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Review

Microbial Diversity and Nitrogen Cycling in Peat and Marine Soils: A Review

Akshatha Soratur [1], Balu Alagar Venmathi Maran [2,3,*], Ahmad Syazni Kamarudin [3] and Kenneth Francis Rodrigues [4]

[1] Department of Ocean Studies and Marine Biology, Pondicherry Central Government University, Port Blair 744103, Andaman and Nicobar, India; 22373004@pondiuni.ac.in or akshasoratur@gmail.com
[2] Institute of Integrated Science and Technology, Nagasaki University, 1-14 Bunkyomachi, Nagasaki 852-8521, Japan
[3] School of Animal Science, Aquatic Science and Environment, Universiti Sultan Zainal Abidin, Besut Campus, Besut 22200, Terengganu, Malaysia; ahmadsyazni@unisza.edu.my
[4] Biotechnology Research Institute, Universiti Malaysia Sabah, Kota Kinabalu 88400, Sabah, Malaysia; kennethr@ums.edu.my
* Correspondence: bavmaran@nagasaki-u.ac.jp or bavmaran@gmail.com

Abstract: Nitrogen is an essential nutrient for living organisms in peat and marine soils, and its transformation within the soil matrix is a complex process mediated by various microbes that inhabit these ecological niches. The metabolism of nitrogen is governed by microbially mediated biogeochemical transformations, such as nitrification, anammox, and denitrification, which contribute to the assimilated pool of nitrogen and fixed nitrogen loss. One of the major challenges facing the field of peat and marine microbiology is the lack of understanding of the correlation between ecosystem-driven nitrogen transformation and microbial diversity. This is crucial because of growing concerns regarding the impacts of human-induced activities and global climate change on microbial nitrogen-cycling processes in peat and marine soils. Thus, this review aimed to provide a comprehensive overview of the current understanding of the microbial communities involved in peat and marine nitrification, anammox, and denitrification; the factors influencing the niche differentiation and distribution of the main functional components; the genes involved; and the main effects of human-induced activities and global climate change on the peat and marine nitrogen cycle. The implications of this review will facilitate an understanding of the complex mechanisms associated with ecosystem function in relation to nitrogen cycling, the role of peat and marine soils as carbon sinks, pollution remediation using naturally occurring populations of diverse microbes, and the development of policies to mitigate the effects of anthropogenic influences in peat and marine soils.

Keywords: microbial diversity; peat soils; marine ecosystem; nitrification; anammox; denitrification; nitrogen-cycling genes

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1. Introduction

Nitrogen is a naturally occurring element that is a constituent of proteins and nucleic acids; as such, it is an essential source for all organisms. Nitrogen exerts a strong influence on the Earth's climate because of its link to cycling processes involving key elements, such as nitrogen [1]. Nitrogen plays a key role in the biogeochemical framework and function of ecosystems. Consequently, nitrogen cycling is one of the most important biogeochemical cycles in ecosystems [2]. This cycling process is guided by abiotic factors, decomposition, nitrogen assimilation, and dissimilation phases. The latter includes different microbe-intervened pathways, such as nitrogen fixation [3], nitrification [4], denitrification [5], ammonification [6], anaerobic ammonium oxidation (anammox) [7], and the complete oxidation of ammonium to nitrate (comammox) [8]. The continued discovery of new pathways and microbial organisms involved in these processes has broadened our understanding of nitrogen cycling.

Peat soils and marine ecosystems are vital for nitrogen cycling. The oxidation states of nitrogen in peat soils and marine ecosystems range from reduced forms, such as ammonium (NH_4^+), to oxidized forms, such as nitrate (NO_3^-), which indicates its significance as both an oxidizing and reducing agent for generating energy from nutrients in marine ecosystems. The major reservoirs of nitrogen in peat soils and marine ecosystems include the reduction of nitrate and anammox [9]. Peat soils contribute to the maintenance of diverse ecosystem facilities, such as the reduction of excess nutrient runoff, conservation of biodiversity, sources of surface water and groundwater, and removal and storage of carbon dioxide [10].

Microbial communities, comprising archaea, bacteria, microbial eukaryotes, and viruses, are crucial contributors to the dynamics of the food web and biogeochemical processes in ecosystems, and they support numerous ecosystem services [11,12]. The nitrogen cycle in peat soils and marine ecosystems is affected by the diversity of nitrogen-cycling microbes. Microorganisms primarily facilitate the redox reactions of nitrogen, altering the concentrations of nitrogen-containing compounds in marine environments. The drainage channel system across peat soils for human-induced purposes regulates the amount of water content in a mass of soil to achieve optimal conditions for different human-induced practices, which affect the distribution of nitrogen and microbial diversity in peat soils [13]. Human-induced shifts in this balance may have a significant effect on the health of peat soils and marine ecosystems, microbial diversity, and climate change.

Although a positive functional link between microbial diversity and the ecosystem has been recognized in many ecosystems [14,15], little is known about the functional relationship between microbial diversity and nitrogen cycling in peat soils and marine ecosystems [16–18]. A general challenge facing the field of peat soils and marine microbiology is the current inability to sufficiently understand how microbial community dynamics and ecosystem-based nitrogen transformations, including processes that maintain the retained nitrogen pool (nitrification), cause a loss of fixed nitrogen (anammox and denitrification) [19]. This understanding requires an amalgamation of research efforts on microbial ecology and biogeochemistry. In addition, because the management of nitrogen is economically and environmentally crucial [9], understanding the ecological and biogeochemical framework of microbial diversity in nitrogen-cycling processes in peat soils and marine ecosystems has received considerable attention in recent years [20,21]. In addition, understanding the link between microbial diversity and nitrogen-cycling processes has been recognized to provide informative insights into changing environmental responses in natural ecosystems [19–22]. These arenas find common ground and collective insights to better understand the underlying processes and their regulation. Moreover, although previous studies demonstrated that the effect of the environment on nitrogen cycling is dependent on the type of ecosystem [23,24], studies on the link between microbial diversity and nitrogen cycling in peat soils and marine ecosystems are lacking [25,26]. Furthermore, there is a paucity of studies on microbial nitrogen-cycling responses to human-induced activities and global climate change in peat soils and marine ecosystems [27,28]. Studies on microbial community dynamics related to nitrogen cycling revealed enormous metabolic versatility within the microorganisms involved in the transformation of nitrogen. Furthermore, the study of nitrogen-cycling genes encoding proteins regulating metabolism, along with measurement rates of nitrogen transformation, has provided important discoveries about the biogeography of microorganisms participating in nitrogen-cycling processes, as well as their activity in peat soils and the marine system [29,30]. However, some discrepancies were observed between the studies, which may be attributed to the use of different approaches. It remains challenging to integrate microbial diversity into existing ecological and nitrogen-cycling frameworks and to progress beyond descriptive research of “which microbes are there” and “what microbiomes are doing?” for a more analytical approach. Thus, it is important to close the existing gap regarding whether nitrogen-cycling processes are related to the diversity of the microbial communities in peat soils and marine ecosystems. The necessity for such an understanding has never been more significant considering the ongoing human-induced activities in ecosystems and global climate change.

The present study aimed to provide an overview of the crucial microbial processes that encompass the nitrogen-cycling processes contributing to the retained nitrogen pool and fixed nitrogen loss, as well as the nitrogen-cycling genes that regulate these processes. Additionally, the ecological framework and distribution of the contributing microorganisms in peat soils and marine ecosystems are also covered in this review. In addition, this study aimed to identify several research gaps that are still encountered in the study of microbial nitrogen processes in peat soils and marine ecosystems. The present paper also discusses the impacts of human-induced activities and climate change on microbially intermediate peat soils and marine nitrogen-cycling processes.

Data Analysis

Keywords were used to search for articles in four databases: SCOPUS, Google Scholar, PubMed, and Web of Science. The domains were title, abstract, and keywords, which were "Microbial diversity, peat soils, marine ecosystem, nitrification, anammox, denitrification, nitrogen cycling genes", and the duration for the search was limited to the years 2000–2024; however, three citations were taken from 1988, 1995, 1997. A total of 17 citations were from 2000 to 2010, and the rest were from 2010 to 2024. A total of 65 citations were retrieved from SCOPUS, 75 from Google Scholar, 20 from PubMed, and 10 from Web of Science.

Publications were screened for duplication, and the publications whose scope was limited to nitrogen fixation in marine ecosystems other than peat soils were excluded from the review. After screening, a total of 55 publications from SCOPUS, 52 publications from Google Scholar, and 14 publications from PubMed, and 10 from Web of Science were retained for the review.

2. Microbial Processes in the Nitrogen Cycle of Peat Soils and the Marine Ecosystem

The nitrogen cycle in peat soils and marine ecosystems is driven by multiple microbial transformation processes, including nitrogen fixation, assimilation, nitrification, denitrification, and anammox (Figure 1). Nitrogen-cycling genes are found in diverse microorganisms that are universally spread throughout peat soils and marine systems. Biogeochemical and microbial dynamics via coupled feedback balance the nitrogen cycle in peat soils and marine systems [31]. However, recent studies strongly indicate a significant imbalance in the availability of nitrogen in peat soils and marine ecosystems due to the microbial conversion of nitrogen compounds; therefore, the knowledge of existing microbial processes, microbial distribution, and the factors influencing these processes is essential to comprehend the fate of peat soils and marine ecosystems [32,33]. The present section provides an overall outline of the biogeochemical and ecological framework of nitrogen-cycling processes, such as nitrification, anammox, and denitrification; the genes that represent these processes (archaeal amoA, bacterial amoA, nirK, nirS, and nosZ); and the microbial community dynamics involved in peat soils and marine nitrogen cycling. The above processes and set of genes were chosen based on their extent of inclusion in research concerning different ecosystems, as well as recent studies reporting beneficial considerations that appear to confirm their selection.

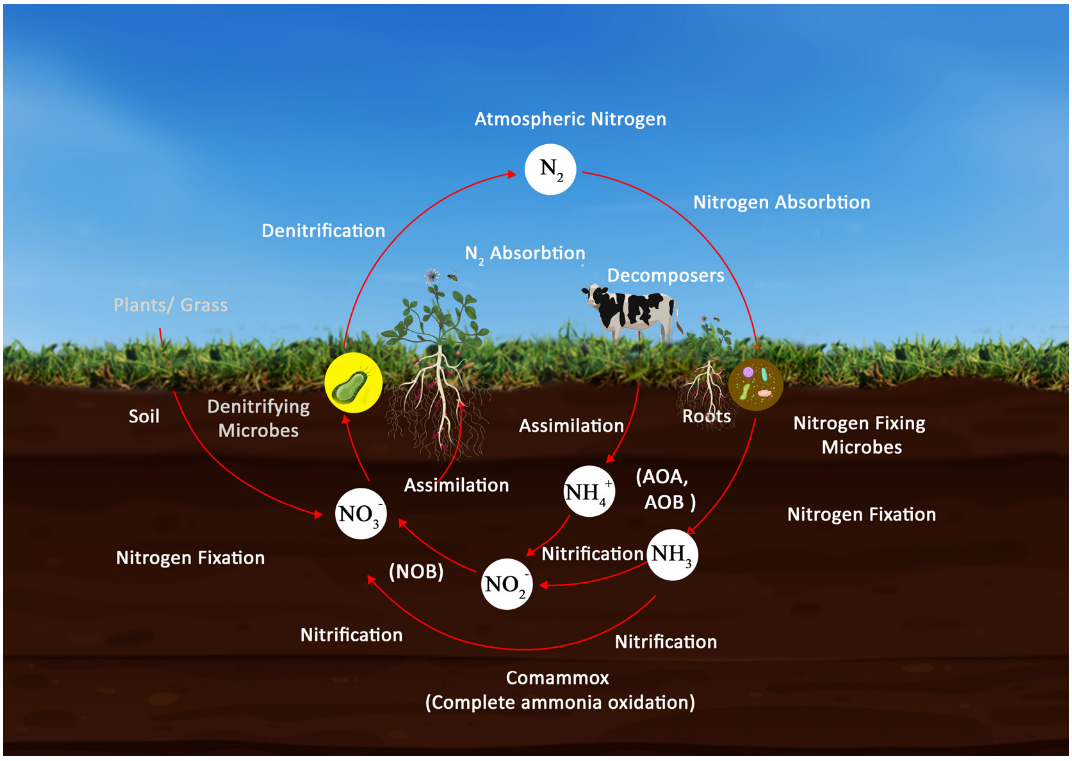

Figure 1. Multiple microbial transformation processes (AOA: ammonia−oxidizing archaea, AOB: ammonia−oxidizing bacteria, NOB: nitrite−oxidizing bacteria).

2.1. Nitrification

Nitrification is an aerobic process that involves the microbe-mediated oxidation of ammonia (NH_3) to nitrite (NO_2^-), followed by the oxidation of NO_2^- to nitrate (NO_3^-) and complete ammonia oxidation (comammox) to NO_3^- through NO_2^-. NH_3 is oxidized by two groups of chemolithotrophs, namely, AOB belonging to classes such as Nitrosomonas, Nitrosospira, and Nitrosococcus; AOA, such as Nitrosopumilus maritimus and Cenarchaeum symbiosum; and heterotrophs, namely, nitrite-oxidizing bacteria (NOB), such as Nitrobacter, Nitrococcus, and Nitrospina species [34,35]. Until recently, nitrification was usually considered to be mediated by AOB, but recent metagenomic studies revealed that AOA are especially important [36]. Previously, the AOB-mediated oxidation of NH_3 was considered to be a two-stage process; however, information regarding the AOA-mediated oxidation of NH_3 is scarce [37]. In the AOB-mediated pathway, the first and usually the slowest stage is the oxidation of NH3 to hydroxylamine (NH_2OH) by ammonia monooxygenase (AMO), whereas the second stage is the oxidation of NH_2OH to NO_2^- catalyzed by hydroxylamine oxidoreductase (HAO). However, recent research indicates the conversion of NH_2OH to nitric oxide (NO) first, and then to NO_2^- [38], increasing the likelihood that the oxidation of NH3 via the AOA pathway also occurs in three stages [39]. AMO is encoded by the amoABC genes. The amoA gene has been widely used to detect ammonia oxidizers in natural ecosystems [40]. Levicnik-Hofferle et al. [41] observed prominent differences between the ammonia oxidizers in the fen and bog peat soils from the Ljubljana marsh. Furthermore, ref. [42] proposed a niche specialization for nitrifiers, where AOA utilized organic nitrogen sources and AOB utilized inorganic nitrogen (Table 1). The nutrient-mix metabolism of AOA in peat soils is also possible but requires further research. The diversity of microbial communities in peat soils has been widely studied through advanced molecular methods; however, the understanding of peat-soil-based microbial community dynamics to nitrification remains limited [43]. Ammonia oxidizers are important producers of nitrous oxide (N_2O) in peat and marine soils [44,45]. However, the exact series of chemical reactions involved in N_2O production remain unclear. In 2015, comammox bacteria were discovered and classified [46] within the Nitrospira lineage II genus, which is the most generous and globally distributed NOB in peat and marine soils [47]. Comammox bacteria have a high affinity for NH_3, and in a recent study by [48], a relatively large supply of these bacteria was identified in coastal water samples, whereas it was untraceable in open-ocean samples [49]. Further studies are required to assess the contribution of comammox bacteria to peat and marine nitrification.

Table 1. Equations in nitrogen cycle.

Sl. No.	Equations	Names of the Steps	Enzymes
A	$NO_3^- + 2e^- + 2H^+ \rightarrow NO_2^- + H_2O$	Denitrification	NAS, NAR, NAP, NXR
B	$NO_2^- + H_2O \rightarrow NO_3^- + 2e^- + 2H^+$	Nitrification	NXR
C	$NO + 2H_2O \rightarrow NO_3^- + 3e^- + 4H^+$	Nitrification	NOD
D	$NO + H_2O \rightarrow NO_2^- + e^- + 2H^+$	Nitrification	Cu-NIR
E	$NO_2^- + e^- + 2H^+ \rightarrow NO + H_2O$	Anammox	Cu-NIR, cd1-NIR
F	$2NO + 2e^- + 2H^+ \rightarrow N_2O + H_2O$	Denitrification	cNOR, qNOR, CuaNOR, HCP, P450, NOR
G	$NH_2OH \rightarrow NO + 3e^- + 3H^+$	Nitrification	HAO, HOX
H	$N_2O + 2e^- + 2H^+ \rightarrow N_2 + H_2O$	Denitirification	NOS
I	$2NO \rightarrow N_2 + O^2$	Anammox	NO-D
J	$NO_2^- + 6e^- + 8H^+ \rightarrow NH_4^+ + 2H_2O$	Assimilation	cNIR, ccNIR, εHAO, ONR, OTR
K	$N_2 + 8e^- + 8H^+ + 16ATP \rightarrow 2NH_3 + H_2^+ 16ADP + 16Pi$	Nitrogen fixation	MoFe, FeFe, VFe
L	$N_2 H_4 \rightarrow N^2 + 4e^- + 4H^+$	Anammox	HDH
M	$NO + NH_4^+ + 3e^- + 2H^+ \rightarrow N_2H_4 + H_2O$	Nitrification	HZS
N	$NH_4^+ + O_2 + 2e^- + H^+ \rightarrow NH_2 OH + H_2O$	Nitrification	AMO, pMMO

2.1.1. Factors Influencing the Niche Differentiation of Nitrifiers in Peat Soils and the Marine Ecosystem

The main factors facilitating the co-existence of key nitrite-oxidizing bacteria (NOB) and separating the two stages of nitrification in peat soils include pH, oxygen availability, organic matter content, soil type, and other environmental factors [33,50]. Fierer et al. [51] observed pH to mostly influence microbial diversity in peat soils. The influence of low pH on nitrogen transformation in tropical peat soils has been reported [52,53]. The niche differentiation of nitrifiers in marine environments is influenced by NH_4^+, NO_2^-, oxygen, water pH, light, temperature, and salinity [54,55]. NO_2^- and oxygen might primarily facilitate the coexistence of marine NOB because these species appear to be relatively adapted to lower concentrations of oxygen and higher concentrations of NO_2^- than non-nitrifier organisms [56]. A light-induced reduction in photosynthesis of marine nitrifier organisms has been reported, but observations of ammonia transformation to nitrate and the frequent recovery of amoA genes close to the marine surface indicate that this is not generally the case. Therefore, light may indirectly affect nitrification [55]. Low temperatures pose difficulties in identifying microbe-mediated pathways that affect specific nitrogen transformation processes in peat soils [57]. High temperatures may facilitate the dissociation of the oxidation of NH_3 and NO_2^-, leading to the aggregation of NO_2^- on some marine coastal surfaces and can affect the distribution of AOA in several marine inlets [58,59].

2.1.2. Distribution of Nitrifiers in Peat and Marine Soils

The distribution and activity of nitrifiers in peat soils and marine environments have been extensively studied. Researchers [60,61] revealed the dominance of AOB in both peat soils while exploring the distribution of microbial diversity in fens and bog peat soils. Despite the differences in the composition of the microbial community and physicochemical parameters between fen and bog peat soils, the microbial distribution was found to be similar. This was in contrast with the trend observed by [41], who observed prominent differences between the ammonia oxidizers in the fen and bog peat soils from the Ljubljana marsh. The abundance of AOB was undetectable in fen and bog peat soils, where the nitrification and growth of AOB were stimulated by pollution in fen peat soils. Conversely, the growth of AOB could not be stimulated in bog peat soils despite the addition of organic or inorganic nitrogen. Similarly, a researcher [62] identified the dominance of AOB in fen peat soil compared with a bog, which could have been due to the labile organic substrate content and higher pH in the fen. Conversely, they [63] observed the dominance of AOA in fen and bog peat soils, irrespective of the addition of ammonium. It was suggested that AOA may outcompete AOB in the presence of low energy levels. Therefore, in peat soils, the ratio of AOA/AOB could serve as an indicator of low vs. high concentrations of nitrates in peat soils, as proposed previously by [64].

In an NH_4^+-limited environment, AOA is distributed throughout the marine environment and dominates over AOB [27,44,65,66], which could be due to their higher affinity for the substrate [36]. However, an exception to this was reported by Li et al. [67], where the dominance of AOB over AOA was found in marine environments. Furthermore, the occurrence of NOB is not clearly understood in marine environments, where only one species of *Nitrococcus* (*Nitrococcus mobilis*) is known to be prevalent in certain marine environments. NOB of the genus *Nitrospina* were found in abundance in different areas of marine environments [68,69]. The rich diversity of ammonia oxidizers in marine environments may be due to nutrient runoff from rivers [59]. Both AOA and AOB are often present in marine environments; however, the AOA community is generally more diverse than the AOB community [70,71]. However, the dominance of ammonia oxidizers (archaeal and bacterial) over each other remains unclear. Peat and marine soils are sites of active nitrification that harbor diverse ammonia-oxidizing microorganisms [66,69,72]. In these environments, AOA is much more abundant than AOB [21,27], although a few exceptions were found [67].

2.2. Anammox

Anammox involves the microbial-mediated conversion of NH_4^+ and NO_2^- to N_2 in an oxygen-depleted environment. The initial conversion of NO_2^- to NO is mediated by nirS [73,74], and the conversion of NH_4^+ and NO to N_2H_4 is mediated by hydrazine synthase (HZS). N_2H_4 is subsequently oxidized to N_2 by hydrazine dehydrogenase (HDH) [75]. The presence of anammox bacteria in marine environments has been widely studied [76,77]. Scalindua-nirS functional genes were used as indicators of anammox activity in marine environments. In a recent study by Rios-Del Toro et al. [77], anammox coupled with sulfate-dependent ammonium oxidation (sulfammox) and iron-dependent ammonium oxidation (feammox) has been reported in marine coastal environments, where both activities may facilitate the significant loss of nitrogen. However, information regarding the distribution and activity of anammox bacteria in peat soils is limited. Humbert et al. [78] detected anammox bacteria in permafrost soils by using a 16S rRNA-based molecular approach. Furthermore, two unknown anammox genera were identified in peat soils deposited with artificial sources of nitrogen [79]. Further studies are essential to reveal the fundamental microbes and processes involved in the production of N_2 via the oxidation of NH_4^+ under reducing conditions. Anammox bacteria have been reported worldwide in intertidal environments that experience a high level of nutrient recycling as a direct consequence of terrestrial runoff into brackish environments. Salt marshes represent an interface wherein a low level of soil oxygen drives nitrogen recycling [80]. Generally, anammox bacteria exhibit a lower diversity when compared with other marine bacteria, as has been reported in different regions of the world; for example, in a study conducted in a tropical and Arctic marine environment, the dominant species was determined to be *Candidatus "scalindua"* [81]. Salinity gradients along an estuary in China were also found to influence the abundance of three species of bacteria: *C. scalindua*, *C. brocadia*, and *C. kuenenia*, where *C. brocadia* was the dominant species in freshwater, *Ca. scalindua* preferred the saline ecosystem, and *C. kuenenia* demonstrated adaptation across a wide range of salinities while preferring a high DIN level [82]. A global study conducted in ten countries and six continents identified *C. brocadia* as the dominant genus across habitats and had a strong ability to survive under nutrient-limiting conditions in groundwater reservoirs [49]. Metagenomic analysis has become the method of choice for the detection of bacteria that are not amenable to culturing in the laboratory [74]; the method was able to successfully identify *C. brocadia* and *C. jettenia* as the dominant species in the lower Yangtze River, and it detects the relative abundance of specific genes in relation to the concentration of ammonium [49]. *C. kuenenia* was determined to be the dominant anammox bacteria in the Indus estuary, and its abundance was correlated with the level of nitrate in the sediment [83]. There has been renewed interest in anammox bacteria because of their biotechnological relevance in nutrient cycling, and *C. uenenia* has emerged as a candidate for bioremediation [35].

Factors Influencing Niche Differentiation of Anammox-Based Microbial Populations and Their Distribution in Peat Soils and Marine Environments

Studies revealed that the presence of anammox bacteria in peat soils depends on the availability of NO_3^-, NO_2^-, and NH_3^+ in the presence of limited oxygen (Figure 2). In several peat soils drained for cultivation, agricultural overflow significantly contributed to NH_3^+ and NO_3^- fluxes [79]. Several studies showed that anammox is highly dependent on the organic matter content in marine environments [83]. For instance, previous studies showed that organic substrates, as sources of nitrogen, can support anammox in oxygen minimum zones (OMZs) [84]. Additionally, anammox is dependent on the salinity [85] and temperature [86]. The contribution of anammox to the loss of N_2 in peat soils seems to be higher owing to low mineralization rates. However, anammox rates tend to decrease in marine environments owing to the limited availability of NH_4^+ [2]. In contrast, a high concentration of organic carbon in peat soils usually causes denitrification, whereas anammox is suppressed due to NO_2^- competition [87]. However, previous studies demonstrated a positive association between anammox and organic carbon content as a result of remineralization and nitrification [88,89]. These ambiguities reflect the debatable nature of the association between anammox and organic matter content. Studies have reported the prevalence of anammox bacteria in marine environments, such as OMZs (Table 2) [90,91] and coastal sediments [92]. In contrast, Bagnoud et al. [93] reported a lower abundance but higher diversity of anammox bacteria compared with ammonia oxidizers in fen peat soils. The distribution of anammox is related to its measurement rates, activity, and diversity in marine environments, which are typically affected by the temperature, salinity, nitrite availability, and nitrogen-containing organic substrates [76,88] (Figure 2).

Table 2. List of enzymes involved and their functions.

Sl. No.	Enzymes Involved and Their Functions	
1	Assimilatory nitrate reductase (1.7.1.1)	
2	Membrane-bound dissimilatory nitrate reductases	NAS, nasA, nirA
3	Periplasmic dissimilatory nitrate reductases	NAR, narGH
4	Nitrite oxidoreductase (1.7.1.15)	NAP, napA
5	Nitric oxide oxidase	NXR, nxrAB
6	Haem-containing nitrite reductases	NOD, hmp
7	Copper-containing nitrite reductases	cd1-NIR, nirS
8	Cytochrome c-dependent nitric oxide reductases	Cu-NIR, nirK
9	Quinol-dependent nitric oxide reductases	cNOR, cnorB
10	Copper-containing quinol-dependent nitric oxide reductases	qNOR, norZ
11	NADH-dependent cytochrome P450 nitric oxide reductase	CuANOR
12	Flavo-diiron nitric oxide reductase	P450NOR, p450nor
13	Hybrid cluster protein	NORvw, norVW
14	Hydroxylamine oxidoreductase	HCP, hcp
15	Hydroxylamine oxidase	HAO, hao
16	Nitrous oxide reductase	HOX, hox
17	Nitric oxide dismutase	NOS, nosZ
18	Assimilatory nitrite reductase	NO-D, norZ
19	Dissimilatory periplasmic cytochrome c nitrite reductase	cNIR, nasB, nirB
20	ε-hydroxylamine oxidoreductase	ccNIR, nrfAH
21	Octahaem nitrite reductase	εHAO, haoA
22	Octahaem tetrathionate reductase (1.8.99.B2)	ONR
23	Molybdenum-iron nitrogenases	OTR
24	Iron-iron nitrogenases (1.18.6.1)	MoFe, nifHDK

Table 2. *Cont.*

Sl. No.	Enzymes Involved and Their Functions	
25	Vanadium-iron nitrogenases (1.18.6.2)	FeFe, anfHGDK
26	Hydrazine dehydrogenase (1.7.2.8)	VFe, vnfHGDK
27	Hydrazine synthase (1.7.2.7)	HDH, hdh
28	Ammonia monooxygenase (1.14.99.39)	HZS, hzsCBA
29	Particulate methane monooxygenase (1.14.13.25)	AMO, amoCAB
30	Cyanase (4.2.1.104)	pMMO, pmoCAB
31	Urease (3.5.1.5)	CYN, cynS

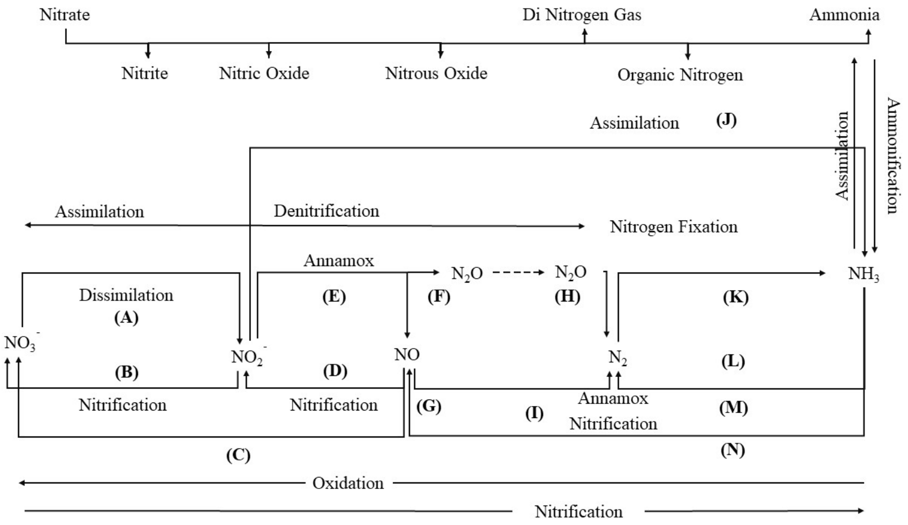

Figure 2. Flow chart showing the nitrogen cycle and microbial processes.

2.3. Denitrification

Denitrification involves the reduction of NO_3^- to nitrogen gases (N_2O and N_2), which is coupled with the oxidation of soil organic matter (SOM), which is a process that is mediated by numerous bacterial species [75]. The reduction of NO_3^- is mediated by narG and napA genes, and the reduction of NO_2^- to NO is mediated by two genes with the same functions but different structures, namely, nirK encoding nitrite reductase (containing copper) and nirS encoding cytochrome cd1 nitrite reductase (containing haem), with some exceptions, such as nirS denitrifiers, which are likely to completely catalyze denitrification and occur at a higher frequency than nirK denitrifiers [94]. The nir genes act as indicators of denitrification and are present in several other microbes, including anammox bacteria, nitrite, AOA, and AOB [95]. Mosier and Francis [96] reported that the dominance of nirS over nirK is an indicator of denitrifiers in marine bay sediments. Palmer et al. [97] reported a higher abundance of nirS in peat soil. A recent study by Pajares et al. [98] reported the coexistence of nirK and nirS microbial communities in peat soil. Furthermore, nirS microbial communities, including the nitric oxide reductase (nor) and nitrous oxide reductase (nos) genes, are more likely to completely reduce NO_2^- to N_2 [94]. The final step involving the reduction of N_2O to N_2 is catalyzed by the nosZ gene encoding nos, which is used as an indicator of denitrifiers in marine environments [99]. Previous studies identified non-denitrifiers with different nosZ genes as potential contributors to the reduction of N_2O in peat soils [100]. Denitrifier and anammox communities facilitate significant but low nitrogen loss in OMZ marine environments [90]. Furthermore, an incomplete denitrification process called nitrifier denitrification, where NO_2^- is reduced to N_2O under a low concentration or absence of oxygen, has been reported in marine environments involving AOA and AOB communities harboring nir and nor genes [101,102]. However, Kozlowski et al. [37] suggested that AOA in marine environments may act as an indicator of N_2O production under low oxygen concentrations. The list of enzymes provided here is involved in various biological processes that are primarily related to nitrogen and oxygen metabolism, as well as other metabolic pathways. The processes associated with each of the enzymes are shown in Table 3. These enzymes are critical for various microbial metabolic pathways and contribute to the cycling of nitrogen, oxygen, and other elements in the environment.

Table 3. Representative studies using key nitrogen processes and nitrogen-cycling genes involved in peat soils and the marine ecosystem.

References	Microbial Nitrogen Process	Genes Analyzed in This Study	Ecosystem	Approaches Used	Conditions Studied	Findings
Bagnoud et al. (2020) [93]	Anammox	16S rRNA	Fen peat soils	qPCR	Distribution and activity of anammox bacteria	A high diversity of anammox bacteria but a lower dominance over ammonia oxidizers. Denitirification contributed more to the loss of nitrogen.
Kujala et al. (2018) [72]	Nitrification	*narG* and *nirB*	Treated peat soils	qPCR and sequencing	Bacterial and archaeal diversity	The abundance of bacteria and archaea associated with a lower prevalence of nitrification-based activities.
Too et al. (2018) [103]	Production of ammonia	16S rRNA	Tropical peat swamp forest	Genomic library and sequencing	Diversity of microbial communities	The relative abundance of microbial diversity at the surface is related to nitrogen, as well as other environmental factors like organic content, oxygen, and pH.
Bristow et al. (2017) [90]	Denitrification and anammox	*amoA*, *nirS*, and 16S rRNA	Oxygen minimum zone (OMZ)	qPCR	Loss of nitrogen	Denitrifier and anammox communities facilitate a significant but low amount of nitrogen loss.
Li et al. (2015) [82]	Nitrification	*amoA* and 16S rRNA	River Colne bay sediments	qPCR, pyrosequencing, and denaturing gradient gel electrophoresis (DGGE)	Diversity of ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB) in the sediments	Differences in nitrification potential with higher abundance of AOB than AOA.
Hou et al. (2013) [88]	Anammox and denitrification	16S rRNA	Yangtze River bay sediments	qPCR and genomic library	Anammox diversity and activity of bacteria	Anammox is related to denitrification and the distribution of anammox denitrifiers is driven by temperature, salinity, and nitrite availability.
Levicnik-Hofferle et al. (2012) [42]	Nitrification	*amoA*	Marsh peat soils	qPCR and DGGE	Activity and abundance of nitrifiers	Higher abundance of archaeal *amoA*, while bacterial *amoA* is undetectable, which, in turn, is related to nitrification.
Lin et al. (2012) [62]	Nitrification and denitrification	16S rRNA	Fen and bog peat soils of Lake Agassiz	qPCR, pyrosequencing, and genomic library	Distribution and activity of the microbial community	Bacterial and archaeal dominance in fen peat soils over bog peat soils.
Palmer et al. (2012) [97]	Denitrification	narG, nirK, nirS, and nosZ	Permafrost tundra peat soils	qPCR and pyrosequencing	Distribution of denitrifiers	Higher abundance of *narG* and *nirS*.
Jensen et al. (2011) [91]	Anammox and denitrification	*nirS* and *Scalindua*-like *nirS*	OMZ in the Arabian sea	RT-PCR and genomic library	Biological nitrogen production	High activity of anammox and undetectable denitrification. Loss of nitrogen through anammox is related to the organic matter content.
Levicnik-Hofferle et al. (2010) [41]	Nitrification	*amoA*	Marsh peat soils in Slovenia with two sample sites (polluted and unpolluted)	qPCR, genomic library, and sequencing	Distribution and activity of ammonia oxidizers	Higher abundance of bacterial *amoA* in polluted peat soil, which is undetectable in the unpolluted peat soil, and this, in turn, is related to nitrification. Archaeal ammonia oxidizers were stratified in both the peat soils.
Mosier and Francis (2010) [96]	Denitrification	*nirK* and *nirS*	San Franciscobay sediment	qPCR and genomic library	Community dynamics of denitrifiers	Higher abundance of *nirS* than *nirK*, which, in turn, is associated with denitrification.
Santoro et al. (2010) [44]	Nitrification	*amoA*, 16S rRNA, and *Nitrospina*	Marine California Current	RT-PCR and genomic library	Activity and occurrence of nitrifiers	Higher abundance of AOA compared with AOB, which is associated with Nitrospina abundance. Prevalence of *amoA* is not related to nitrification.

Table 3. *Cont.*

References	Microbial Nitrogen Process	Genes Analyzed in This Study	Ecosystem	Approaches Used	Conditions Studied	Findings
Stopnisek et al. (2010) [63]	Nitrification	*amoA* and 16S rRNA	Peat soils from Ljubljana marsh	qPCR, RT-PCR, cloning, and sequencing	Diversity and activity of AOA and AOB	Increased abundance of AOA is associated with nitrification and this is not influenced by ammonium addition.
Ausec et al. (2009) [61]	Nitrification and denitrification	16S rRNA	Fen and bog peat soils in a temperate marsh	T-RFLP and genomic library	Distribution of microbial community	A high abundance of acidobacteria.
Dale et al. (2009) [76]	Anammox and denitrification	16S rRNA	Cape Fear River bay sediments	qPCR, terminal restriction fragment length polymorphism (T-RFLP), and genomic library	Diversity and activity of anammox bacteria	Diversity is affected by salinity and the abundance of anammox bacteria is related to the rate measurements of anammox.
Caffrey et al. (2007) [65]	Nitrification	*amoA* and 16S rRNA	Sediments from six bays	qPCR and nitrification potential	The abundance of AOA and AOB	A higher abundance of AOA is related to nitrification.
Nakagawa et al. (2007) [66]	Nitrification	*amoA*	Deep-sea sediments	PCR and genomic library	Diversity and activity of nitrifiers	Higher abundance of AOA than AOB, which, in turn, is associated with nitrification.
Kraigher et al. (2006) [60]	Nitrification and denitrification	16S rRNA	Fen peat soils from Ljubljana Marsh	T-RFLP	Diversity of microbial community	Higher abundance of proteobacteria and acidobacteria.

Factors Affecting Denitrification-Related Microbial Populations and Their Distribution in Peat Soils and Marine Environments

The quantification of nitrogen-cycling genes involved in denitrification to explain the relative importance of environmental factors in the distribution of denitrifiers was studied in peat soils [104,105] (Table 2). These studies demonstrated that the distribution of denitrifiers and rate measurements of denitrification in peat soils depend on the pH, humidity, soil texture, and availability of nitrogen and oxygen. However, the interdependency of these factors with microbial populations concerning denitrification in peat soils and marine systems is still largely unclear [106]. For instance, Pal et al. [107] reported low nitrate concentrations, irrespective of a high carbon content, but a high potential for denitrification in peat soils of the Ljubljana marsh, which could be attributed to the addition of external sources of organic matter. The high potential for nitrate removal in peat soils is significant for preventing the leaching of nitrate into groundwater, despite the decrease in the potential for denitrification with soil depth [108]. In addition, Yu et al. [104] found that the abundance of norB and nosZ genes is associated with soil pH. Moreover, the abundance of nirS and nosZ genes is associated with nitrogen concentrations in peat soils [109]. Furthermore, the availability of O_2 is associated with the division of limited resources of reducers of NO_{2-} and N_2O, with nirS- and nosZ-type denitrifiers being dominant under lower O_2 concentrations in marine environments [99].

3. Effects of Human-Induced Activities and Climate Change on Microbial Nitrogen-Cycling Processes in Peat Soils and the Marine Ecosystem

Compared with the natural processes of nitrogen production, human-induced activities stimulate a nearly threefold increase in global nitrogen production (Figure 3). Since nitrogen is one of the most fundamental elements for all life forms, an imbalance in its production can affect the balance of peat soils and the marine environment in terms of productivity and competition for the coexistence between species in the ecosystem [110]. Human-induced activities have encouraged many ecological studies to focus on the link between microbial diversity and nitrogen-cycling processes [111]. As such, concerns regarding the influence of ecosystem-based responses on human-induced activities are also receiving increasing attention. Direct changes due to human-induced activities include an imbalance in the nitrogen budget through atmospheric deposition and riverine discharges, which leads to eutrophication and the formation of areas with low or no oxygen concentrations in marine ecosystems [112]. It also includes an increase in the temperature, precipitation regime, and nitrogen mineralization in peat soils. For example, high temperatures stimulate increased denitrification rates in peat soils [113]. Human-induced activities also cause indirect changes, such as deoxygenation, acidification, and ocean warming. The effects of these direct and indirect changes on peat soils and the marine nitrogen cycle remain uncertain [114] and were investigated in recent studies [1,115,116]. In a recent study by Fasching et al. [117], weighted gene correlation network analysis (WGCNA) was used to identify specific groups of functions related to land use, indicating changes in microbial composition and loss of microbial diversity in peat soils. In addition to human-induced activities, global climate change has had profound effects on peatland and marine communities and biogeochemistry [33]. Global climate change has numerous potential effects on microbial structure and nitrogen-cycling processes in these ecosystems, such as precipitation in peat soils [118] and the freshening of open oceans [119]. Although metagenomic studies and rRNA sequencing have started to focus on understanding the taxonomic and functional composition of peat soils and marine ecosystems [28,120,121], an amalgamation of these studies, along with experimental techniques and modeling, is essential to provide important insights into microbial responses to human-induced influences and climate change on peat soils and marine systems.

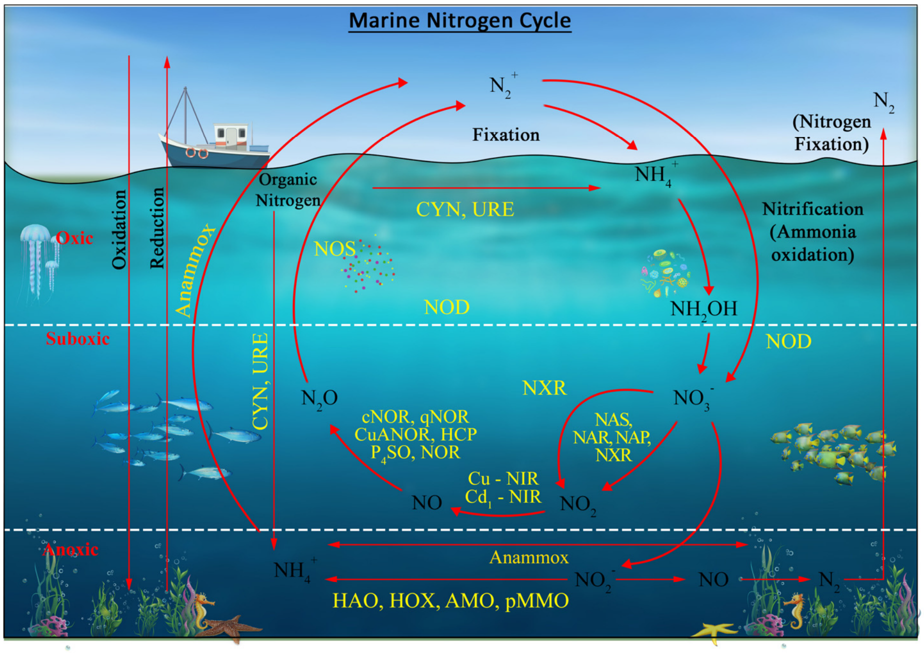

Figure 3. Microbial diversity in peat soils and marine ecosystem.

4. Remediation of Degraded Peat Soils

Peat soils have been documented to restore twice the amount of carbon compared with forest soils, and thus, the restoration of degraded peat soils is central to any strategy to offset carbon and reverse the effects of climate change [122,123]. Studies have reported that degraded sites can be restored in a manner that facilitates net carbon sequestration; however, the complete restoration of biological diversity and the biogeochemical processes may not be fully restored in decades [124]. Nevertheless, ecological restoration projects have reported different levels of success in restoring peat soils. A study in Indonesia on policies and practices emphasized the success of the 3R strategy, which involves rewetting, revegetation, and revitalization of local livelihoods [125]. The actual process of restoring peat soils commences with understanding the hydrological processes, followed by the establishment of blockages to limit the release of water from a peat swamp and the introduction of plant species that were present in the original ecosystem [126]. Studies demonstrated remediation using chemical-based approaches using phenolic inhibitors of phenolic oxidases to limit the rate of degradation below that of photosynthetic productivity [127]. Field studies showed that the addition of wood chips from trees, such as Spruce (*Picea mariana*), Larch (*Larix laricina*), and Cedar (*Thuja occidentalis*), have reduced carbon flux in peatland soils without any detrimental effects on the extant populations of Sphagnum moss [128]; nevertheless, this approach may not be practical on a large scale, which leads to the alternative, which is the application of microbial consortia for the remediation of peat soils. The process of remediation with microbes commences with the development of a model of the distribution of microbes at various trophic levels within the peat soil. The decomposition of organic matter in peat soils is driven by prokaryotes from the phyla Proteobacteria, Acidobacteria, Verrucomicrobia, and Planctomycetes, which dominate the acidic surface layer. Extensive studies in Indonesia noted that there are significant differences between the diversity in natural peat swamp forest soil, disturbed peat soil, and mineral soil, with natural peat swamps having the highest level of diversity and richness of Ascomycota, Basidiomycota, Zygomycota, and Glomeromycota, whereas degraded peat soil hosts pathotrophs that have been associated with the spread of pathogens among crop plants cultivated in drained peat soils [129]. The potential candidate microbes that can be introduced in the surface layers for bioremediation include Ascomycota, which has also been used in the bioremediation of contaminated peat soils due to its ability to degrade aromatic compounds [130]. A very innovative approach to the restoration of peat soils is the WETSCAPES method [131], which relies on a holistic approach to understanding the effects of rewetting peat soils based on the primary productivity, matter transformation via microbial and chemical processes, gas exchange, peat formation, and integration of data from multiple sources. The distribution and activity of nitrifiers in peat soils and marine environments have been extensively studied and the representative studies using key nitrogen processes and nitrogen-cycling genes involved in peat soils and the marine ecosystem is provided in Table 3.

5. Conclusions and Future Perspective

In this review, we provide a view of the ecology, distribution, and genetics of peat and marine nitrogen-cycling microbial diversity and the processes they mediate. These processes, involving nitrogen assimilation and loss, are more broadly distributed than previously assumed given that they have been found in unexpected peat and marine environments. Additionally, new metabolic nitrogen pathways have been reported over the past few years, changing the framework of the typical peat and marine nitrogen-cycling processes. Additionally, the potential effects of human-induced activities and global climate change on microbial nitrogen processes have led to an imbalance in natural peat and marine nitrogen transformation, with consequences that are at the initial stages of comprehension. Thus, a deeper insight into microbially mediated nitrogen processes in peat soils and the marine ecosystem is crucial, as nitrogen transformation in these environments impacts the dynamics of food production and environmental change. Moreover, future studies should focus on the functioning of the microorganisms involved in peat and marine nitrogen transformations to build holistic frameworks, taking into consideration all future scenarios and processes within various natural ecosystem settings. Furthermore, the present study revealed research gaps regarding microbially mediated nitrogen transformation processes in peat soils and the marine ecosystem, where these gaps represent critical future research directions. For instance, more data are needed to accurately demonstrate the regulation of nitrogen cycling in a much broader range of ecosystems than those currently studied.

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