.3 to 7.94	-	-	[97]		
10110 1012 1012 1012 1012 1012 1012 1012 1012 1012 1012 1012 1012 1012 1012	Mai Po Wetland, Hong Kong, China	6.61 to 7.48	-	-	[98]		
Dava Bay, Guangdong, China 7.5 to 8.1 20.6 to 22.6 26.7 to 31.9 [99]	Daya Bay, Guangdong, China	7.5 to 8.1	20.6 to 22.6	26.7 to 31.9	[99]		
Ribandar, Mandovi Estuary, Goa, India 6.5 to 6.7 35 - [100]	Ribandar, Mandovi Estuary, Goa, India	6.5 to 6.7	35	-	[100]		
Sahakorn Canal, Bangkok, Thailand 7.3 33 33 [101]	Sahakorn Canal, Bangkok, Thailand	7.3	33	33	[101]		
Dongzhai Bay, Hainan, China 3.19 to 7.1 [102]	Dongzhai Bay, Hainan, China	3.19 to 7.1	-	-	[102]		
Mai Po Wetland, Hong Kong, China 5.82 to 8.17 [103]	Mai Po Wetland, Hong Kong, China	5.82 to 8.17	-	-	[103]		
Rantau Abang, Terengganu, Malaysia 5.1 [31]	Rantau Abang, Terengganu, Malaysia	5.1	-	-	[31]		
Ar-Ravis and Yanbu, Saudi Arabia 8.4 to 8.5 31.7 to 33.4 15.9 to 19.2 [104]	Ar-Ravis and Yanbu, Saudi Arabia	8.4 to 8.5	31.7 to 33.4	15.9 to 19.2	[104]		
Darwin Harbour, Australia - 25.5 to 31.7 18.4 to 39.2 [105]	Darwin Harbour, Australia	-	25.5 to 31.7	18.4 to 39.2	[105]		
Yellow River Delta, Shandong, China 7.5 to 8.7 11.7 to 12.6 0.4~3.4 [106]	Yellow River Delta, Shandong, China	7.5 to 8.7	11.7 to 12.6	0.4~3.4	[106]		
Coastal Zones of Singapore 6.37 to 8.61 27.1 to 28.3 - [107]	Coastal Zones of Singapore	6.37 to 8.61	27.1 to 28.3	-	[107]		
Mai Po Wetland, Hong Kong, China 6.8 to 5.8 - 27.7 to 35 [108]	Mai Po Wetland, Hong Kong, China	6.8 to 5.8	-	27.7to 35	[108]		
Bertioga, Sao Paulo State, Brazil 64 to 7.1 - 55.6 to 88.4 [109]	Bertioga, Sao Paulo State, Brazil	6.4 to 7.1	-	55.6 to 88.4	[109]		
Netidhopani Island, Sundarban, India 8.1 - 7.22 [110]	Netidhopani Island, Sundarban, India	8.1	-	7.22	[110]		
Todos os Santos Bay, Bahia, Brazil 3.6 to 7.5 [111]	Todos os Santos Bay, Bahia, Brazil	3.6 to 7.5	-	=	[111]		

-: no data provided. Publications are sorted according to published year.

The effect of environmental parameters can be observed among the AOB which is an important component of the nitrogen cycle within the mangrove ecosystem. It has been documented that their diversity decreased with the increase in salinity. Some studies show that freshwater sediment bacteria when exposed to a saline environment may influence the species richness (an increase of Chao1 index) of specific bacteria [62,63]. Salinity is theorized to constrain functional changes such as mineralization rates, reproduction rates, and cell physiology while facilitating a more diverse bacterial colonization and limiting the domination of certain lineages [112].

3.2. Physicochemical Parameters in Restored Mangroves

Restored mangrove sites have a similar alkaline pH to well-preserved mangroves as highlighted in the literary materials compiled in Table 2 (sampling coordinates are listed in Table S3). The physiochemical parameters in restored mangroves of 10 published articles

shows that restored mangroves were mostly studied at riverine landscapes and deltas where the salinity was mostly brackish and the soil temperature fluctuated depending on the locations of sampling. Some reports noted that the concentration of ammonia (NH₃) significantly correlated with the bioavailability of diazotrophs [113]. The effects of pH were observed in the report by Zhang et al. (2012) [114], where AOB abundance was documented to be low when the soil sediment was acidic, while the abundance of ammonia-oxidizing archaea (AOA) was higher. Thus, demonstrating AOA might have a more significant role in autotrophic nitrification processes in a more acidic ecosystem [114,115].

It was found that AOB such as genera *Vibrio* and *Methylophaga* had a more profound proposition in a lower tidal mudflat of artificial restored mangrove wetland, remedying the coastal area by removing N from the eutrophicated and polluted surroundings into nutrients for the mangrove trees [79]. Studies in the Matang Mangrove Forest Reserve (MMFR) showed that mangroves managed by a rotating thinning process for commercial use are found to have a similar pH value compared to well-preserved mangroves [68]. The model in the MMFR showed that managed logging may change nutrient input to the soil sediments and to physiochemical parameters but that the mangrove sediment microbial structures were relatively similar, providing a sustainable model of managing a productive mangrove forest.

3.3. Physicochemical Parameters in Disturbed Mangroves

In our context, mangrove forests exposed to anthropogenic pressure, the presence of invasive species, and pollution, which includes oil, wastewater, heavy metals, microplastics, and Bisphenol A (BPA) contamination, are classified as disturbed mangrove environments. The discharge of anthropogenic fertilizer contributes to increased phosphorus (P) levels, for instance, which promotes eutrophication in marine and transitional ecosystems such as mangroves [116–118]. As eutrophication and anaerobic conditions are caused by mainly agriculture runoff, the dynamics of mangrove nutrient cycles are distorted by the increasing rate of algae blooms which degenerate the water quality.

Furthermore, the balance of organic and inorganic matter will be distorted when both domestic and industrial pollutants are introduced into the environment [117,119]. Aquaculture and human industrial activities lead to the dispersal of pollutants adjacent mangrove to the area, thus influencing the functional framework of microbes in the sediment. While most mangrove forests are slightly alkaline, the literature shows that a disturbed mangrove environment, such as in Table 2 (sampling coordinates are provided in Supplementary Materials) has a lower pH value and is relatively more acidic than a well-preserved mangrove (Table 2), thus pH was suggested as an indicator for the spatial variation of microbial distributions [120].

Since pH has such a significant impact on the soil microbial community, and the tendency of acidification of the marine environment with global warming and ocean acidification due to CO₂ increases [121], research on the influence of pH on ammonia-oxidizing prokaryotes (AOP) such as the phylums Proteobacteria, Chloroflexi, Nitrospira, and Cyanobacteria for the bacteria domain [122] and Crenarchaeota [123] and Thaumarchaeota [114] for Archaea, is essential.

Zhang et al. (2022) [124] reported that the calcium content within sediment samples has a significant contribution to the microbial communities in high-urban-human activity Jiulong river mangrove patches and calcium ions are needed to maintain basic metabolisms such as cell division and control the permeability of cell membranes [124]. Therefore, the high content of calcium discharged from urban areas served as a nutrient for the microbes in the sediment. These microbial communities played positive roles in accommodating contaminated intertidal ecosystems overseeing the nutrient input caused by wastewater and industrial contaminants.

PAHs (polycyclic aromatic hydrocarbons) and hydrocarbon incubation mangrove sediment studies show Gram-negative bacteria have potential key roles in the degradation of PAH and hydrocarbons. *Anaerolineaceae* of Choloflexi have a high tolerance to a

range of phenanthrene (a colorless and low molecular weight PAH) concentrations (150 to 1200 mg kg⁻¹ sediment). These microbial community serve as an important component in oil-contaminated mangrove sediment [84].

Gram-negative bacteria were able to use phenanthrene and other hydrocarbons as their carbon source. Seasonal comparisons of sediment hydrocarbon incubation showed that wet season mangrove sediment accommodates a more diverse biodegrading bacterial capacity mainly constituted of Gram-negative bacteria that might have a higher hydrocarbon degradation rate. This is caused by the higher diversity of bacteria that are adept to utilized the differential of hydrocarbon within the environment [84].

Microplastic contamination is profound on a global scale and polycondensing resin has been widely employed in countless industrial uses. Ye et al. (2021) [125] demonstrated that it induces microbial dysbiosis and dysfunction in mangrove sediment contaminated with microplastic, and the huge amount of microsized polymer products pose a threat to the balance of the ecological environment and its subordinate biota. The physical weathering of mangrove sediment and tidal inundation results in flaked microplastics being the most recovered microplastic in a study by Chen et al. (2022) [126], their study also shows that the physical and chemical properties of soil were altered by the microplastic contamination, causing microscopic changes to the biota nutrient cycles and ecosystem. While the chemotrophic selectivity colonization of mangrove rhizosphere microorganisms was mainly formed by Gammaproteobacteria and Deltaproteobacteria in different microplastics, it shows various biodegradation rates of microplastic which effected the surrounding mangrove ecosystem health, thus suggesting mangrove sediment microbes as a plausible candidate for industrial plastic-degradation processes and related applications [127].

In a conclusion, upon reviewing all 69 articles, there is no clear pattern that the physical parameters control the diversity and structural composition of microbes in disturbed mangrove sediments, but few studies show a variety of explanations in justifying the main factors shaping the sediment microbial structure.

4. Microbial Communities in Different Types of Mangrove Forests

The main microbial element cycles in mangrove ecosystems include carbon, sulfur, and nitrogen cycles, the distinct element cycles are strongly interconnected and their relative contribution to nutrient dynamics varies depending on the environmental conditions. Microbial communities in mangrove sediments are characterized by environmental gradients and bioavailability of nutrients. We acknowledge that the advancement of metagenomic diversity studies of bacteria and other biotics yield different results due to the dissimilarity of primers, sequencing methods such as 454 pyrosequencing [128,129], Illumina tagged 16S rRNA gene sequencing [95,108], and targeted groups of studies in each study. However, metagenomics studies are culture-independent and diverse at a taxonomic resolution compared to traditional isolation and cultivation of microorganisms.

4.1. The Trends in Microbial Communities across Mangrove Forest Types

In terms of microbial diversity, similar to well-preserved and restored mangrove forests, Proteobacteria dominated, with random reports of Firmicutes and Chloroflexi as the dominating phyla and archaea present in all reported articles. Indeed, the class Gammaproteobacterial dominated (56% of all published articles with mentioned class abundance), meanwhile there seemed to be a fair share of presence in Alpha- (12%) and Deltaproteobacteria (26%) as well. The phylum Chloroflexi was represented by *Anaerolineae* while the Firmicutes were represented by *Clostridium* and *Bacilli*. Interestingly, several reports show Firmicutes as the most dominant phyla [85,130,131]. All reports of Firmicutes as the most dominant phyla [85,130,131]. All reports of Firmicutes as the most dominant phyla were from South America and further investigation is needed to define its spatial and temporal relationship. One way or another, it is almost certain that the proportion of Proteobacteria will be followed as the second most dominant bacteria phyla with minute differences in percentage to Firmicutes.

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The taxonomic class level shows that most Proteobacteria were reported to come from Gammaproteobacterial followed by Deltaproteobacteria and Alphaproteobacteria. The diverse function and the phylogenic variation of Gammaproteobacteria which consisted of orders such as *Alteromonadales* [104,107,131] and *Vibrionales* [76,127] are found in marine and coastal regions and are high in abundance in mangrove sediments functioning as nutrient recyclers. Members of Deltaproteobacteria found in mangrove soil are mostly sulfur-related, consisting of *Desulfobacterales*, *Desulfuromonadales*, *Desulfovibrionales*, and *Desulfarculales* among others.

On the other hand, archaea represent a lesser amount compared to the bacterial domain. Reports from Luis et al. (2019) [60] and Zhang et al. (2022) [81] show that as high as 20% to 40% of sediment 16S rDNA genes were affiliated with archaea in stratified sediment layers, while other results show a much lower composition with roughly 2% to 12% [102,131,132] in the surface samples. The main archaea phylum was mostly annotated to either Euryarchaeota or Crenarachaeota. Euryarchaeota is a methanogen-related archaea with some members reported to have halophilic properties which help them survive in the highly fluctuating salinity of mangrove sedimentation and they are reported to have integral roles in phosphorus cycles [133]. Crenarchaeota were also vastly reported in the reviewed database, they tend to have a higher abundance when there is higher sulfur content, indicating their sulfur-dependent role in the mangrove sediment environment and other extreme environments including hot springs [134]. The taxonomy of archaea is still constantly changing and evolving thus the classifications of taxonomic names have been reported differently across publications. This indicates that the research on archaea diversity and its relationship to environment and metabolism needs a more in-depth investigation.

Figure 5 and Table 3 show that the diverse parameters influencing the structure dynamics and diversity of microbes in mangrove sediment are conducive to the nature where the adaptability and resilience of microbial communities within well-preserved and pristine mangrove environments is high due to long-term succession, and subtle changes in the diversity and community structure of mangrove tree stands, where an equilibrium between the nutrient from mangrove trees and microbial communities was achieved. Hence a much lower diversity in both tree counts, and prokaryotes communities was observed [86,111,130,135].



Figure 5. The key function of mangrove sediment microbes using nutrient exudates from tree roots and the surrounding environment. (**a**) Well-preserved mangrove sediment has lower microbial diversity compared to (**b**) disturbed mangrove sediment which has a more diverse structural composition adapting and utilizing different nutrient sources in the environment.

Well-Preserved		Disturbed		Sampling Criteria			
Shannon	Chao1	Shannon	Chao1	Cores Collected per Plot	Total Cores	Sediment Sample Depth	References
-	16,439.80	-	12,172.76	3	6	2 cm	[113]
5.83	-	5.69	-	3	18	10 to 30 cm	[110]
2.9	-	2.85	-	3	12	30 cm	[108]
5.81	7645.06	7.58	11,710.45	-	-	-	[130]
10.8	8905.00	11.1	10,662.00	3	45	15 cm	[115]
7.4	-	9.9	-	3	18	10 cm	[99]
394.4	326.20	417.53	223.27	2	10	10 cm	[124]
-	-	-	-	2	39	-	[132]
-	-	-	-	3	15	15 cm	[117]

Table 3. Comparison of reported bacterial diversity indices and sampling criteria of disturbed and well-preserved mangrove sediments.

-: no data provided.

A larger amount of Acidobacteria and Gemmatimonadetes were observed in relatively well-preserved mangrove sediment [38,100]. Strains of Acidobacteria are linked with carbon and nitrogen consumption in the decomposition of deadwood [136] and are reported in other various soil sediments. The distribution of Gemmatimonadetes is present in a range of natural habitats and are more abundant in high nutrient input habitats including aquatic and agricultural soil habitats [137].

Mangrove restoration work has been performed in small patches around the world and has been mainly concentrated in Asia [138]. While mangrove restoration often emphasizes forest coverage and seedling numbers while leaving out biodiversity and stand structures as the main focal point, and monospecies replantation approaches have been used to ease plantation and produce a uniform harvest for timber [139], multiple studies have been completed to elevate mangrove restoration success and environmental impact ratios [140,141]. Many studies have pointed out that through mangrove restoration of native species, the microbial structure composition could increase the microbial structure of native, mature, mangrove forests [58,75]. The selection of mangrove restoration species have an effect on both the nutrients and microbial diversity caused by the enrichment of organic matter and induced biogeochemical cycles [77]. Restored mangroves have been found to have accelerated rates of carbon acquisition and ultimately higher sequestration rates compare to matured mangroves, while at the same time having a higher emission of methane [78], thus providing a clue to increase mangrove restoration as an alternative solution to increase carbon sequestration rates in coastal regions.

Restored mangrove forests have a similar prokaryote composition compared to wellpreserved mangrove areas but have different diazotroph structures when the restored mangrove was planted in a previously invasive species vegetation, the differences in vegetation type shape the nutrient availability and prokaryotes succession [75]. Feedback adjustments of microorganisms are highly sensitive to the surrounding nutrients and the restoration of mangroves.

Gammaproteobacteria and Deltaproteobacteria have a higher proportion in disturbed environments compared to those found in well-protected mangrove sediments [102] and replace *Anaerolineae* in microcosm hydrocarbon incubation conducted by Taketani (2010) [111]. Sulfur-dependent prokaryotes of Gammaproteobacteria and Deltaproteobacteria are abundant in both before and after pollutants such as hydrocarbon but orders such as *Alteromonadales* were reported to have increased in amount as a response to oil contamination [72]. A significant upsurge in the diversity of bacteria has been detected in contaminated mangrove sediment which was attributed to the dispersed nutrient availability artificially introduced into the environment. Spatiotemporal factors such as salinity, nutrients, and metabolism inhibitor obstruction lower the productivity of the mangrove ecosystem and its dependent communities [135,142]. The diversity of bacteria in disturbed mangroves are reported to be higher than in well-preserved mangroves, as shown in Table 3. Studies comparing mangroves in different conservation states show that bacterial composition in disturbed mangrove sediment alters its structure leading to a functional equilibrium, where the dynamics of chemicals in mangrove soils lead to the remodeling of its microbial structure [95,97,130]. Mangrove soil bacteria variation found in different mangrove conditions are shown in Table S2.

In contrast, only Haldar et al. (2018) [100] report that mangrove sediments from the Mandovi river which is heavily influenced by raw sewage and anthropogenic activities have a lower diversity and taxonomical richness compared to sediment samples from the Zuari river which are deemed to have less human interventions. Thus, the evaluation and comparison of bacterial diversity and its surrounding conditions is much needed to parse into the feedback controls of bacterial diversity towards long-term environmental changes.

A Venn diagram was used to illustrate the differences of unique taxon orders found in the three mangrove conditions (well-preserved, restored, and disturbed), as shown in Figure 6. Well-preserved mangroves had similar counts of unique taxon orders compared to restored mangroves, with 33 and 38 taxon orders, respectively. Members from *Desulfobacterales* and *Chromatiales* were the most abundant taxon. Only a minute number of bacterial taxon orders were distinctively found in well-preserved mangrove conditions (seven taxon orders) and a large portion of taxon orders were found in restored and disturbed mangrove conditions. This may indicate that the unique taxon order found in well-preserved mangroves served as the core component of mangrove microbes. External nutrient input indirectly induced and promoted microbial diversity causing disturbed mangroves to have a higher unique order reported due to the imbalance in nutrient recycling causing niched nutrients for a variety of microbes to thrive and survive.



Figure 6. Venn diagram showing the summary of the number of unique taxonomic orders found in the three different mangrove conditions.

The Venn diagram in Figure 6 shows the unique taxon order found in three different mangrove conditions. Well-preserved mangrove condition has the least unique taxon order with 33 taxonomic orders quantified, followed by restored with 38, while the disturbed

mangrove condition has the most number of microbial taxonomic orders totaled at 70. The diverse nutrients in the disturbed mangrove area induced the variations of microbial diversity in disturbed mangroves, with high unique taxon orders of 35 found solely in disturbed mangrove condition.

To summarize, we observed a diverse and high abundance of microbial taxon in mangrove sediments regardless of the mangrove type. Well-preserved mangroves shared a similar bacteria taxon order count with restored mangroves, while disturbed mangrove exhibited a more diverse microbial diversity. We acknowledge that the current dataset does not allow us to suggest the criteria to select suitable species considering the effects of microbial diversity on reforestation and for restoration of mangrove ecosystems. Generally, the tree species for planting would be selected considering its natural habitat in the focal region. The present study result, however, suggested that the diversity of soil microbes can differ depending on human disturbance. The interactions among planted mangrove species, environmental settings, and soil microbes have not been fully studied yet, and further studies on the interactions among them and their impacts on the mangrove ecosystem functions are necessary.

4.2. Specific Roles of Mangrove Associated Microbes

The circulation and storage of "Blue Carbon" in mangroves are the largest by service value according to the calculations by Macreadie et al. [143]. Carbon sequestration is one of the main functions of mangroves and prokaryotes such as bacteria and archaea supply the nutrients, and regulate the carbon flux by removing inorganic carbon such as CO₂ from the atmosphere and from the mangrove sediment while emitting methane and other greenhouse gases (GHGs) as a byproduct of their distinct metabolisms [144–146]. Bacteria serve as the fundamental decomposer controlling the transformation of organic carbon to inorganic carbon and vice versa [13,147]. Meng et al. (2022) [148], using the functional gene correlation method, found that mangrove bacteria have the highest correlation in carbon cycles which includes carbon fixation, degradation, and methanogenesis.

Aerobic methanotrophs including *Methylacidiphilum* and *Methylacidimicrobium* from Verrucomicrobia are some of the rare members of methane oxidizers outside the Proteobacteria lineage [149]. The grouping of aerobic methanotrophs is phylogenetically separated into two divisions, namely, Type I constitute members of Gammaproteobacteria, where they combine oxygen and methane as part of their carbon assimilation pathway, and Type II including the genus *Methylosinus* and genus *Methylocystis* methanotrophic Alphaproteobacterium [150] and, according to Yang and colleagues, the cell carbon largely originates from CO₂ [151]. The absence of oxygen in mangrove sediment provides a suitable environment, meeting the needs of several groups of anaerobic prokaryotes which include methanogens [152]. It is acknowledged that recent studies show methanotrophs survive under both conditions either with or without the presence of free-flowing oxygen [153]. The distinct metabolism of methanogens provides a degradation solution for a complex carbon-borne substrate such as polycyclic aromatic hydrocarbons (PAH) thus linking it as part of the carbon cycle.

Nitrogen is an integral nutrient component in mangrove growth limitations [154,155]. Nitrogen cycles in the mangrove ecosystem largely depend on the microbial community in the recycling of N, which includes nitrification, N-fixation, and denitrification. Diazotrophs are a community of organisms that fixes atmospheric nitrogen gas into bioavailable organic molecules such as ammonium (NH4⁺). They play an integral role in rhizosphere nutrient cycles [156], diazotroph communities acting as an intermediaries for free-flowing nitrogen gases, and useful ammonium as a nutrient for plants [109,157]. The bacterial symbiotic fixation of nitrogen (N₂) is reported to affiliate with various plants [158]. The isolations of diazotrophs genera such as *Oceanomonas, Marinobacterium*, and *Pseudomonas*, have been described to have crucial roles in maintaining the soil–plant nitrogen cycle in the mangrove ecosystem.

On the other hand, nutrient parameters in Tables 4 and S2 show that the percentages of sulfur account for a minute amount representing less than 0.5% of soil content. In contrast to the amount reported in mangrove soil sediment, there have been a large number of S-cycle involvers such as members of the order *Desulfobacterales*, *Desulfuromonadales*, *Desulfovibrionales* and *Desulfarculales* reported as part of dominant bacterial orders in mangrove sediments [75,102,108]. These major groups of bacteria utilized sulfur as the primary resource for sulfur cycles in the environment using a variety of assimilation methods [159].

Sampling Site	Condition Categorized	TS	References
Mai Po Wetland, Hong Kong, China	Disturbed	0.59% to 0.86%	[98]
Yunxiao Zhangjiangkou Nature Reserve, Fujian, China	Disturbed	4.27 g/kg	[91]
Coastal Zones of China	Disturbed	0.19% to 1.33%	[94]
Mangalavanam, India	Disturbed	0.26% to 0.04%	[56]
Rantau Abang, Terengganu, Malaysia	Disturbed	1.374 g/kg	[31]
Valle de Los Cangrejos, La Guajira, Colombia	Disturbed	0.523 to 0.849 g/kg	[85]
La Guajira, Colombia	Disturbed	0.803 to 0.324 g/kg	[97]
Bertioga, Sao Paulo State, Brazil	Disturbed	0.17% to 0.34%	[95]
Bertioga, Sao Paulo State, Brazil	Disturbed	0.13% to 0.45%	[109]
Quanzhou bay, Fujian, China	Restored	1.59 to 4.09 g/kg	[75]
Quanzhou bay, Fujian, China	Restored	1.59 to 6.08 g/kg	[58]
Matang Virgin Jungle Forest, Perak, Malaysia	Well Preserved	3.64 to 3.84 g/kg	[68]
Saint Vincent Bay, New Caledonia	Well Preserved	0.72% to 0.99%	[60]
Saint Vincent Bay, New Caledonia	Well Preserved	0.21% to 0.23%	[60]
Ilha do Cardoso, Sao Paulo, Brazil	Well Preserved	0.14% to 0.19%	[73]
Estuary of Cananéia, São Paulo, Brazil	Well Preserved	0.1% to 0.2%	[71]

Table 4. Total sulfur content of sampled mangrove soil.

TS: Total Sulfur.

While there is a considerable number of research efforts focusing on microbial communities in different mangrove conditions and their corresponding environmental factors and element cycles shaping the microbiome groups, we strongly support more research into the role and distribution of these microbial communities on a global scale and the establishment of standardized mangrove microbiome research in a broader scope as the foundation for a more diverse and transdisciplinary perspective.

5. Suggestions for Future Mangrove Microbial Diversity Research

Despite many research advancements in mangrove sediment bacterial metagenomics diversity in various conditions over the past few years, bridging the research gap and expanding our knowledge towards the relationship between microbes mainly constituted of bacteria and its nutrient cycles in the mangrove sediment and direct and indirect impacts on mangrove growth and stand-structures as coastal barriers and other ecological service providers. Thus, based on our systematic review, here we suggest sampling improvements and a fundamental environmental index for future reference.

- 1. Southeast Asian nations (ASEAN) have high mangrove coverage and tree diversity, and are the epicenter of most mangrove deforestation [160,161] and small patch mangrove restoration efforts [138]. We suggest for an increase mangrove sediment bacterial diversity studies in these rapidly changing and developing areas. The increment of studies will provide a clearer insight to understand the ecological and social values of mangroves and their subordinates in different succession stages. Furthermore, there is a need to explore the polluted sediments of different species of mangroves and their interaction and impact on microbial diversity, thus finding suitable and highly adaptive mangrove species for quick remediation of contaminated mangrove areas and coastal protection.
- 2. We recommend increased research and development of the biogeochemical behaviors of coastal mangrove sediment microbes and the main drivers to cultivate a "fertilizer"

to enhance a higher rate of success in mangrove restoration and conservation. Mangrove forests are subject to high salinity and constant inundation, hence the "fertilizer" developed must premeditate the hydrodynamics, bioavailability, and feedback adjustment of sediment microbes and their reciprocal mangrove trees. The accomplishment of mangrove restoration can reduce the rate of climate change and help nations to realize sustainable development goals (SDG) [162]. We suggest public, private, and governmental organizations join hands and promote mangrove restoration in coastal regions around land–sea margins for sustainable development and to benefit ethically from the ecosystem.

- 3. Further, we should deepen the current understanding of the relationship between geolocation and mangrove species and their microbial diversity. Microbes in mangrove sediments have a symbiotic relationship with their corresponding mangrove environment. While studies have shown that mangrove tree species contribute to the ecosystem by controlling the supply and demand of vital resources, the nutrient transformation from different mangrove tree species also alters microbial diversities and structures in a phenomenon where the microbial community selection force is driven by mangrove plant species [163]. Here we suggest adding mangrove tree species and their growth status such as diameter at breast height (DBH) and estimated tree height as part of the criteria and factors affecting and controlling the diversity of the microbial community. The differential of mangrove tree age [58,75] and species [78,90] have proven to induce vital changes in controlling the microbiota structure compositions.
- 4. We recommend unified physio-chemical indices units for better regional and ultimately global-scale comparison. We acknowledge the constraints of methodological differences in research equipment and objectives, here suggestions are made to encourage the universalization and protocol of units such as TC, TN, TS, and TP. These indices are important for environmental nutrient factors dictating the directive changes of microbial communities. Such developments and unification of standard units will benefit all sediment microbes research and have significant value in constructing a conducive comparison meanwhile further bridging research gaps and encouraging research development.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/f13122160/s1, Table S1: Bacteria Taxon Order Classifications; Table S2: Mangrove Condition nutrient Parameters; Table S3: Detailed Publications and Sampling Coordinates; Table S4: Mangrove Condition Unique Taxon Order.

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