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Review

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

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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_2O), 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_2O). 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_2O 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 CO_2 [3]. However, soil can also be a source of greenhouse gases such as N_2O and CH_4, 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 CO_2 from organic matter. In aerobic soil environments, microbes use oxygen (O_2) as an electron acceptor and reduce it to water (H_2O). 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 (CH_4) [5–7]. In addition, soil organic N in aerobic environments can be mineralized with organic C decomposition to form ammonium (NH_4^+), then be nitrified into nitrate (NO_3^-) [8]. In anoxic conditions, NO_3^- can serve as an alternative electron acceptor, and be denitrified to N_2 and some intermediate gases such as NO and N_2O [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 CO_2 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 CO_2 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 CO_2 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 Malaysia	Mangrove Mangrove	572 1059
[35]	FL, USA	Mangrove	307
[46]	Global	Mangrove	749
[38]	Australia	Mangrove Tidal marsh Seagrass	66 87 24
[39]	Brazil	Mangrove Salt marsh	341 257
[47]	MD, USA	Salt marsh (*S. patens*) Salt marsh (*S. alterniflora*)	24 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 CO_2 emission from mangrove forests was calculated to be 0.7–3 g C m^{-2} d^{-1} [58–61], which is comparable to CO_2 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).

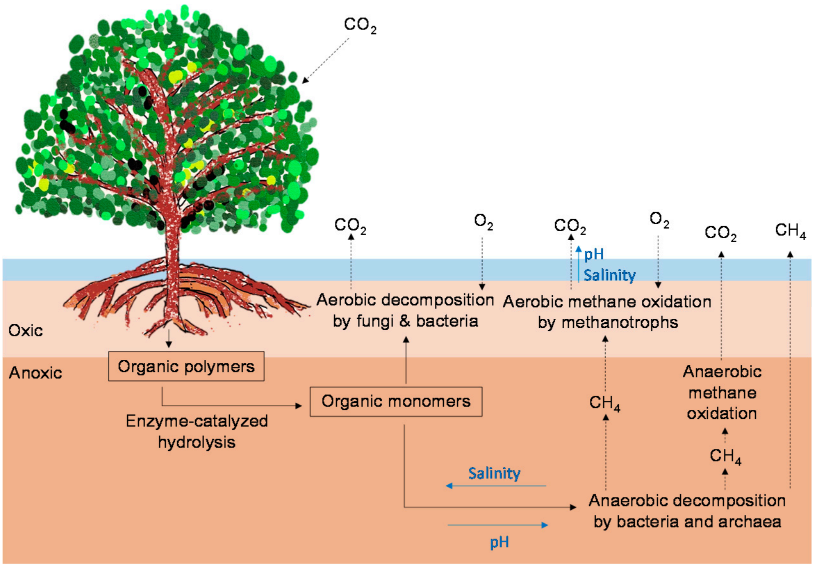

Figure 1. Possible pathways for CO_2 and CH_4 emissions from mangrove forests (modified from Vepraskas and Craft [63]). The black arrows indicate the C pathways. The blue arrows indicate the direction in which increases in environmental factors (salinity, pH) may affect the C pathways.

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**	**CO_2 Efflux (mg C m^{-2} h^{-1})**	**CH_4 Efflux (mg C m^{-2} h^{-1})**	**N_2O Efflux (mg N m^{-2} h^{-1})**	**Global Warming Potential (GWP) (mg $CO_{2\text{-eq}}$ m^{-2} h^{-1})**
[64]	Mangrove (Taiwan)			0.14		
[65]	Mangrove (China)		31–74			
[66]	Mangrove (India)				0.018–0.034	
[67]	Mangrove (Australia)		−11–128			
[68]	Mangrove (Hong Kong)	15–21	10–1,374		0.032–0.534	
[69]	Mangrove (Australia)	17–25 *	36.9–59.0	0–0.06	0–0.05	136–245
[70]	Mangrove (China)		16–267			
[71]	Mangrove (New Caledonia)		36–44			
[72]	Mangrove (Colombia)	2.7–23.4		0–23.68	0.009–0.375	
[58]	Mangrove (Philippines)	16.8–79.3	108–151	0.06–0.12	0–0.084	396–604
[73]	Mangrove (China)	12–14	−9–140	0–4.02	0–0.016	−33–889
[74]	Mangrove (China)	10–21	0–55	0.35–23.09	0–0.017	32–2,326
[59]	Mangrove (Vietnam)	7–16	Wet season: 112 Dry season: 25			
[60]	Mangrove (New Caledonia)		40.2	0.22		
[61]	Mangrove (Australia)		28			
[75]	Mangrove (Australia)	9–35 *		0.04–1.18	0.004–0.13	
[76]	Mangrove (China)	8.4–14.8		0.63–4.12		
[77]	Mangrove (China)	12–26	11–114	0–0.17		
[78]	Mangrove (Indonesia)	25–34	−16.8–46.6	−0.003–0.007	−0.17–0.37	−139–344
[56]	Brackish salt marsh (NC, USA)	22.5	−45–88	−0.17–0.23	−0.046–0.048	−202–366
[62]	Tidal freshwater wetland (GA, USA)	0.4–2.1	15–59	0.04–0.24	−0.009–0.012	54–244
[79]	Rice paddies (Vietnam)			0–75	0–0.132	
[80]	Rice paddies (China)			0–630		
[81]	Ponds (Sweden)			0.75–40.50		

* 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}) [56], 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].

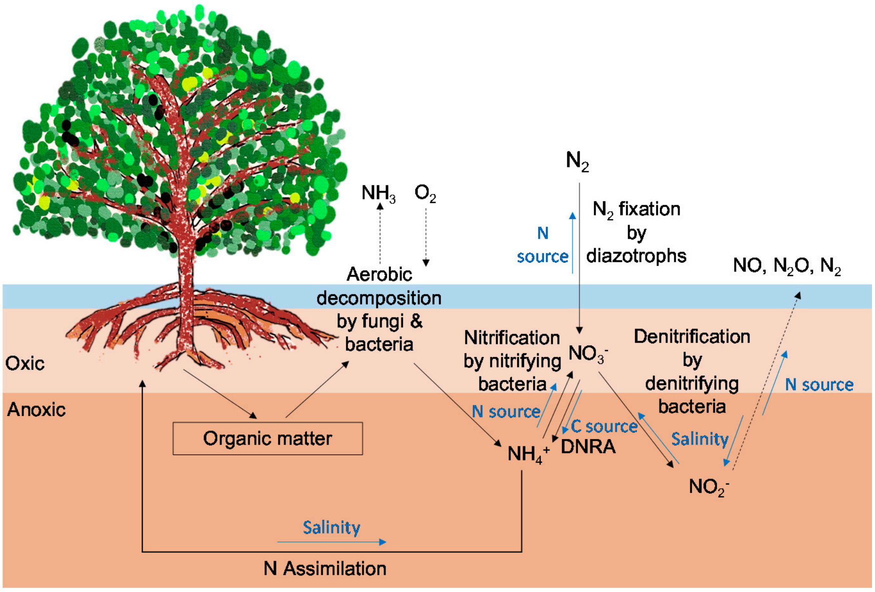

Figure 2. Potential pathways for the N cycle in mangrove forests (modified from Vepraskas and Craft [63]). The black arrows indicate the N pathways. The blue arrows indicate the direction in which increases in environmental factors (salinity, C source, N source) may affect the N pathways.

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. N_2 Fixation in Mangrove Soils

As many mangrove forests are N-limited, soil microbial N_2 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 N_2 fixation is an energy-consuming process, previous studies have shown that the N_2 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 N_2-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 obovata*	6.96	[111] *
	Dwarf *Kandelia obovata*	1.56	
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 N_2-fixation potential was estimated using the acetylene reduction method with a conversion factor of 4 [121].

Laboratory experiments using MoO_4, 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 N_2 fixation in mangrove ecosystems [111,118,125]. Moreover, experiments that used the inhibitors chloramphenicol and nalidixic acid further revealed that N_2 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_2 fixation in mangrove ecosystems [126]. Furthermore, in environments with sufficient sunlight, diatoms and cyanobacteria also contribute considerably to N_2 fixation in coastal ecosystems [115,127].

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

Along with microbial N_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_3^- 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^{-1} h^{-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^{-1} h^{-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_3^- [13].

Microbial denitrification in mangrove forests may be significantly impacted by the increasing loads of NO_3^- from upland drainages to estuaries and the potential salt water intrusion due to climate change. Under these conditions, N_2O may be released into the atmosphere because it is an intermediate product of microbial denitrification processes [140]. Previous studies have shown N_2O efflux in mangrove forest soils to be 0–0.534 mg N m^{-2} h^{-1} [63,69] (Table 1), which is considerably higher than the rates from tidal and brackish marshes [56,62]. N_2O 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_2O is basically lower than those of CH_4 and CO_2 from the same mangrove forests. However, considering that the global warming potential of N_2O is 298 times higher than that of CO_2 [133], the N_2O 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^{-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^{-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.

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