Biogeochemical Processes of C and N in the Soil of Mangrove Forest Ecosystems

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Received: 19 February 2020; Accepted: 22 April 2020; Published: 27 April 2020

Abstract: The mangrove forest provides various ecosystem services in tropical and subtropical regions. Many of these services are driven by the biogeochemical cycles of C and N, and soil is the major reservoir for these chemical elements. These cycles may be influenced by the changing climate. The high plant biomass in mangrove forests makes these forests an important sink for blue C storage. However, anaerobic soil conditions may also turn mangrove forests into an environmentally detrimental producer of greenhouse gases (such as CH$_4$ and N$_2$O), especially as air temperatures increase. In addition, the changing environmental factors associated with climate change may also influence the N cycles and change the patterns of N$_2$ fixation, dissimilatory nitrate reduction to ammonium, and denitrification processes. This review summarizes the biogeochemical processes of C and N cycles in mangrove forest soils based on recently published studies, and how these processes may respond to climate change, with the aim of predicting the impacts of climate change on the mangrove forest ecosystem.

Keywords: mangrove; greenhouse gas; blue carbon; N cycle; C cycle

1. Introduction

The greenhouse effect occurs when solar radiation is reflected from the Earth’s surface and transformed into heat by greenhouse gases (GHG) such as carbon dioxide (CO$_2$), methane (CH$_4$), and nitrous oxide (N$_2$O). Over the past 150 years, human activities have increased the CO$_2$ concentration in the atmosphere by over 40%; this has resulted in an increase in mean air temperature, which has broad climate implications [1].

The 2013 Intergovernmental Panel on Climate Change (IPCC) report found that in the past century the global average CO$_2$ concentration has increased from 280 to 400 ppm and average global air temperature has increased by 0.74 °C. Moreover, the temperature is likely to increase 1.1–6.4 °C in the next hundred years if the trajectory does not change, resulting in disasters such as rising sea levels, changing ecosystems, drought or flooding, and melting Antarctic sea ice [1,2].

Research has shown that the combustion of fossil fuels for electricity, transportation, and industry accounts for over 80% of human-produced CO$_2$ emissions [1]. In addition, 60% of global methane emissions comes from human activity, about 70% of which is from industry, agriculture, and landfills [1,2]. About 40% of total N$_2$O emissions is from human activity, 75% of which comes from agriculture [1,2].

Soil is the reservoir for the chemical elements that form the structures of all organisms on land. Different organisms utilize, absorb, or transfer inorganic chemical elements in different forms to complete the biogeochemical cycles that support all consumers in ecosystems, such as animals and humans. Most importantly, soil contains chemical elements that are essential to soil organisms, such as
C and N, and, in most cases, it is believed to be a net sink for atmospheric CO₂ [3]. However, soil can also be a source of greenhouse gases such as N₂O and CH₄, especially in anoxic environments, where soil microorganisms undergo anaerobic respirations and fermentations [4].

Soil microorganisms oxidize electron sources such as organic C through various oxidation-reduction reactions to generate adenosine tri-phosphate (ATP) and release oxidized products such as CO₂ from organic matter. In aerobic soil environments, microbes use oxygen (O₂) as an electron acceptor and reduce it to water (H₂O). In anaerobic environments, on the other hand, oxidized chemical elements can serve as alternative electron acceptors. Methanogenesis is an important biogeochemical process by which acetate or hydrogen is oxidized to produce methane (CH₄) [5–7]. In addition, soil organic N in aerobic environments can be mineralized with organic C decomposition to form ammonium (NH₄⁺), then be nitrified into nitrate (NO₃⁻) [8]. In anoxic conditions, NO₃⁻ can serve as an alternative electron acceptor, and be denitrified to N₂ and some intermediate gases such as NO and N₂O [9].

Coastal wetlands provide various ecosystem services such as habitat restoration, ecosystem remediation, and flood mitigation [10–13]. Coastal wetlands also contain a wide range of anoxic conditions that other upland ecosystems do not have, which can facilitate various biogeochemical processes along both spatial and temporal scales, thereby playing an important role in global C, N, and P cycles [14–16]. Atmospheric CO₂ in coastal ecosystems is fixed through plant photosynthesis, then buried as organic matter in soil for several decades to centuries; this process may reduce overall atmospheric CO₂ concentrations, and thus the buried C is also called blue carbon. Research suggests that sediments in oceans and soil in coastal ecosystems store over 3.8 billion tons of C, making them the most important C sink on Earth [17].

Mangrove forests are one of the major types of coastal wetland, occupying over 16.4 million hectares worldwide [18] and mostly existing in tropical and subtropical regions [19]. More than one third of the global mangrove forests occur in South-East Asia [20], and these forests include more than 46 different mangrove species [21]. Globally, they only cover a small area, but mangrove forests perform many ecosystem functions in nature, such as dissipating excess nutrients from nearby uplands [13,22–24]. Therefore, they provide valuable ecosystem services worth over US$194,000 ha⁻¹ yr⁻¹ [25]. However, mangrove forest coverage has largely decreased over the past century due to changes in land use [18,26]. Moreover, mangrove forests are being threatened by increasing anthropogenic nutrient loadings, which may be altering biogeochemical processes and related soil microbial functions [27,28]. These changes may threaten the mangrove forest dynamics of net blue C storage (hereafter just “carbon” or “C”) and greenhouse emissions.

Many reviews have addressed the impacts of anthropogenic and natural changes on mangrove forests [25,29], but few have approached this from a soil microbial ecology perspective. The purpose of this review is to assess the soil microbial and biogeochemical cycles in mangrove ecosystems, their adaptations to different anthropogenic and natural changes, and how these adaptations may affect C and N cycling in mangrove ecosystems.

2. C Dynamics in Mangrove Forests

2.1. C Storage in Mangrove Forests

There are several reasons why mangrove forest ecosystems have high ecosystem C stocks. Coastal ecosystems sequester CO₂ from the atmosphere through plant primary production and store it in plant biomass (mostly for woody plants) and soil [30]. Although C accumulation rates vary among coastal wetlands, plant primary production in coastal wetlands in general is comparable to that of terrestrial forests [29]. However, the low decomposition rate of soil C gives coastal wetlands a higher potential to sequester C in sediments [29]. Thus, coastal ecosystems are generally believed to accumulate C up to 100 times faster than terrestrial forest ecosystems [19,31–33]. Compared to other coastal ecosystems, mangrove forests are believed to have higher organic C stocks because of their high growth rates [34].
Furthermore, unlike the herbaceous salt marshes, where most organic C stocks are stored in soil, C stocks in mangrove forests are distributed more in plant biomass than soil [35]. Previous research found that most mangrove plant-fixed C is stored in biomass and only 3%–11.7% of it is transferred to and stored in sediment [36].

The soil C stored in mangrove forests can vary widely, but it is generally higher in the tropical regions than the sub-tropical ones [35,37–40] (Table 1). Different environmental and soil physicochemical factors may explain this difference. Different tidal ranges may create different soil anaerobic conditions among mangrove forests, and thus affect C decomposition rates [40,41]. Moreover, fine soil texture in some mangrove forests may also reduce groundwater drainage and facilitate soil C accumulation [42].

Table 1. Comparison of the soil C stocks in different types of ecosystems.

| Study | Site          | Ecosystem                 | Average Soil C Stock (Mg C ha\(^{-1}\)) |
|-------|---------------|----------------------------|----------------------------------------|
| [43]  | Mexico        | Mangrove                   | 622                                    |
| [44]  | Global        | Mangrove                   | 650                                    |
| [45]  | Philippines   | Mangrove                   | 442                                    |
| [37]  | Indonesia     | Mangrove                   | 572                                    |
|       | Malaysia      | Mangrove                   | 1059                                   |
| [35]  | FL, USA       | Mangrove                   | 307                                    |
| [46]  | Global        | Mangrove                   | 749                                    |
| [38]  | Australia     | Mangrove                   | 66                                     |
|       | Tidal marsh   |                            | 87                                     |
|       | Seagrass      |                            | 24                                     |
| [39]  | Brazil        | Mangrove                   | 341                                    |
|       | Salt marsh    |                            | 257                                    |
| [47]  | MD, USA       | Salt marsh (\(S.\ patens\))| 24                                     |
|       | Salt marsh (\(S.\ alterniflora\)) |                | 22                                     |
| [48]  | FL, USA       | Salt marsh                 | 72                                     |

Aboveground and belowground biomass production in mangrove plants is another major contributor to the ecosystem C stocks in mangrove forests. Unlike herbaceous plants, which have a fast C turnover rate, mangrove plants may be able to fix atmospheric CO\(_2\) and store it as biomass for a long period of time (i.e., up to centuries); this would lead to a considerable amount of C stock [49]. Mangrove plants have different degrees of root volumes and aboveground structures that may create a wide range of C storage rates [22,50]. Indeed, field surveys from previous studies in Atlantic coastal mangrove forests showed that aboveground plant biomass comprised 50–250 Mg C ha\(^{-1}\) and the belowground biomass comprised 10–50 Mg C ha\(^{-1}\) [35,39].

The abundant C that mangrove forests provide facilitates the development of soil microbial communities. Studies have shown that the microbial genus \(Bacteroidetes\) is abundant in the mangrove rhizosphere, which may be due to the high particulate organic matter in the environment [51,52]. Furthermore, the abundant root systems of mangrove plants may create environmental niches for \(Proteobacteria\), one of the important microbial genera for N and S cycling in mangrove ecosystems [52,53].

2.2. \(CO_2\) and \(CH_4\) Emissions in Mangrove Soils

Although mangrove forests provide high ecosystem C stocks, their wide ranges of anoxic soil conditions also make them a considerable source of greenhouse gases and decrease their net contribution to \(CO_2\) reduction (Figure 1). In addition, the presence of sulfate (SO\(_4^{2-}\)) in the saline water can serve as an alternative electron acceptor and help soil microbes yield more energy than methanogens, resulting in \(CO_2\) efflux in coastal ecosystems [54–56]. As a result, the ecosystem respiration rates in tide-influenced
coastal forest wetlands are typically higher than those observed in inland freshwater wetlands [57]. The average CO₂ emission from mangrove forests was calculated to be 0.7–3 g C m⁻² d⁻¹ [58–61], which is comparable to CO₂ emissions from coastal marshes (0.3–2 g C m⁻² d⁻¹) [56,62], but slightly higher than those from inland wetlands (0.8–1.6 g C m⁻² d⁻¹) [57] (Table 2).

Figure 1. Possible pathways for CO₂ and CH₄ emissions from mangrove forests (modified from Vepraskas and Craft [63]). The black arrows indicate the C pathways. The blue arrows indicate the direction in which increases in environmental factors (salinity, pH) may affect the C pathways.

Table 2. Comparison of greenhouse gas effluxes across various salinity ranges. (The absence of data means that the study analyzed did not report these data.)

| Study                     | Ecosystem                  | Salinity | CO₂ Efflux (mg C m⁻² h⁻¹) | CH₄ Efflux (mg C m⁻² h⁻¹) | N₂O Efflux (mg N m⁻² h⁻¹) | Global Warming Potential (GWP) (mg CO₂eq m⁻² h⁻¹) |
|---------------------------|----------------------------|----------|---------------------------|---------------------------|---------------------------|-----------------------------------------------|
| [64] Mangrove (Taiwan)    |                            |          |                           |                           |                           |                                               |
| [65] Mangrove (China)     |                            | 31–74    |                           |                           |                           |                                               |
| [66] Mangrove (India)     |                            |          |                           |                           |                           |                                               |
| [67] Mangrove (Australia) |                            | 15–21    |                           |                           |                           |                                               |
| [68] Mangrove (Hong Kong) |                            | 10–1,374 |                           |                           |                           |                                               |
| [69] Mangrove (Australia) |                            | 36.9–59.0| 0.0–0.06                  |                           |                           |                                               |
| [70] Mangrove (China)     |                            | 16–267   |                           |                           |                           |                                               |
| [71] Mangrove (New Caledonia) |                        | 36–44    |                           |                           |                           |                                               |
| [72] Mangrove (Colombia)  |                            | 2.7–23.4 |                           |                           |                           |                                               |
| [73] Mangrove (Philippines)|                            | 16.8–79.3| 108–151                   |                           |                           |                                               |
| [74] Mangrove (China)     |                            | 12–14    |                           |                           |                           |                                               |
| [75] Mangrove (China)     |                            | 10–21    |                           |                           |                           |                                               |
| [76] Mangrove (Vietnam)   |                            | 7–16     |                           |                           |                           |                                               |
| [77] Mangrove (New Caledonia) |                        | 40.2     |                           |                           |                           |                                               |
| [78] Brackish salt marsh (NC, USA) |                |          |                           |                           |                           |                                               |
| [79] Tidal freshwater wetland (GA, USA) |            |          |                           |                           |                           |                                               |
| [80] Rice paddies (Vietnam) |                            | 0–75     |                           |                           |                           |                                               |
| [81] Rice paddies (China) |                            | 0–630    |                           |                           |                           |                                               |

* data were converted from electrical conductivity (EC).
CH$_4$ efflux in coastal wetlands is considerably lower than in freshwater wetlands, mostly because of the presence of SO$_4^{2-}$ [56,82]. The CH$_4$ fluxes reported from previous literature show a decreasing trend with increasing salinity (Table 2). Compared to other coastal ecosystems, mangrove forests generally emit 0–23.68 mg C m$^{-2}$ h$^{-1}$ of CH$_4$ [58,60,65,74,76,77,83], which is generally higher than in brackish marshes (0.17–0.23 mg C m$^{-2}$ h$^{-1}$) [36], but lower than in tidal freshwater marshes (0.01–10.8 mg C m$^{-2}$ h$^{-1}$) [62,84] and freshwater ecosystems such as rice paddies (0–630 mg C m$^{-2}$ h$^{-1}$) [79,80,85] or ponds (0.75–40.5 mg C m$^{-2}$ h$^{-1}$) [81] (Table 2). In addition, species in mangroves with pneumatophores had significantly lower CH$_4$ emission rates than in mangroves without pneumatophores because pneumatophores increase soil aeration [86]. Moreover, anthropogenic nutrient loading from upland drainage also contributes to the high CH$_4$ emission rates [72,78].

CO$_2$ in mangrove soils is generated by chemoheterotrophs during respiration, but the CH$_4$ fluxes are mainly attributed to methane-producing archaea in soils. However, until now, few studies have focused specifically on identifying the quantity, composition, and environmental niches of methanogenic communities in mangrove soils. The soil total organic C concentrations may stimulate CH$_4$ production and increase the mcrA gene expression (i.e., methanogenic population) in soil [87]. Furthermore, studies on other coastal ecosystems also found that methanogens may be sensitive to soil pH and showed optimum growth at soil pH 6.5–7.5 [88,89].

Along with high SO$_4^{2-}$ concentrations, CH$_4$ efflux can be reduced by methanotrophs in surface mangrove soils that use CH$_4$ as an energy source and oxidize it into CO$_2$ (Figure 1) [90]. This mechanism can reduce CH$_4$ before it reaches the atmosphere [91–93]. However, most previous studies on methanotrophs have been performed in freshwater, not coastal, ecosystems. In fact, mangrove soils may have high CH$_4$ oxidation potentials that are comparable to those of freshwater ecosystems, such as rice paddies and lakes [94–98].

Compared to freshwater ecosystems, mangrove forest soils typically contain more Type I methanotrophic communities [97], which are believed to have higher CH$_4$ oxidation potentials, than Type II methanotrophs, which are typically found in freshwater ecosystems [99–101]. Moreover, the Type I methanotrophs *Methylosarcina*, *Methylomonas*, and *Methylobacter* in mangrove forest soils contained the most active CH$_4$-oxidizing genes, despite the fact that the dominant methanotrophs in mangrove soils were uncultured and their genes belong to the deep-sea 5 cluster, which is one of the five major sequence clusters retrieved from marine environments [102]. The presence of NaCl in mangrove soils was proven to be one of the reasons why this environmental niche contains more Type I methanotrophs than Type II ones [103]. As shown in a previous study, *Methylobacter* is better adapted to various salinity conditions and can be found in water with NaCl concentrations up to 3% [104]. In addition, alkaline environmental conditions may also be an important factor influencing the growth of Type I and Type II methanotrophs [98]. Previous studies revealed that the Type I methanotrophs *Methylomonas* and *Methylobacter* are mostly adapted to pH 6.5–7.55, which is generally the pH of saline ecosystems [97,104,105]. This ecological niche provided by the coastal mangrove forests may be one of the key factors resulting in the large Type I methanotrophic populations and low CH$_4$ emissions in this ecosystem.

3. N Dynamics in Mangrove Forests

3.1. N Assimilation Rates of Mangrove Plants

Mangrove forests and coastal marshes are typically considered N-limited ecosystems because of their high primary production [106,107]. Therefore, mangrove plants are highly efficient at utilizing soil N, making them an important sink for excess N from upstream [108,109]. However, different mangrove species may still utilize N at different efficiencies [65], even though they share similar N pathways (Figure 2). Reported N assimilation rates in mangrove plants ranged from 2 to 8 µmol g$^{-1}$ h$^{-1}$ under ambient N conditions [110], and 19 to 251 µmol g$^{-1}$ h$^{-1}$ when the N supply was unlimited [111].
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Figure 2. Potential pathways for the N cycle in mangrove forests (modified from Vepraskas and Craft [63]). The black arrows indicate the N pathways. The blue arrows indicate the direction in which increases in environmental factors (salinity, C source, N source) may affect the N pathways.

In addition to species variation, different environmental conditions can also affect the N assimilation rates in mangrove plants. Because Cl− ions can reduce protein synthesis and N assimilation [112], soil pore water salinity appears to be a negative factor that significantly alters the N uptake rates of mangrove plants [111,113].

3.2. N2 Fixation in Mangrove Soils

As many mangrove forests are N-limited, soil microbial N2 fixation can be a major external source of N into the ecosystem (Figure 2) [114], in addition to excess N from upland drainage. Because microbial N2 fixation is an energy-consuming process, previous studies have shown that the N2 fixation rates in mangrove soils can vary widely depending on the availabilities of soil C and N (Table 3).

Table 3. Nitrogenase activity among different coastal ecosystems.

| Location                  | Dominant Plant                  | Soil N2-Fixation Potential (µmol N m−2 h−1) | Reference |
|---------------------------|---------------------------------|--------------------------------------------|-----------|
| Mangrove (Tanzania)       | -                               | 21.6–26.4                                   | [115] *   |
| Mangrove (Malaysia)       | Rhizophora apiculata            | 0–125                                       | [116]     |
| Mangrove (Belize)         | Rhizophora mangle               | 128                                         | [117] *   |
| Mangrove (Taiwan)         | Tall Kandelia obvata            | 6.96                                        | [111] *   |
| Salt marsh (Arcachon, Fr) | Zostera noltii                  | 72–152                                      | [118] *   |
| Salt marsh (Belize)       | Eleocharis spp.                 | 20–24                                       | [119] *   |
| Natural salt marsh (VA, USA) | Spartina alterniflora       | 72–420                                      | [120] *   |

* the soil N2-fixation potential was estimated using the acetylene reduction method with a conversion factor of 4 [121].

Laboratory experiments using MoO4−, which inhibits sulfate-reducing bacterial activity [122–124], found that sulfate-reducing bacteria are important diazotrophs in coastal ecosystems and may contribute up to 50% of the total N2 fixation in mangrove ecosystems [111,118,125]. Moreover, experiments that used the inhibitors chloramphenicol and nalidixic acid further revealed that N2 fixation in mangrove soils is mainly attributed to the activity of diazotrophs rather than the reproduction of their biomass [111]. In addition, studies on mangrove soils at the molecular scale also indicate that members
of Vibrio may be important contributors to N\textsubscript{2} fixation in mangrove ecosystems [126]. Furthermore, in environments with sufficient sunlight, diatoms and cyanobacteria also contribute considerably to N\textsubscript{2} fixation in coastal ecosystems [115,127].

3.3. Dissimilatory Nitrate Reduction to Ammonium and Denitrification in Mangrove Soils

Along with microbial N\textsubscript{2} fixation, dissimilatory nitrate reduction to ammonium (DNRA) has been shown to be an important process in mangrove forest soils that helps plants retain N [128]. The pathways of NO\textsubscript{3}\textsuperscript{-} dissimilation by denitrification or DNRA are basically determined by the availability and compositions of soil C and N (Figure 2) [129–131]. Therefore, in the typical C-rich and N-limited mangrove ecosystem, N retention through DNRA can help all the living organisms efficiently re-circulate N and overcome limitations in coastal ecosystems [128,132,133]. In C-rich environments, DNRA is the major nitrate-reducing pathway, and denitrification is relatively minor [128,133,134].

The major pathway of nitrate reduction may shift from DNRA to denitrification in the soils of estuarine mangroves that have been heavily impacted by humans, and are therefore more N-rich [135]. Studies have suggested that the denitrification potential is higher (i.e., 0.18–8.75 µg N g\textsuperscript{-1} h\textsuperscript{-1}) in some estuarine mangrove soils—which have relatively high excess N [13,68]—than in other coastal ecosystems with less N loading (i.e., 0–1.25 µg N g\textsuperscript{-1} h\textsuperscript{-1}) [56,136,137]. Although the exact reason may not be well understood from a microbial metabolism standpoint, studies suggest that the reason for this difference in denitrification potential may be that the ecosystems need to conserve N in N-limited environments [138,139]. In addition, the general denitrification capacities of mangrove forest soils were shown to be under 2–3 mM NO\textsubscript{3}\textsuperscript{-} [13].

Microbial denitrification in mangrove forests may be significantly impacted by the increasing loads of NO\textsubscript{3}\textsuperscript{-} from upland drainages to estuaries and the potential salt water intrusion due to climate change. Under these conditions, N\textsubscript{2}O may be released into the atmosphere because it is an intermediate product of microbial denitrification processes [140]. Previous studies have shown N\textsubscript{2}O efflux in mangrove forest soils to be 0–0.534 mg N m\textsuperscript{-2} h\textsuperscript{-1} [63,69] (Table 1), which is considerably higher than the rates from tidal and brackish marshes [56,62]. N\textsubscript{2}O efflux from mangrove forests was also found to be higher in summer and fall than winter and spring [141], which may be correlated with seasonal air temperatures.

The efflux of N\textsubscript{2}O is basically lower than those of CH\textsubscript{4} and CO\textsubscript{2} from the same mangrove forests. However, considering that the global warming potential of N\textsubscript{2}O is 298 times higher than that of CO\textsubscript{2} [133], the N\textsubscript{2}O efflux from mangrove forests is another non-negligible factor that decreases the climate mitigation effect of C storage in the mangrove ecosystem.

4. Mangrove C and N Dynamics under Climate Change

Global warming and climate change are expected to lead to increases in N loading from uplands, salinity from salt water intrusion, and overall temperature (2–4 °C) in mangrove forests [2,142]. Although the litter quality (i.e., C/N ratios) of mangrove plants may not change with increased N loading and warming temperature [143], the growth rates of mangrove plants may increase with warming temperature, resulting in higher soil C and N immobilization rates [144–146]. Furthermore, the increase in air temperature may shift the distributions of mangrove species [147]. Studies have shown that mangrove plant abundance is positively correlated with air temperature [148], and that mangrove forest coverage is projected to expand to temperate zones as the climate warms [35,149].

Warming temperatures may also stimulate fungal and bacterial activities [150], thus accelerating litter decomposition [143]. For example, mesocosm experiments in one study demonstrated that litter decomposition rates of mangrove plants were 20%–40% faster when atmosphere temperature and N loading increased by 3 °C and 25 mg N L\textsuperscript{-1}, respectively [143]. In addition, the activation energy of soil denitrification in mangrove forests fitted with the Arrhenius equation went from 68 to 92 kJ mol\textsuperscript{-1} when temperature increased by 10 °C, which shows a faster increase than activation energy changes...
observed in other ecosystems [13]. This result implies that soil denitrification in mangrove forests can be sensitive to increasing air temperatures.

All of these factors may dramatically alter the soil microbial community in mangrove forests via the C and N cycles, and in turn accelerate both cycles. Whether the net C sink that mangrove forests provide will change or not with climate change is still unknown. Consequently, several mesocosm studies have disclosed some of the effects of climate change on the microbial communities in mangrove ecosystems, e.g., salinization, increased nutrient loads, and changes in C sources [13,97,111,143–145].

Our changing climate may influence mangrove ecosystems in a myriad of ways that are difficult to predict because individual microbes or plants have different reactions and tolerances to change. Our current pool of evidence and knowledge on mangrove ecosystems is not enough to conclude the overall impact that climate change may have on this ecosystem. Therefore, more comprehensive and systematic studies are needed to further investigate the microbial dynamics in mangrove forests under the impacts of climate change.

Thus, we suggest that future research on mangrove ecosystems focus on the following topics:

♦ Evaluating the impact of warming temperature on the compositions and distributions of C and N in mangrove forest litter and soil.
♦ Determining the diel and diurnal cycles of C and N fluxes in tide-influenced coastal ecosystems.
♦ Discovering the compositions and activities of C- and N-related microorganisms associated with increases in nutrient load, salinity, and temperature in mangrove forest soils.

Author Contributions: Preparation of first draft, Y.-J.S.; Supervision and editing, C.-Y.C. All authors have read and agreed to the published version of the manuscript.

Funding: Ministry of Science and Technology of Taiwan.

Acknowledgments: The authors thank the Ministry of Science and Technology of Taiwan, Republic of China, for financially supporting this research under contract numbers MOST 107-2621-M-001-001, MOST 108-2621-M-001-002 and MOST 108-2621-M-002-027. The authors also thank Noah Last of Third Draft Editing for his English language editing.

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

References
1. IPCC. AR4 Climate Change 2007: Synthesis Report; The Intergovernmental Panel on Climate Change: Geneva, Switzerland, 2007.
2. IPCC. Climate Change 2013: The Physical Science Basis; The Intergovernmental Panel on Climate Change: Geneva, Switzerland, 2013.
3. Bradford, M.A. A leaky sink. Nat. Clim. Chang. 2017, 7, 475–476. [CrossRef]
4. Whiting, G.J.; Chanton, J.P. Greenhouse carbon balance of wetlands: Methane emission versus carbon sequestration. Tellus B 2001, 53, 521–528. [CrossRef]
5. Gujer, W.; Zehnder, A.J.B. Conversion processes in anaerobic digestion. Water Sci. Technol. 1983, 15, 127–167. [CrossRef]
6. Schlesinger, W.H.; Bernhardt, W.S. Biogeochemistry: An Analysis of Global Change; Academic Press: Cambridge, MA, USA, 2013.
7. Smith, P.H.; Mah, R.A. Kinetics of acetate metabolism during sludge digestion. Appl. Microbiol. 1966, 14, 368–371. [CrossRef]
8. Paul, E.A.; Clark, F.E. Soil Biology and Biochemistry; Academic Press: San Diego, CA, USA, 1996.
9. Stein, L.Y. Surveying N2O-producing pathways in bacteria. Method. Enzymolog. 2011, 486, 131–152.
10. Brix, H. Do macrophytes play a role in constructed treatment wetlands? Water Sci. Technol. 1997, 35, 11–17. [CrossRef]
11. Etheridge, J.R.; Birgand, F.; Burchell, M.R., II. Quantifying nutrient and suspended solids fluxes in a constructed tidal marsh following rainfall: The value of capturing the rapid changes in flow and concentrations. Ecol. Eng. 2015, 78, 41–52. [CrossRef]
1. Mumby, P.J.; Edwards, A.J.; Ernesto Arias-González, J.; Lindeman, K.C.; Blackwell, P.G.; Gall, A.; Gorczynska, M.I.; Harborne, A.R.; Pescod, C.L.; Renken, H.; et al. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 2004, 427, 533. [CrossRef]

2. Shiau, Y.J.; Dham, V.; Tian, G.; Chiu, C.Y. Factors influencing removal of sewage nitrogen through denitrification in mangrove soils. *Wetlands* 2016, 36, 621–630. [CrossRef]

3. He, J.-Z.; Zhang, L. Advances in ammonia-oxidizing microorganisms and global nitrogen cycle. *Shengtai Xuebao/Acta Ecol. Sin.* 2009, 29, 406–415.

4. Liu, N.; Wang, K.; Xie, Y.; Yang, G.; Duan, Y. Characteristics of the soil environment of Dongting Lake wetlands and its response to the converting farmland to lake project. *Shengtai Xuebao/Acta Ecol. Sin.* 2011, 31, 3758–3766.

5. Steger, D.; Wentrup, C.; Braunegger, C.; Deevong, P.; Hofer, M.; Richter, A.; Baranyi, C.; Pester, M.; Wagner, M.; Loy, A. Microorganisms with novel dissimilatory (Bi) sulfite reductase genes are widespread and part of the core microbiota in low-sulfate peatlands. *Appl. Environ. Microbiol.* 2010, 77, 1231–1242. [CrossRef]

6. Emmer, I.; von Unger, M.; Needelman, B.; Crooks, S.; Emmett-Mattox, S. A Manual for Using the VCS Methodology for Tidal Wetland and Seagrass Restoration VM0033; Restore America’s Estuaries: Arlington, VA, USA, 2015.

7. Hamilton, S.E.; Casey, D. Creation of a high spatio-temporal resolution global database of continuous mangrove forest cover for the 21st century (CGMFC-21). *Glob. Ecol. Biogeogr.* 2016, 25, 729–738. [CrossRef]

8. Pidgeon, E. *Carbon Sequestration by Coastal Marine Habitats: Important Missing Sinks*; IUCN: Gland, Switzerland, 2009; pp. 47–51. [CrossRef]

9. Pandisamy, R.; Saxena, A.; Jayaraj, R.; Mohan, P.M.; Ravichandran, K.; Saravanan, S.; Vijayaraghavan, A. A review of the mangrove floristics of India. *Taiwania* 2016, 61, 224–242. [CrossRef]

10. Duarte, C.M.; Losada, I.J.; Hendriks, I.E.; Mazarrasa, I.; Marbà, N. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Chang.* 2013, 3, 961–968. [CrossRef]

11. Lovelock, C.E.; Adame, M.F.; Bennion, V.; Hayes, M.; O’Mara, J.; Reef, R.; Santini, N.S. Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of south east queensland, australia. *Estuaries Coasts* 2014, 37, 763–771. [CrossRef]

12. Vo, Q.T.; Kuenzer, C.; Vo, Q.M.; Moder, F.; Oppelt, N. Review of valuation methods for mangrove ecosystem services. *Ecol. Indic.* 2012, 23, 431–446. [CrossRef]

13. Costanza, R.; de Groot, R.; Sutton, P.; van der Ploeg, S.; Anderson, S.J.; Kubiszewski, I.; Farber, S.; Turner, R.K. Changes in the global value of ecosystem services. *Glob. Environ. Chang.* 2014, 26, 152–158. [CrossRef]

14. Thomas, N.; Lucas, R.; Bunting, P.; Hardy, A.; Rosenqvist, A.; Simard, M. Distribution and drivers of global mangrove forest change, 1996–2010. *PLoS ONE* 2012, 7, e0179302. [CrossRef]

15. Chiu, C.Y.; Lee, S.C.; Juang, H.T.; Hur, M.T.; Hwang, Y.H. Nitrogen nutritional status and fate of applied N in mangrove soils. *Bot. Bull. Acad. Sin.* 1996, 37, 191–196.

16. Jing, H.; Xia, X.; Liu, H.; Zhou, Z.; Wu, C.; Nagarajan, S. Anthropogenic impact on diazotrophic diversity in the mangrove rhizosphere revealed by nifH pyrosequencing. *Front. Microbiol.* 2015, 6. [CrossRef]

17. Meleod, E.; Chmura, G.L.; Bouillon, S.; Salm, R.; Björk, M.; Duarte, C.M.; Lovelock, C.E.; Schlesinger, W.H.; Silliman, B.R. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Front. Ecol. Environ.* 2011, 9, 552–560. [CrossRef]

18. Alongi, M.D. Impact of global change on nutrient dynamics in mangrove forests. *Forests* 2018, 9, 596. [CrossRef]

19. Shiau, Y.-J.; Burchell, M.R.; Krauss, K.W.; Broome, S.W.; Birgand, F. Carbon storage potential in a recently created brackish marsh in eastern North Carolina, USA. *Ecol. Eng.* 2019, 127, 579–588. [CrossRef]

20. Chmura, G.L.; Anisfeld, S.C.; Cahoon, D.R.; Lynch, J.C. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* 2003, 17. [CrossRef]

21. Kennedy, H.; Björk, M. *Seagrass Meadows*; IUCN: Gland, Switzerland, 2009; pp. 23–30.

22. Turner, R.E. Geographic variations in salt marsh macrophyte production: A review. *Contrib. Mar. Sci.* 1976, 20, 47–68.
35. Simpson, L.T.; Osborne, T.Z.; Duckett, L.J.; Feller, I.C. Carbon storages along a climate induced coastal wetland gradient. *Wetlands* 2017, 37, 1023–1035. [CrossRef]
36. Li, S.-B.; Chen, P.-H.; Huang, J.-S.; Hsieh, M.-L.; Hsieh, L.-Y.; Lee, C.-L.; Lin, H.-J. Factors regulating carbon sinks in mangrove ecosystems. *Glob. Chang. Biol.* 2018, 24, 4195–4210. [CrossRef]
37. Murdiyarso, D.; Purbopuspito, J.; Kaufman, J.B.; Warren, M.W.; Sasmito, S.D.; Donato, D.C.; Manuri, S.; Krisnawati, H.; Taberima, S.; Kurnianto, S. The potential of Indonesian mangrove forests for global climate change mitigation. *Nat. Clim. Chang.* 2015, 5, 1089–1092. [CrossRef]
38. Ewers Lewis, C.J.; Carnell, P.E.; Sanderman, J.; Baldock, J.A.; Macreadie, P.I. Variability and vulnerability of coastal ‘blue carbon’ stocks: A Case Study from Southeast Australia. *Ecosystems* 2018, 21, 263–279. [CrossRef]
39. Kaufman, J.B.; Bernardino, A.F.; Ferreira, T.O.; Giovannoni, L.R.; Gomes, L.E.D.O.; Romero, D.J.; Jimenez, L.C.Z.; Ruiz, F. Carbon stocks of mangroves and salt marshes of the Amazon region, Brazil. *Biol. Lett.* 2018, 14, 20180208. [CrossRef] [PubMed]
40. Nehren, U.; Wicaksono, P. Mapping soil carbon stocks in an oceanic mangrove ecosystem in Karimunjawa Islands, Indonesia. *Estuar. Coast. Shelf Sci.* 2018, 214, 185–193. [CrossRef]
41. Nobrega, G.N.; Ferreira, T.O.; Siqueira Neto, M.; Queiroz, H.M.; Artur, A.G.; Mendonça, E.D.S.; Silva, E.D.O.; Otero, X.L. Edaphic factors controlling summer (rainy season) greenhouse gas emissions (CO2 and CH4) from semiarid mangrove soils (NE-Brazil). *Sci. Total Environ.* 2016, 542, 685–693. [CrossRef]
42. Schmidt, M.W.I.; Torn, M.S.; Abiven, S.; Dittmar, T.; Guggenberger, G.; Janssens, I.A.; Kleber, M.; Kögel-Knabner, I.; Lehmann, J.; Manning, D.A.C.; et al. Persistence of soil organic matter as an ecosystem property. *Nature* 2011, 478, 49–56. [CrossRef]
43. Kaufman, J.B.; Hughes, R.F.; Heider, C. Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics. *Ecol. Appl.* 2009, 19, 1211–1222. [CrossRef]
44. Donato, D.C.; Kaufman, J.B.; Murdiyarso, D.; Kurnianto, S.; Stidham, M.; Kanninen, M. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 2011, 4, 293–297. [CrossRef]
45. Thompson, B.S.; Clubbe, C.P.; Primavera, J.H.; Curnick, D.; Koldewey, H.J. Locally assessing the economic viability of blue carbon: A case study from Panay Island, the Philippines. *Ecosyst. Serv.* 2014, 8, 128–140. [CrossRef]
46. Kaufman, J.B.; Bhomia, R.K. Ecosystem carbon stocks of mangroves across broad environmental gradients in West-Central Africa: Global and regional comparisons. *PLoS ONE* 2017, 12, e0187749. [CrossRef]
47. Elsey-Quirk, T.; Seliskar, D.M.; Sommerfield, C.K.; Gallagher, J.L. Salt marsh carbon pool distribution in a mid-atlantic lagoon, USA: Sea level rise implications. *Wetlands* 2011, 31, 87–99. [CrossRef]
48. Radabaugh, K.R.; Moyer, R.P.; Chappel, A.R.; Powell, C.E.; Bociu, I.; Clark, B.C.; Smoak, J.M. Coastal blue carbon assessment of mangroves, Salt Marshes, and Salt Barrens in Tampa Bay, Florida, USA. *Estuaries Coasts* 2018, 41, 1496–1510. [CrossRef]
49. Doughty, C.L.; Langley, J.A.; Walker, W.S.; Feller, I.C.; Schaub, R.; Chapman, S.K. Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries Coasts* 2016, 39, 385–396. [CrossRef]
50. Comeaux, R.S.; Allison, M.A.; Bianchi, T.S. Mangrove expansion in the Gulf of Mexico with climate change: Implications for wetland health and resistance to rising sea levels. *Estuar. Coastal. Shelf Sci.* 2012, 96, 81–95. [CrossRef]
51. Pinhasi, J.; Sala, M.M.; Havskum, H.; Peters, F.; Guadayol, Ö.; Malits, A.; Marrasé, C. Changes in bacterioplankton composition under different phytoplankton regimens. *Appl. Environ. Microbiol.* 2004, 70, 6753. [CrossRef]
52. Gomes, N.C.M.; Cleary, D.F.R.; Pinto, F.N.; Egas, C.; Almeida, A.; Cunha, A.; Mendonca-Hagler, L.C.S.; Smalla, K. Taking root: Enduring effect of rhizosphere bacterial colonization in mangroves. *PLoS ONE* 2010, 5. [CrossRef]
53. Lyimo, T.J.; Pol, A.; Jetten, M.S.M.; Op den Camp, H.J.M. Diversity of methanogenic archaea in a mangrove sediment and isolation of a new Methanococcoides strain. *FEMS Microbiol. Lett.* 2009, 291, 247–253. [CrossRef]
54. Weston, N.B.; Dixon, R.E.; Joye, S.B. Ramifications of increased salinity in tidal freshwater sediments: Geochemistry and microbial pathways of organic matter mineralization. *J. Geophys. Res. Biogeosci.* 2006, 111. [CrossRef]
55. Chambers, L.; Reddy, K.; Osborne, T. Short-term response of carbon cycling to salinity pulses in a freshwater wetland. *Soil Sci. Soc. Am. J.* 2011, 75, 2000–2007. [CrossRef]
56. Shiau, Y.J.; Burchell, M.R.; Krauss, K.W.; Birgand, F.; Broome, S.W. Greenhouse gas emissions from a created brackish marsh in eastern North Carolina. *Wetlands* 2016, 36, 1009–1024. [CrossRef]

57. Lu, W.; Xiao, J.; Liu, F.; Zhang, Y.; Liu, C.A.; Lin, G. Contrasting ecosystem CO2 fluxes of inland and coastal wetlands: A meta-analysis of eddy covariance data. *Glob. Chang. Biol.* 2017, 23, 1180–1198. [CrossRef]

58. Castillo, J.A.A.; Apan, A.A.; Maraseni, T.N.; Salmo, S.G. Soil greenhouse gas fluxes in tropical mangrove forests and in land uses on deforested mangrove lands. *CATENA* 2017, 159, 60–69. [CrossRef]

59. Hien, H.T.; Marchand, C.; Aimé, J.; Cuc, N.T.K. Seasonal variability of CO2 emissions from sediments in planted mangroves (Northern Viet Nam). *Estuar. Coast. Shelf Sci.* 2018, 213, 28–39. [CrossRef]

60. Jacotot, A.; Marchand, C.; Allenbach, M. Tidal variability of CO2 and CH4 emissions from the water column within a Rhizophora mangrove forest (New Caledonia). *Sci. Total Environ.* 2018, 631–632, 334–340. [CrossRef] [PubMed]

61. Rosentreter, J.A.; Maher, D.T.; Erler, D.V.; Murray, R.; Eyre, B.D. Seasonal and temporal CO2 dynamics in three tropical mangrove creeks—A revision of global mangrove CO2 emissions. *Geochim. Cosmochim. Acta* 2018, 222, 729–745. [CrossRef]

62. Krauss, K.W.; Whitbeck, J.L. Soil greenhouse gas fluxes during wetland forest retreat along the Lower Savannah River, Georgia (USA). *Wetlands* 2012, 32, 73–81. [CrossRef]

63. Vepraskas, M.J.; Craft, C.B. *Wetland Soils: Genesis, Hydrology, Landscapes, and Classification*, 2nd ed.; CRC Press: Boca Raton, FL, USA, 2015.

64. Chang, T.-C.; Yang, S.-S. Methane emission from wetlands in Taiwan. *Atmos. Environ.* 2003, 37, 4551–4558. [CrossRef]

65. Alongi, D.M.; Pfitzner, J.; Trott, L.A.; Tiredi, F.; Dixon, P.; Klumpp, D.W. Rapid sediment accumulation and microbial mineralization in forests of the mangrove Kandelia candel in the Jiulongjiang Estuary, China. *Estuar. Coast. Shelf Sci.* 2005, 63, 605–618. [CrossRef]

66. Krithika, K.; Purvaja, R.; Ramesh, R. Fluxes of methane and nitrous oxide from an Indian mangrove. *Curr. Sci.* 2008, 94, 218–224.

67. Lovelock, C.E. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 2008, 11, 342–354. [CrossRef]

68. Chen, G.C.; Tam, N.F.Y.; Ye, Y. Spatial and seasonal variations of atmospheric N2O and CO2 fluxes from a subtropical mangrove swamp and their relationships with soil characteristics. *Soil Biol. Biochem.* 2012, 48, 175–181. [CrossRef]

69. Livesley, S.J.; Andrusiak, S.M. Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store. *Estuar. Coast. Shelf Sci.* 2012, 97, 19–27. [CrossRef]

70. Jin, L.; Lu, C.-Y.; Ye, Y.; Ye, G.-F. Soil Respiration in a subtropical mangrove wetland in the Jiulong River Estuary, China. *Peloskys* 2013, 23, 678–685. [CrossRef]

71. Konnerup, D.; Marchand, C.; Deborde, J.; Chaduteau, C.; Allenbach, M. Influence of mangrove zonation on CO2 fluxes at the sediment-air interface (New Caledonia). *Geoderma* 2013, 202–203, 62–70. [CrossRef]

72. Krithika, K.; Purvaja, R.; Ramesh, R. Fluxes of methane and nitrous oxide from an Indian mangrove. *Curr. Sci.* 2008, 94, 218–224.

73. Chen, G.; Chen, B.; Dan, Y.; Tam, N.; Ye, Y.; Shunyang, C. Soil greenhouse gas emissions reduce the contribution of mangrove plants to the atmospheric cooling effect. *Environ. Res. Lett.* 2016, 11, 124019. [CrossRef]

74. Wang, H.; Liao, G.; D’Souza, M.; Yu, X.; Yang, J.; Yang, X.; Zheng, T. Temporal and spatial variations of greenhouse gas fluxes from a tidal mangrove wetland in Southeast China. *Environ. Sci. Pollut. Res.* 2016, 23, 1873–1885. [CrossRef]

75. Allen, D.; Dalal, R.C.; Rennenberg, H.; Schmidt, S. Seasonal variation in nitrous oxide and methane emissions from subtropical estuary and coastal mangrove sediments. *Aust. Plant Biol.* 2011, 13, 126–133. [CrossRef]

76. Chen, G.C.; Tam, N.F.Y.; Wong, Y.S.; Ye, Y. Effect of wastewater discharge on greenhouse gas fluxes from mangrove soils. *Atmos. Environ.* 2011, 45, 1110–1115. [CrossRef]

77. Zheng, X.; Guo, J.; Song, W.; Feng, J.; Lin, G. Methane Emission from mangrove wetland soils is marginal but can be stimulated significantly by anthropogenic activities. *Forests* 2018, 9, 738. [CrossRef]

78. Chen, G.C.; Ulumuddin, Y.I.; Pramudji, S.; Chen, S.Y.; Chen, B.; Ye, Y.; Ou, D.Y.; Ma, Z.Y.; Huang, H.; Wang, J.K. Rich soil carbon and nitrogen but low atmospheric greenhouse gas fluxes from North Sulawesi mangrove swamps in Indonesia. *Sci. Total Environ.* 2014, 487, 91–96. [CrossRef]
79. Tariq, A.; Vu, Q.D.; Jensen, L.S.; de Tourdonnet, S.; Sander, B.O.; Wassmann, R.; Van Mai, T.; de Neergaard, A. Mitigating CH4 and N2O emissions from intensive rice production systems in northern Vietnam: Efficiency of drainage patterns in combination with rice residue incorporation. *Agric. Ecosyst. Environ.* 2017, 249, 101–111. [CrossRef]

80. Liu, J.; Xu, H.; Jiang, Y.; Zhang, K.; Hu, Y.; Zeng, Z. Methane emissions and microbial communities as influenced by dual cropping of Azolla along with Early Rice. *Sci. Rep.* 2017, 7, 40635. [CrossRef] [PubMed]

81. Stadmark, J.; Leonardson, L. Emissions of greenhouse gases from ponds constructed for nitrogen removal. *Ecol. Eng.* 2005, 25, 542–551. [CrossRef]

82. Bridgham, S.D.; Megonigal, J.P.; Keller, J.K.; Bliss, N.B.; Trettin, C. The carbon balance of North American wetlands. *Wetlands* 2006, 26, 889–916. [CrossRef]

83. Chauhan, R.; Datta, A.; Ramanathan, A.L.; Adhya, T.K. Factors influencing spatio-temporal variation of methane and nitrous oxide emission from a tropical mangrove of eastern coast of India. *Atmos. Environ.* 2015, 107, 95–106. [CrossRef]

84. Bartlett, K.B.; Bartlett, D.S.; Harriss, R.C.; Sebacher, D.I. Methane emissions along a salt-marsh salinity gradient. *Biogeochemistry* 1987, 4, 183–202. [CrossRef]

85. Liu, H.; Wu, X.; Li, Z.; Wang, Q.; Liu, D.; Liu, G. Responses of soil methanogens, methanotrophs, and methane fluxes to land-use conversion and fertilization in a hilly red soil region of southern China. *Environ. Sci. Pollut. Res.* 2017, 24, 8731–8743. [CrossRef]

86. He, Y.; Guan, W.; Xue, D.; Liu, L.; Peng, C.; Liao, B.; Hu, J.; Zhu, Q.A.; Yang, Y.; Wang, X.; et al. Comparison of methane emissions among invasive and native mangrove species in Dongzhaihaigang, Hainan Island. *Sci. Total Environ.* 2019, 697, 133945. [CrossRef]

87. Arai, H.; Yoshioka, R.; Hanazawa, S.; Minh, V.Q.; Tuan, V.Q.; Tinh, T.K.; Phu, T.Q.; Jha, C.S.; Rodda, S.R.; Dadhwal, V.K.; et al. Function of the methanogenic community in mangrove soils as influenced by the chemical properties of the hydrosphere. *Soil Sci. Plant Nutr.* 2016, 62, 150–163. [CrossRef]

88. Sowers, K.R.; Baron, S.F.; Ferry, J.G. Methanosarcina acetivorans sp. nov., an acetotrophic methane-producing bacterium isolated from marine sediments. *Appl. Environ. Microbiol.* 1984, 47, 971–978. [CrossRef]

89. Lyimo, T.J.; Pol, A.; Op den Camp, H.J.; Harhangi, H.R.; Vogels, G.D. Methanosarcina semesiae sp. nov., a dimethylsulfide-utilizing methanogen from mangrove sediment micrographs. *Int. J. Syst. Evol. Microbiol.* 2000, 50, 171–178. [CrossRef] [PubMed]

90. Coyne, M. *Soil Microbiology: An Exploratory Approach*; Delmar Publishers: New York, NY, USA, 1999.

91. Rosslev, P.; King, G.M. Regulation of methane oxidation in a freshwater wetland by water table changes and anoxia. *FEMS Microbiol. Ecol.* 1996, 19, 105–115. [CrossRef]

92. Le Mer, J.; Roger, P. Production, oxidation, emission and consumption of methane by soils: A review. *Eur. J. Soil Biol.* 2001, 37, 25–50. [CrossRef]

93. Megonigal, J.P.; Schlesinger, W.H. Methane-limited methanotrophy in tidal freshwater swamps. *Glob. Biogeochem. Cycles* 2002, 16. [CrossRef]

94. Cai, Y.; Zheng, Y.; Bodelier, P.L.E.; Conrad, R.; Jia, Z. Conventional methanotrophs are responsible for atmospheric methane oxidation in paddy soils. *Nat. Commun.* 2016, 7. [CrossRef]

95. Pandit, P.S.; Ranade, D.R.; Dhakephalkar, P.K.; Rahalkar, M.C. A pmoA-based study reveals dominance of yet uncultured Type I methanotrophs in rhizospheres of an organically fertilized rice field in India. *3 Biotech* 2016, 6, 135. [CrossRef]

96. Oswald, K.; Graf, J.S.; Littmann, S.; Tienken, D.; Brand, A.; Wehrli, B.; Albertsen, M.; Daims, H.; Wagner, M.; Kuyper, M.M.M.; et al. Crenothrix are major methane consumers in stratified lakes. *ISME J.* 2017, 11, 2124–2140. [CrossRef]

97. Shiau, Y.J.; Cai, Y.F.; Lin, Y.T.; Jia, Z.; Chiu, C.Y. Community structure of active aerobic methanotrophs in Red Mangrove (Kandelia obovata) soils under different frequency of tides. *Microb. Ecol.* 2017. [CrossRef]

98. Shiau, Y.J.; Cai, Y.F.; Jia, Z.J.; Chen, C.L.; Chiu, C.Y. Phylogenetically distinct methanotrophs modulate methane oxidation in rice paddies across Taiwan. *Soil Biol. Biochem.* 2018, 124, 59–69. [CrossRef]

99. He, R.; Wooner, M.J.; ROHLMAN, J.W.; CATRANIS, C.; QUENSEN, J.; TIEJDJE, J.M.; LEIGH, M.B. Identification of functionally active aerobic methanotrophs in sediments from an arctic lake using stable isotope probing. *Environ. Microbiol.* 2012, 14, 1403–1419. [CrossRef]

100. Dumont, M.G.; Luke, C.; Deng, Y.; Frenzel, P. Classification of pmoA amplicon pyrosequences using BLAST and the lowest common ancestor method in MEGAN. *Front. Microbiol.* 2014, 5. [CrossRef]
101. Zheng, Y.; Jia, Z. The application of biomarker genes for DNA/RNA-stable isotope probing of active methanotrophs responsible for aerobic methane oxidation in six paddy soils. *Acta Pedol. Sin.* 2016, 53, 490–501. [CrossRef]

102. Lüke, C.; Frenzel, P. Potential of pmoA amplicon pyrosequencing for methanotroph diversity studies. *Appl. Environ. Microbiol.* 2011, 77, 6305. [CrossRef] [PubMed]

103. Ho, A.; Mo, Y.L.; Lee, H.J.; Sauheitl, L.; Jia, Z.; Horn, M.A. Effect of salinity stress on aerobic methane oxidation and associated methanotrophs; a microcosm study of a natural community from a non-saline environment. *Soil Biol. Biochem.* 2018, 125, 210–214. [CrossRef]

104. Bowman, J.P. Methylobacter. In *Bergey’s Manual of Systematics of Archaea and Bacteria*; Whitman, W.B., Ed.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2015.

105. Bowman, J.P. Methylophonas. In *Bergey’s Manual of Systematics of Archaea and Bacteria*; Whitman, W.B., Ed.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2015.

106. Feller, I.C.; McKee, K.L.; Whigham, D.F.; O’Neill, J.P. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 2003, 62, 145–175. [CrossRef]

107. Vitousek, P.M.; Aber, J.D.; Howarth, R.W.; Likens, G.E.; Matson, P.A.; Schindler, D.W.; Schlesinger, W.H.; Tilman, D. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecol. Appl.* 1997, 7, 737–750. [CrossRef]

108. De-Leon-Herrera, R.; Flores-Verdugo, F.; Flores-de-Santiago, F.; Gonzalez-Farias, F. Nutrient removal in a closed silvofishery system using three mangrove species (Avicennia germannia, Laguncularia racemosa, and Rhizophora mangle). *Mar. Pollut. Bull.* 2015, 91, 243–248. [CrossRef]

109. Reef, R.; Feller, I.C.; Lovelock, C.E. Nutrition of mangroves. *Tree Physiol.* 2010, 30, 1148–1160. [CrossRef]

110. Datta, R.; Datta, B.K. Desiccation induced nitrate and ammonium uptake in the red alga *Catenella repens*. *Tree Physiol.* 2017, 109. [CrossRef]

111. Shiau, Y.J.; Lin, M.F.; Tan, C.C.; Tian, G.; Chiu, C.Y. Assessing N2 fixation in estuarine mangrove soils. *Environ. Microbiol.* 2011, 123, 619–628. [CrossRef] [PubMed]

112. Parida, A.K.; Das, A.B.; Mittra, B. Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove, *Bruguiera parviflora*. *Trees Struct. Funct.* 2004, 18, 167–174. [CrossRef]

113. Khan, M.A.; Aziz, I. Salinity tolerance in some mangrove species from Pakistan. *Wetlands Ecol. Manag.* 2001, 9, 229–233. [CrossRef]

114. Holguin, G.; Vazquez, P.; Bashan, Y. The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: An overview. *Biol. Fertil. Soils* 2001, 33, 265–278. [CrossRef]

115. Kyruzi, J.J.; Kyewalyanga, M.; Muruke, M. Cyanobacteria composition and impact of seasonality on their in situ nitrogen fixation rate in a mangrove ecosystem adjacent to Zanzibar Town. *Western Indian Ocean J. Mar. Sci.* 2003, 2, 35–44. [CrossRef]

116. Alongi, D.M.; Sasekumar, A.; Chong, V.C.; Pfitzner, J.; Trott, L.A.; Triendl, F.; Dixon, P.; Brunskill, G.J. Sediment accumulation and organic material flux in a managed mangrove ecosystem: Estimates of land–ocean-atmosphere exchange in peninsular Malaysia. *Mar. Geol.* 2004, 208, 383–402. [CrossRef]

117. Romero, I.C.; Jacobson, M.; Fuhrman, J.A.; Fogel, M.; Capone, D.G. Long-term nitrogen and phosphorus fertilization effects on N-2 fixation rates and nifH gene community patterns in mangrove sediments. *Mar. Ecol. Evolut. Perspect.* 2012, 33, 117–127. [CrossRef]

118. Welsh, D.T.; Bourgues, S.; de Wit, R.; Herbert, R.A. Seasonal variations in nitrogen-fixation (acetylene reduction) and sulphate-reduction rates in the rhizosphere of *Zostera noltii*: Nitrogen fixation by sulphate reducing bacteria. *Mar. Biol.* 1996, 125, 619–628. [CrossRef]

119. Šantruková, H.; Rejmáneková, E.; Pivničková, B.; Snyder, J.M. Nutrient enrichment in tropical wetlands: Shifts from autotrophic to heterotrophic nitrogen fixation. *Biogeochemistry* 2010, 101, 295–310. [CrossRef]

120. Tyler, A.C.; Mastronica, T.A.; McGlathery, K.J. Nitrogen fixation and nitrogen limitation of primary production along a natural marsh chronosequence. *Oecologia* 2003, 136, 431–438. [CrossRef]

121. Postgate, J.R. *The Fundamentals of Nitrogen Fixation*; CUP Archive: Cambridge, UK, 1982.

122. Oremland, R.S.; Capone, D.G. Use of specific inhibitors in biogeochemistry and microbial ecology. In *Advances in Microbial Ecology*; Marshall, K.C., Ed.; Plenum Press: New York, NY, USA, 1988; Volume 10, pp. 285–383.

123. Riederer-Henderson, M.-A.; Wilson, P.W. Nitrogen fixation by sulphate-reducing bacteria. *J. Gen. Microbiol.* 1970, 61, 27–31. [CrossRef]
124. Taylor, B.F.; Oremland, R.S. Depletion of adenosine triphosphate in Desulfovibrio by oxygenans of group VI elements. *Curr. Microbiol.* 1979, 3, 101–103. [CrossRef]
125. Bertics, V.J.; Sohm, J.A.; Treude, T.; Chow, C.-E.T.; Capone, D.G.; Fuhrman, J.A.; Ziebis, W. Burrowing deeper into benthic nitrogen cycling: The impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Mar. Ecol. Prog. Ser.* 2010, 409, 1–15. [CrossRef]
126. Flores-Mireles, A.; Winans, S.; Holguín, G. Molecular characterization of diazotrophic and denitrifying bacteria associated with mangrove roots. *Appl. Environ. Microbiol.* 2007, 73, 7308–7321. [CrossRef] [PubMed]
127. Currin, C.A.; Joye, S.B.; Paerl, H.W. Diel Rates of N2-fixation and denitrification in a transplanted Spartina alterniflora marsh: Implications for N-flux dynamics. *Estuar. Coast. Shelf Sci.* 1996, 42, 597–616. [CrossRef]
128. Fernandes, S.O.; Michotey, V.D.; Guasco, S.; Bonin, P.C.; LokaBharathi, P.A. Denitrification prevails over anammox in tropical mangrove sediments (Goa, India). *Mar. Environ. Res.* 2012, 74, 9–19. [CrossRef] [PubMed]
129. Tiedje, J.M. cology of denitrification and dissimilatory nitrate reduction to ammonium. In *Biology of Anaerobic Microorganisms;* Zehnder, A.J., Ed.; John Wiley and Sons Inc.: New York, NY, USA, 1988; pp. 179–244.
130. Fazzolari, F.; Nicoldobut, B.; Germon, J.C. Simultaneous effects of increasing levels of glucose and oxygen partial pressures on denitrification and dissimilatory nitrate reduction to ammonium in repacked soil cores. *Eur. J. Soil Biol.* 1998, 34, 47–52. [CrossRef]
131. Yin, S.X.; Chen, D.; Chen, L.M.; Edis, R. Dissimilatory nitrate reduction to ammonium and responsible microorganisms in two Chinese and Australian paddy soils. *Soil Biol. Biochem.* 2002, 34, 1131–1137. [CrossRef]
132. Bonin, P.; Omnes, P.; Chalamet, A. The influence of nitrate and carbon inputs on the end products of bacterial nitrate dissimilation in marine sediment. *Toxicol. Environ. Chem.* 1999, 73, 67–79. [CrossRef]
133. Balk, M.; Laverman, A.M.; Keuskamp, J.A.; Laanbroek, H.J. Nitrate ammonification in mangrove soils: A hidden source of nitrite? *Front. Microbiol.* 2015, 6, 166. [CrossRef]
134. Fernandes, S.O.; Gonsalves, M.-J.; Michotey, V.D.; Bonin, P.C.; LokaBharathi, P.A. Denitrification activity is closely linked to the total ambient Fe concentration in mangrove sediments of Goa, India. *Estuar. Coast. Shelf Sci.* 2013, 131, 64–74. [CrossRef]
135. Giblin, A.E.; Tobias, C.R.; Song, B.; Weston, N.; Banta, G.T.; Rivera-Monroy, V.H. The importance of dissimilatory nitrate reduction to ammonium (DNRA) in the nitrogen cycle of coastal ecosystems. *Oceanography* 2013, 26, 124–131. [CrossRef]
136. Cao, Y.; Green, P.G.; Holden, P.A. Microbial community composition and denitrifying enzyme activities in salt marsh sediments. *Appl. Environ. Microbiol.* 2008, 74, 7585–7595. [CrossRef] [PubMed]
137. Marton, J.M.; Herbert, E.R.; Craft, C.B. Effects of salinity on denitrification and greenhouse gas production from laboratory-incubated tidal forest soils. *Wetlands* 2012, 32, 347–357. [CrossRef]
138. Fernandes, S.O.; Bonin, P.C.; Michotey, V.D.; Garcia, N.; LokaBharathi, P.A. Nitrogen-limited mangrove ecosystems conserve N through dissimilatory nitrate reduction to ammonium. *Sci. Rep.* 2012, 2, 419. [CrossRef] [PubMed]
139. Weng, B.; Xie, X.; Yang, J.; Liu, J.; Lu, H.; Yan, C. Research on the nitrogen cycle in rhizosphere of Kandelia obovata under ammonium and nitrate addition. *Mar. Pollut. Bull.* 2013, 76, 227–240. [CrossRef]
140. Maier, R.M.; Pepper, I.L.; Gerba, C.P. *Environmental Microbiology;* Academic Press: San Diego, CA, USA, 2000.
141. Huang, C.-M.; Yuan, C.-S.; Yang, W.-B.; Yang, L. Temporal variations of greenhouse gas emissions and carbon sequestration and stock from a tidal constructed mangrove wetland. *Mar. Pollut. Bull.* 2019, 149, 110568. [CrossRef]
142. Chen, W.-B.; Liu, W.-C.; Hsu, M.-H. Modeling assessment of a saltwater intrusion and a transport time scale response to sea-level rise in a tidal estuary. *Environ. Fluid Mech.* 2015, 15, 491–514. [CrossRef]
143. Yang, Z.; Song, W.; Zhao, Y.; Zhou, J.; Wang, Z.; Luo, Y.; Li, Y.; Lin, G. Differential responses of litter decomposition to regional excessive nitrogen input and global warming between two mangrove species. *Estuar. Coast. Shelf Sci.* 2018, 214, 141–148. [CrossRef]
144. Lu, W.; Chen, L.; Wang, W.; Fung-Yee Tam, N.; Lin, G. Effects of sea level rise on mangrove Avicennia population growth, colonization and establishment: Evidence from a field survey and greenhouse manipulation experiment. *Acta Oecol.* 2013, 49, 83–91. [CrossRef]
145. Krauss, K.W.; McKee, K.L.; Lovelock, C.E.; Cahoon, D.R.; Saintilan, N.; Reef, R.; Chen, L. How mangrove forests adjust to rising sea level. *New Phytol.* 2014, 202, 19–34. [CrossRef]
146. Reef, R.; Slot, M.; Motro, U.; Motro, M.; Motro, Y.; Adame, M.F.; Garcia, M.; Aranda, J.; Lovelock, C.E.; Winter, K. The effects of CO2 and nutrient fertilisation on the growth and temperature response of the mangrove Avicennia germinans. *Photosynth. Res.* 2016, 129, 159–170. [CrossRef] [PubMed]

147. Hughes, L. Climate change and Australia: Trends, projections and impacts. *Austral Ecol.* 2003, 28, 423–443. [CrossRef]

148. Osland, M.; Feher, L.; López-Portillo, J.; Day, R.; Suman, D.; Guzmán Menéndez, J.; Rivera-Monroy, V. Mangrove forests in a rapidly changing world: Global change impacts and conservation opportunities along the Gulf of Mexico coast. *Estuar. Coast. Shelf Sci.* 2018, 214. [CrossRef]

149. Gabler, C.; Osland, M.; Grace, J.; Stagg, C.; Day, R.; Hartley, S.; Enwright, N.; From, A.; McCoy, M.; McLeod, J. Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nat. Clim. Chang.* 2017, 7. [CrossRef]

150. Feng, X.; Simpson, A.; Wilson, K.; Williams, D.; Simpson, M. Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nat. Geosci.* 2008, 1, 836–839. [CrossRef]

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